Biol Invasions (2014) 16:1387–1395
DOI 10.1007/s10530-013-0576-y

ORIGINAL PAPER

An invasive stink bug as an evolutionary trap for an indigenous egg parasitoid

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Received: 16 June 2013 / Accepted: 22 October 2013 / Published online: 27 October 2013

Abstract Invasive alien species can act as 'evolutionary traps' for indigenous parasites and predators when the alien species is accepted as prey or a host but is unsuitable for consumption or development. We tested the relationship between acceptance and suitability of eggs of the invasive alien *Halyomorpha halys* (Hemiptera: Pentatomidae) in North America relative to eggs of the indigenous *Podisus maculiventris* (Pentatomidae) for the indigenous generalist egg parasitoid *Telenomus podisi* (Hymenoptera: Scelionidae). *T. podisi* accepted 0–24 h old *H. halys* eggs at a rate similar to *P. maculiventris* eggs (87.5 ± 6.0 and 70.2 ± 9.1 %, respectively). Successful development of *T. podisi* occurred in 98.3 % of attacked *P. maculiventris* eggs, but was not observed in *H. halys* eggs. Oviposition by *T. podisi* did, however, reduce the developmental success of *H. halys* embryos relative to unattacked controls by 24.1 % in 0–24 h old eggs and 29.6 % in 24–48 h old eggs. We suggest that as *H. halys* spreads and increases in abundance in North America, it could operate as an evolutionary trap for indigenous egg parasitoids, thereby indirectly causing an increase in population levels of indigenous pentatomids. This predicted indirect effect would be a result of *H. halys* eggs acting as an egg sink for *T. podisi*. We also introduce the concept of a 'time sink', which may be particularly relevant for parasitoids such as *T. podisi* that spend considerable time protecting their reproductive investments.

Keywords Biological invasion · Egg sink · Evolutionary trap · *Halyomorpha halys* · Host-parasitoid relationship · Host acceptance · *Telenomus podisi* · Time sink

Introduction

A forager's utilization of resources is shaped by past selective pressures that link the behaviours necessary to exploit a resource, such as the utilization of cues related to resource acceptance, and the profitability of that resource (i.e. the resulting fitness payoff) (Schlaepfer et al. 2002). Introduction of an invasive alien species may add a resource to the environment that a forager has never encountered and break the link between resource acceptance and profitability; for

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example, when cues for acceptance of an invasive alien prey by an indigenous predator are present but the prey is unsuitable for consumption (Schlaepfer et al. 2005). The invasive alien prey is then referred to as an 'evolutionary trap' (Schlaepfer et al. 2005), and causes indigenous predators to invest energy or reproductive resources that result in a lower profitability than that normally associated with the investment.

Evolutionary traps may have consequences for the population dynamics of indigenous parasitoids, their indigenous hosts, and the invasive alien host species through their mediation of indirect effects. For example, the North American parasitoid *Dinocampus coccinellae* (Hymenoptera: Braconidae) shows similar levels of acceptance of the invasive *Harmonia axyridis* (Coleoptera: Coccinellidae) and the indigenous *Coleomegilla maculata* (Coccinellidae) (Firlej et al. 2010; Hoogendoorn and Heimpel 2002), but the former host species has high levels of resistance to parasitism via haemocytic encapsulation while the latter does not (Firlej et al. 2012). Rather than the more common situation where the presence of *H. axyridis* would cause an increase in parasitism of *C. maculata* via augmentation of populations of *D. coccinellae* (i.e., apparent competition), *H. axyridis* rather acts as an 'egg sink' for *D. coccinellae*, reducing levels of parasitism of *C. maculata* by causing foraging *D. coccinellae* to become egg-limited (Hoogendoorn and Heimpel 2002; Heimpel et al. 2003). Thus, according to the model of Heimpel et al. (2003), the presence of *H. axyridis* actually increases the equilibrium population levels of *C. maculata*, while the presence of *C. maculata* has a small negative effect on population levels of *H. axyridis* (Hoogendoorn and Heimpel 2002). This situation is referred to an indirect (+, −) interaction, or 'apparent predation' (Holt 1977; Heimpel et al. 2003). Similar examples of parasitoids showing high levels of acceptance of unsuitable invasive alien species, and predictions about the resulting indirect ecological consequences, are lacking in the literature.

Halyomorpha halys Stål (Hemiptera: Pentatomidae), the brown marmorated stink bug, is a pest of Asian origin that has recently become established in North America (Hoebeke and Carter 2003) and Central Europe (Wermelinger et al. 2008). This species has already become very common in invaded areas and has caused substantial economic losses in fruit orchards in the Northeastern United States (Nielsen and Hamilton 2009; Leskey et al. 2012). *H. halys* is also a nuisance for homeowners when large numbers of the bugs move indoors for overwintering (Leskey et al. 2012). *H. halys* continues to spread, and based on climate modeling is expected to expand its range to large geographic areas of North America and Europe (Zhu et al. 2012). The first established Canadian population of *H. halys* was found in the summer of 2012 in Southern Ontario (T. Gariepy and H. Fraser, unpublished data). While there are some reports of indigenous parasitoids being reared from *H. halys* eggs in the United States (Hoelmer and Tatman 2011; Leskey et al. 2012), no published studies have directly tested the acceptance and suitability of *H. halys* eggs to these parasitoid species.

Telenomus podisi Ashmead (Hymenoptera: Scelionidae) is a common indigenous egg parasitoid usually responsible for the majority of parasitism of several pentatomid species' eggs in North America (Yeargan 1979; McPherson 1982; Orr et al. 1986; Koppel et al. 2009). In the current study, the relationship between acceptance and suitability of *H. halys* eggs for *T. podisi* relative to eggs of the indigenous predatory species *Podisus maculiventris* Say (Pentatomidae) was tested under laboratory conditions. Following Keeler and Chew (2008), there are three general outcomes (with intermediate outcomes possible between each): (1) *T. podisi* will not recognize the invasive *H. halys* as a host, (2) *T. podisi* will recognize *H. halys* eggs as suitable hosts and offspring will successfully develop, and (3) *T. podisi* will recognize *H. halys* as a suitable host but offspring will be unable to develop. Whether or not *H. halys* eggs are accepted by and suitable for *T. podisi* development could have important ecological consequences for the parasitoid, its indigenous pentatomid hosts, and *H. halys*.

Materials and methods

Insects

Halyomorpha halys were originally collected from a population in Hamilton, Ontario, Canada in the summer of 2012 (~200 individuals). They were then reared continuously at a containment facility at the Southern Crop Protection and Food Research Centre in London, Ontario at 24 ± 1 °C, 50 ± 10 % RH and under a 16:8 h L:D photoperiod. First-instar nymphs were housed in 3 L plastic tubs and provided with lettuce and raw peanuts. Adults and 2nd–5th instar nymphs were housed in ventilated cages (47.5 cm^3) with water, lettuce, sunflower seeds, peanuts, and apples. Eggs laid by females on paper towel and the sides of the cages were collected daily for experiments and to perpetuate the rearing.

Podisus maculiventris were originally collected as adults (~50 individuals) from several locations in the London region in 2011–2012 and reared continuously. Nymphs and adults were reared in plastic tubs, fed with mealworm (*Tenebrio molitor* L.) larvae and lettuce, and provided with water. Crumpled newspaper was used as oviposition substrate and eggs were collected daily.

Telenomus podisi were originally reared from ~100 field-exposed sentinel egg masses of *P. maculiventris* and *Euschistus* spp. (Hempitera: Pentatomidae) in the London region in 2011. No *H. halys* populations were detected in Ontario until the summer of 2012, so it is most likely that these *T. podisi* populations had never encountered *H. halys*. Identifications of colony foundresses were confirmed by Dr. Lubomir Masner (National Collection of Insects, Arachnids, and Nematodes, Ottawa, ON, Canada). *Telenomus podisi* were reared continuously on eggs of *P. maculiventris* by offering egg masses (<3 days old) to groups of *T. podisi* housed in large ventilated cages for 48 h. To collect females used in experiments, parasitized egg masses from the colony were kept in small Petri dishes (diameter: 5.0 cm, height: 1.0 cm). Within 24 h of emergence, females that had emerged in the presence of males were separated into 1.2 mL Eppendorf tubes with a small drop of honey water for 2 days before being used in experiments. This allowed time for ovariole maturation, since this strain of *T. podisi* is largely synovigenic and females often emerge without any mature eggs (P. Abram, unpublished results). 2–3 day-old, naïve females have between 9 and 15 mature eggs in their ovarioles and are consistently able to parasitize up to 16 host eggs in the subsequent 24-h period (P. Abram, unpublished results). This colony of *T. podisi* retains the ability to parasitize and develop in other species of stink bugs indigenous to North America despite being reared for several generations on *P. maculiventris* eggs (T. Gariepy, personal observations).

Test arenas and host treatments

Pentatomid eggs were removed from the oviposition substrate with forceps and glued to squares of filter paper in masses of eight (two rows of four) with a small amount of white non-toxic glue (LePage White Glue). The squares of filter paper with eggs were then glued to the center of the bottom of a small Petri dish (diameter: 5.0 cm, height: 1.0 cm). Artificial egg masses were either (1) 24–48 h old *P. maculiventris* eggs, (2) 0–24 h old *H. halys* eggs, or (3) 24–48 h old *H. halys* eggs. Two ages of *H. halys* eggs were tested because preliminary observations indicated that eggs were accepted at a much lower rate when >24 h old. 0–24 h old *P. maculiventris* eggs were not tested (i.e., a control for egg age) because we have previously determined that acceptance and suitability of *P. maculiventris* eggs to *T. podisi* does not differ with host egg age, even until the eggs are 5 days old (Y. Zhou and P. Abram, submitted). For each replicate exposed to parasitoids, an unexposed egg mass of the same host treatment was set up in an identical arena. These served as controls for host developmental success (see below).

Behavioural observations

Experiments were performed at ambient laboratory temperature (23–25 °C) and lighting between 3 and 8 h after the start of the photophase. It was ensured that no movement occurred in the vicinity of the trials, since this affected parasitoid behaviour in preliminary experiments. Single female *T. podisi* were released into the Petri dish arenas containing one of the three host egg treatments. Their behaviour was filmed for 2 h, which is more than twice the time required to completely exploit a host patch of eight eggs (Table 1). Each treatment was replicated 21 times. Treatments were spread out evenly with respect to day and time of day over the 5-day experimental period. Films were played back and, using Cowlog software (Hänninen and Pastell 2009), the occurrence and duration of the following behaviours were recorded (see Field 1998 for a detailed description of scelionid patch exploitation behaviour): (1) adoption of oviposition posture, (2) drilling (insertion of ovipositor into a host egg), (3) marking of a host egg, indicating egg deposition, (4) patch guarding (repeated bouts of stationary and patrol behaviour; see Field 1998). The assumption that host

Table 1 Behavioural parameters of *T. podisi* exploiting patches of *P. maculiventris* (24–48 h old) and *H. halys* (0–24 h old or 24–48 h old) eggs

Treatment	Mean % acceptance[a]	Mean rejection rate[b]	Mean incomplete oviposition rate[c]	# patches fully exploited (/21)	Mean time to exploit patch (min)[d]	Proportion of females defending patch[d]
P. maculiventris (24–48 h old)	70.2 ± 9.1^{a}	0.232 ± 0.037^{b}	0.298 ± 0.039^{a}	13	47.81 ± 4.35^{a}	0.615
H. halys (0–24 h old)	87.5 ± 6.0^{a}	0.097 ± 0.024^{c}	0.100 ± 0.026^{b}	16	40.73 ± 1.94^{a}	0.625
H. halys (24–48 h old)	23.8 ± 9.0^{b}	0.276 ± 0.035^{a}	0.069 ± 0.027^{b}	3	50.72 ± 4.91^{a}	0

Within a column, means (±SE) followed by different letters are significantly different ($p < 0.05$; see text for details of statistical tests)

[a] Number of eggs oviposited by the parasitoid/total number of eggs in the patch

[b] Number of rejections/total number of initiated ovipositions

[c] Number of incomplete ovipositions/total number of initiated ovipositions

[d] Of replicates where host patches were fully exploited

marking indicates a successful oviposition has been confirmed several times in different species of scelionid parasitoids attacking different host species, and is a well-established convention in the study of scelionid behaviour (Rabb and Bradley 1970; Bin et al. 1993; Colazza et al. 1996; Weber et al. 1996; Field 1998; Agboka et al. 2002; Hirose et al. 2003; Wajnberg et al. 2004). We defined each oviposition attempt as a: (1) successful oviposition (adoption of oviposition posture + drilling + marking), (2) rejection (adoption of oviposition posture + drilling, not followed by marking) (Colazza et al. 1996; Wajnberg et al. 2004), (3) unsuccessful oviposition attempt (adoption of oviposition posture not followed by drilling). All rejections were of unparasitized host eggs; drilling was not observed in already-parasitized eggs. Only one incidence of superparasitism was observed, and was discarded from the analysis. Eggs on which rejections and/or unsuccessful oviposition attempts occurred were often subsequently parasitized by the same female. Therefore, rejections and incomplete ovipositions did not necessarily indicate levels of final acceptance; rather, they are indications of how readily/efficiently the wasps parasitized host eggs.

Assessment of developmental outcomes

Following the filming period, females were removed from the arenas and both exposed an unexposed control eggs were incubated under standard rearing conditions (see above). Emergence of host nymphs and parasitoids was recorded as it occurred. After 30 days (7–8 days after the last parasitoid emergence), all eggs from which there was no emergence were dissected to record the contents of the egg: (1) undeveloped (liquid contents with no discernible stink bug nymph or parasitoid), (2) fully developed pentatomid nymph that failed to emerge, (3) fully developed parasitoid that failed to emerge. Category (1) may have included dead early-instar parasitoid immatures that we were unable to distinguish, but dead late-stage parasitoid larvae or pupae were not observed in any of the treatments. Since gluing the eggs to filter paper was previously observed to affect emergence rate (but not development) of pentatomid nymphs, and all unemerged parasitoids (12.0 % of all observed) were completely developed and still alive inside the host egg shell, completion of development rather than emergence was used as the final measure of developmental outcome. These parasitoids may not have emerged if the egg mass was left undisturbed, but since we never found parasitoids of any stage in *H. halys* eggs or unattacked controls (see below), using completion of development rather than emergence as the developmental outcome did not meaningfully affect any of the comparisons of host suitability for *T. podisi*.

Data analysis

Acceptance rate of host eggs in each replicate was calculated by dividing the number of accepted eggs by eight (the total number of eggs in the patch) and treatment rank-averages were compared with a

Kruskall–Wallis test; data could not be normalized with transformations. Rejection rate and incomplete oviposition rate for each replicate were calculated by dividing the number of each behaviour by the total number of initiated ovipositions, and rank-averages were compared with Kruskall–Wallis tests. Following significant ($p < 0.05$) Kruskall–Wallis tests, post hoc differences between rank averages were compared by calculating the Tukey least significant differences (LSD) between mean ranks ($\alpha = 0.05$). For replicates where females parasitized every egg (see Table 1 for the number in each host treatment), the mean time to exploit host patches (the time from the initiation of the first oviposition to the end of the last) was calculated and compared between treatments with a one-way analysis of variance (ANOVA). Also, in replicates where every egg was parasitized, the number of females that exhibited patch guarding behaviour was tallied. The proportion of guarding versus non-guarding females was compared between the three host-treatments with a 2 × 3 Fisher exact test.

For each replicate, whether each egg was apparently parasitized (from analysis of the videos) was related to its developmental outcome. For each host treatment, the developmental outcomes of parasitized eggs was pooled from all replicates, and the proportions of each developmental outcome (undeveloped, pentatomid embryo development, parasitoid development) were compared with the outcomes of the unexposed control eggs (also with replicates pooled) with 2 × 3 (when parasitoid development occurred) or 2 × 2 (when parasitoid development did not occur) Fisher exact tests. Statistical tests were performed with R software (R Core Team 2013).

Results

Behavioural observations

The mean acceptance rate of host eggs (Kruskall–Wallis test, $H = 18.29$, $p < 0.001$, $df = 2$), mean rejection rate ($H = 25.09$, $p < 0.001$, $df = 2$), and mean incomplete oviposition rate ($H = 19.63$, $p < 0.001$, $df = 2$) of *T. podisi* varied significantly among host treatments (Table 1). *Podisus maculiventris* eggs and 0–24 h old *H. halys* eggs were accepted at similar levels, while acceptance of 24–48 h old *H. halys* eggs was significantly lower (Tukey LSD, $p < 0.05$). The greatest proportion of initiated ovipositions resulted in rejections on 24–48 h *H. halys* eggs, while rejection rate of 0–24 h *H. halys* eggs was significantly lower than that of *P. maculiventris* eggs (Tukey LSD, $p < 0.05$). A significantly larger proportion of initiated oviposition attempts were unsuccessful on *P. maculiventris* eggs than on either age of *H. halys* eggs (Tukey LSD, $p < 0.05$).

In replicates where every egg in the patch was parasitized, the time required to exploit the patch did not differ significantly between host treatments (ANOVA, $F_{2,29} = 1.76, p = 0.19$) (Table 1). In these replicates, the proportion of females exhibiting patch guarding behaviour, ranging from 0 on 24–48 h old *H. halys* eggs to 0.625 on 0–24 h old *H. halys* eggs, was also independent of host treatment (Fisher exact test, $p = 0.19$) (Table 1).

Assessment of developmental outcomes

The proportion of each developmental outcome was significantly different between eggs in which parasitism was observed and unexposed controls in *P. maculiventris* eggs (Fisher exact test, $p < 0.001$), 0–24 h old *H. halys* eggs (Fisher exact test, $p < 0.001$), and 24–48 h *H. halys* eggs (Fisher exact test, $p < 0.001$) (Fig. 1). Parasitoid offspring successfully developed in 98.3 % (117/119) of *P. maculiventris* eggs in which *T. podisi* oviposition was observed. While *T. podisi* did not ever successfully develop in either age of *H. halys* eggs, successful host nymph development was reduced by 24.1 and 29.6 % in parasitized eggs relative to unexposed control eggs for host ages of 0–24 and 24–48 h old, respectively (Fig. 1). The reduced proportions of pentatomid embryo developmental success were attributable to higher proportions of 'undeveloped' eggs, where there was no discernible development of either a pentatomid nymph or a parasitoid.

Discussion

Telenomus podisi females accepted eggs (<24 h old) of the invasive alien *H. halys* as hosts at a high rate, but their offspring were unable to complete development. We propose that in invaded regions where *H. halys* becomes common, it could act as an evolutionary trap

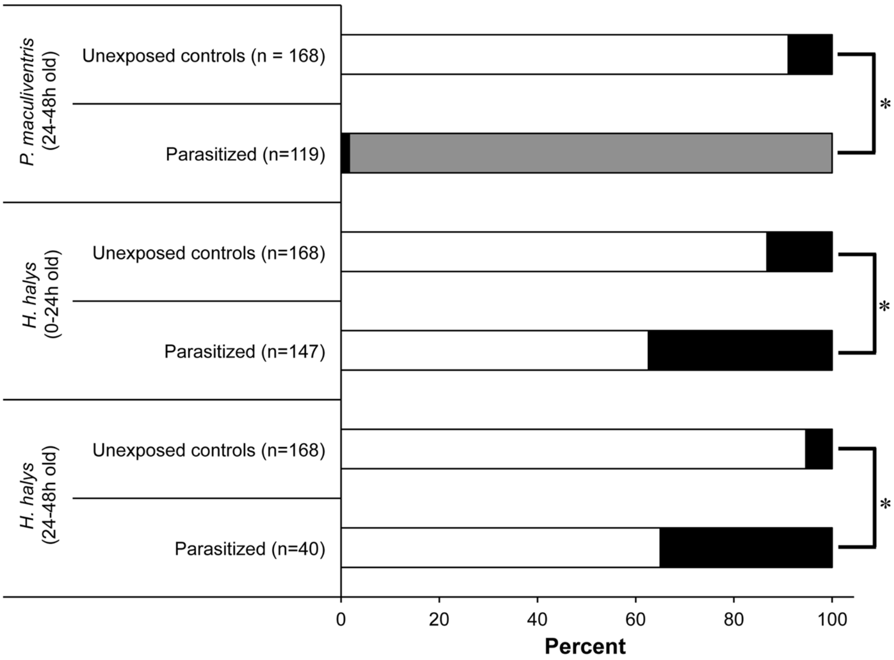

Fig. 1 Percentage of each developmental outcome in parasitized eggs (in which parasitoid oviposition was observed) and unexposed control eggs of *P. maculiventris* (24–48 h old) and *H. halys* (0–24 h old or 24–48 h old). *White* pentatomid embryo, *grey* parasitoid, *black* undeveloped (no discernible development of pentatomid embryo or parasitoid). *Asterisks* indicate significantly different proportions of each developmental outcome (Fisher exact test, $p < 0.001$)

for *T. podisi*, with potential ecological consequences for the indigenous community of pentatomid hosts.

Behavioural acceptance of *H. halys* eggs by *T. podisi* indicates that the short-range cues necessary for parasitism are present. The fact that the presence of short range host cues alone seems to be sufficient for host location by *T. podisi* in nature (Okuda and Yeargan 1988; Bruni et al. 2000; Koppel et al. 2009) suggests that the attack of recently-laid *H. halys* eggs could commonly take place under natural conditions in environments where both species occur.

Acceptance of *H. halys* eggs was significantly lower when they were 24–48 h old than when they were 0–24 h old (Table 1). On 24–48 h old *H. halys* egg patches, parasitoids often (14/21 replicates) rejected several eggs (2.71 ± 0.24; mean ± SE) and then left the patch, making no further parasitism attempts. This change in acceptance levels by *T. podisi* in different ages of *H. halys* eggs constrasts with our previous observations showing no difference in acceptance and suitability of different ages of *P. maculiventris* eggs. The mechanism behind this result is unknown, but the fact that the insertion of the ovipositor was used to mediate rejections indicates that the cue causing the rejection of older *H. halys* eggs is likely internal, rather than, for example, being mediated by a change in the composition of external kairomones.

Parasitism by *T. podisi* prevented the development of some *H. halys* embryos, but never resulted in successful parasitoid development (Fig. 1). Mortality of *H. halys* embryos could have been caused by damage to the host immature or the egg chorion by the developing parasitoid larva (Boivin 2010), or injection of compounds by the ovipositing parasitoid that liquefy the embryo or arrest its growth (Strand et al. 1983; Moreau and Guillot 2005). Although we did not determine the basis of the developmental unsuitability of *H. halys* eggs for *T. podisi*, the fact that we did not find dead late-stage parasitoid immatures in parasitized host eggs indicates that mortality occurred early in parasitoid development. This could be due to the absence of necessary developmental cues or nutritional resources (Lawrence 1990; Vinson 2010), a host egg chorion structure that prevented immature parasitoid respiration (Nénon et al. 1995), or an innate immune response by the host egg (Abdel-latief and Hilker 2008). To ensure that the complete developmental failure of parasitoids we observed was not due to the small number of females tested, we subsequently exposed over 1,200 0–24 h old *H. halys* eggs (~45 egg masses) to a colony of >300 *T. podisi* over a period of 3 weeks, each egg mass being exposed for

48–72 h. Although no parasitoid offspring emerged from these egg masses, corroborating our prior results, we found dead *T. podisi* pupae or fully-developed, dead adults in 4 (<0.33 %) of the exposed eggs upon subsequent dissection. Very low levels of developmental success may thus be possible. Indeed, there is a report of rearing *T. podisi* from field-collected *H. halys* eggs in the northeastern United States at very low rates (Hoelmer and Tatman 2011). Geographic populations/biotypes of *T. podisi* other than the ones in our colony may have the capacity to develop in *H. halys* eggs, a possibility requiring further testing.

Halyomorpha halys has the potential to become very common and widespread in its invaded ranges of Central Europe and North America (Zhu et al. 2012), and is already much more common than all indigenous pentatomid species combined at some sites in the Northeastern United States (Nielsen and Hamilton 2009). In such areas, it could act as an evolutionary trap for *T. podisi* by causing the parasitoid to invest eggs that do not result in offspring production. Since *T. podisi* is the most common parasitoid of several species of pentatomid bugs in North America (Yeargan 1979; McPherson 1982; Okuda and Yeargan 1988; Koppel et al. 2009), the invasive *H. halys* could have indirect effects on the populations of indigenous pentatomids. When a 'marginal' (relatively unsuitable for development) host species is introduced to a system comprising a parasitoid and a suitable host species, and when both species are accepted by the parasitoid at a similar rate, it is predicted that the equilibrium population levels of the suitable host species will increase (Heimpel et al. 2003). This effect is dependant on low parasitoid fecundity (egg-limitation), since the benefit to the suitable host species is due to the parasitoid allocating eggs to the unsuitable host and becoming egg-limited (Heimpel et al. 2003). The suitable host species is predicted to exert a slightly negative effect on the marginal host species, since it augments populations of the parasitoids that are able to cause some mortality of the marginal species (Hoogendoorn and Heimpel 2002; Heimpel et al. 2003). The overall interaction is of the (+, −) type, or 'apparent predation' (Holt 1977; Heimpel et al. 2003). The general conditions of the model predictions in Heimpel et al. (2003) are satisfied in the present system, since (1) *H. halys* (the marginal host) is attacked by *T. podisi* at a similar rate to *P. maculiventris* (the suitable host) but is less suitable for development; (2) *T. podisi* has a low fecundity relative to the size of host egg masses and is therefore likely to experience egg-limitation in nature; and (3) the presence of suitable host species such as *P. maculiventris* is slightly detrimental to *H. halys*, since *T. podisi* is capable of causing some mortality (24–29 %, Fig. 1) of *H. halys* eggs. We therefore suggest that the invasive *H. halys*, via the indigenous parasitoid *T. podisi*, could cause an increase in population levels of pentatomid species such as *P. maculiventris* that are indigenous to North America. Whether this prediction is validated will depend on many ecological factors, including the importance of direct competitive interactions between *H. halys* and indigenous pentatomids. The fact that *H. halys* eggs are only accepted by *T. podisi* for a limited time during their development could also diminish the ecological impact of this interaction.

Post-exploitation patch guarding, including pre-emptive aggressive behaviours by *T. podisi* occurred on patches of *H. halys* eggs with a frequency comparable to that on *P. maculiventris* eggs. The incidence and duration of patch guarding in scelionids increases with maternal investment (Field 1998), and the patch size used in this experiment was smaller than generally laid by both pentatomid species tested (Yeargan 1979; Orr et al. 1986; Nielsen et al. 2008). Our methodology did not allow a quantification of patch guarding duration (patch-guarding individuals were still on the patch at the end of the experiment), but we have previously observed up to 7 h of patch guarding on patches of 12 *P. maculiventris* eggs (P. Abram, unpublished data). *H. halys* egg masses contain a median of 28 eggs (Nielsen et al. 2008). Therefore, in addition to acting as an 'egg sink' (following Hoogendoorn and Heimpel 2002), patches of *H. halys* eggs could be particularly potent evolutionary traps for *T. podisi* by also acting as a 'time sink', since they would cause parasitoids to invest time that does not result in any fitness payoff. The time sink effect is costly, and would potentially magnify the above-mentioned indirect ecological effects, if patch guarding increases predation risk or wastes time that could be used to find other host patches. This time sink concept should be integrated into models of indirect ecological effects mediated by species such as *T. podisi* that are likely to waste considerable time, in addition to reproductive resources, as a result of evolutionary traps.

There are two ways parasitoids could ‘escape’ an evolutionary trap. One possibility would be to evolve behavioural, physiological, or morphological barriers to acceptance of the invasive host species (Phillips and Shine 2004). Alternatively, parasitoids could evolve the capacity to develop in the invasive host species (Keeler and Chew 2008). The likelihood of either of these occurring depends, in part, on whether enough heritable genetic variability exists within and among populations of the parasitoid for the tendency to reject the invasive host species and the capacity to successfully develop in them (Henter 1995). In contrast, any (1) trade-off between a capacity to develop in the invasive host species and suitable indigenous host species, (2) correlation between an increased tendency to reject the invasive host species and the tendency to reject suitable host species, or (3) trade-off between increased virulence of the parasitoid in the invasive host species and other life history traits (Kraaijeveld and Godfray 1997), would prevent an escape from the evolutionary trap, since these trade-offs would inhibit the evolution of barriers to acceptance or increased developmental capacity.

Halyomorpha halys has also recently been accidentally introduced to central Europe (Wermelinger et al. 2008), and preliminary results indicate that the native European *Telenomus chloropus* Thomson accepts its eggs but is unable to develop in them (Tim Haye, personal communication). This emerging biological system thus presents the opportunity to study the ecological consequences, specifically the indirect effects, of evolutionary traps simultaneously in two invaded areas with different native host and parasitoid communities. In the coming years, indigenous pentatomid population levels before and after *H. halys* arrival in different regions should be measured, as should parasitism levels of *H. halys* and indigenous pentatomids. Behavioural acceptance levels and developmental success of indigenous egg parasitoids inside and outside of invaded areas over time could also be measured to test for between-population differences, and for whether there is any evidence of escape from the evolutionary trap *H. halys* represents.

Acknowledgments The authors wish to thank Allison Bruin for technical assistance. This work was supported by a Natural Sciences and Engineering Council of Canada postgraduate scholarship to P. K. Abram.

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