Learning can be detrimental for a parasitic wasp

Valeria Bertoldi¹, Gabriele Rondoni¹, Ezio Peri², Eric Conti¹, Jacques Brodeur³*

¹ Dipartimento di Scienze Agrarie, Alimentari e Ambientali, Università degli Studi di Perugia, Perugia, Italy, ² Dipartimento di Scienze Agrarie e Forestali,Università degli Studi di Palermo, Palermo, Italy, ³ Département de Sciences Biologiques, Institut de Recherche en Biologie Végétale, Université de Montréal, Montréal, Québec, Canada

* jacques.brodeur@umontreal.ca

Abstract

Animals have evolved the capacity to learn, and the conventional view is that learning allows individuals to improve foraging decisions. The parasitoid Telenomus podisi has been shown to parasitize eggs of the exotic stink bug Halyomorpha halys at the same rate as eggs of its coevolved host, Podisus maculiventris, but the parasitoid cannot complete its development in the exotic species. We hypothesized that T. podisi learns to exploit cues from this non-coevolved species, thereby increasing unsuccessful parasitism rates. We conducted bioassays to compare the responses of naïve vs. experienced parasitoids on chemical footprints left by one of the two host species. Both naïve and experienced females showed a higher response to footprints of P. maculiventris than of H. halys. Furthermore, parasitoids that gained an experience on H. halys significantly increased their residence time within the arena and the frequency of re-encounter with the area contaminated by chemical cues. Hence, our study describes detrimental learning where a parasitoid learns to associate chemical cues from an unsuitable host, potentially re-enforcing a reproductive cul-de-sac (evolutionary trap). Maladaptive learning in the T. podisi—H. halys association could have consequences for population dynamics of sympatric native and exotic host species.

1. Introduction

Animal decision-making, which is involved in processes such as resource and habitat selection, mate choice and progeny allocation, relies on innate behaviour (instinct), stochastic processes, physiological feedbacks (e.g., hormonal signalling) and learning (reviewed in [1]). Insect parasitoids have been used as model systems to explore both proximate and ultimate perspectives of optimal foraging. In order to cope with spatial and temporal variability in resources, parasitic wasps have evolved the capacity to associate host-related chemical cues to host availability and suitability [2–6]. They further consolidate and improve this capacity through learning processes [7–10], resulting in increased reproductive success [3, 11–13]. The probability of including a new stimulus in the behavioural repertoire of a parasitoid female depends on its reliability in host location [2], with oviposition having been shown to consolidate a change in foraging behaviour and host acceptance [3, 9, 14]. For example, scelionid parasitoids use host
chemical cues on the egg surface or those deposited on plant surfaces by gravid females (foot-prints) to locate hosts in the habitat (reviewed by [15]). Following detection of host chemical cues, experienced scelionid females show stronger arrestment response (increased residence time, slower walking and increased turning tendency) than naïve females, a behaviour that is re-enforced by successful oviposition [16, 17].

Biological invasions generate novel interactions which can have negative consequences on populations of native species [18–21]. This occurs, for example, when an invasive exotic species becomes accepted as a host by native parasitoids but is unsuitable for offspring development. The introduced species then acts as an egg sink [22] for indigenous parasitoids, and negatively impact their reproductive success. We hypothesized that such an evolutionary trap [23, 24] could be exacerbated if foraging parasitoid females learn to exploit cues from a novel but unsuitable host. To our knowledge, there are no examples where associative learning actually results in costs to the foraging success of an animal.

To test this hypothesis we used Telenomus podisi Ashmead (Hymenoptera: Scelionidae), a common egg parasitoid of several North American stink bugs (Hemiptera: Pentatomidae) [25, 26]. As previously reported, T. podisi females accept and parasitize eggs of the brown marmored stink bug, Halyomorpha halys Stål (Pentatomidae) [27], a recently established pest from eastern Asia [28], at a similar rate to that of its coevolved host, the predator Podisus maculiventris (Say) (Pentatomidae). But the parasitoid progeny rarely develop successfully in H. halys [27, 29–34], except for a nonconforming T. podisi population in California [35]. Halyomorpha halys is progressively spreading in invaded areas, thereby increasing the probability of native T. podisi encountering this novel but unsuitable host. We examined the learning capacity of T. podisi towards its coevolved host, P. maculiventris, and non-coevolved host, H. halys, and discussed consequences on interacting species.

2. Material and methods

2.1 Hosts and parasitoid

A colony of H. halys reared continuously on raw pumpkin seeds, carrots, green beans, grapes and potted soybean plants, was established from adults collected in Ontario (Canada) in 2012. The P. maculiventris colony was initially established using adults collected in Ontario in 2011 and 2012 and supplemented with bugs from Anatis Bioprotection (Canada). They were fed with live mealworm, Tenebrio molitor L. (Coleoptera: Tenebrionidae) larvae reared in the laboratory, fresh green beans and bean plants. Nymphs were kept in plastic cylinders and fed with mealworm and green beans. For both stink bug species, freshly laid eggs (< 24 h old) were used for the experiments.

The T. podisi colony was established with individuals collected in 2011 and 2012 in Ontario. Adult parasitoids were provided with a 1:1 (vol/vol) honey:water solution rubbed on a small piece of ParaFilm®. Each week, 1–2 days-old egg masses of P. maculiventris (stuck on filter paper using Pritt® stick glue) were exposed to T. podisi females for 24 h to maintain the colony. After emergence, male and female parasitoids were kept together in glass tubes for mating and provided with the honey-water solution. Naïve (i.e. without oviposition experience), 3–8 days-old females were randomly assigned to the different experimental treatments. Females T. podisi from our laboratory colony are synovigenic (ovigeny index < 0.05), typically emerging with very few mature oocytes (mean of approximately 2.0 [36]), and can survive for up to 100 days under laboratory conditions [37]. Unpublished data (M. Gaudreau, pers. com.) further show that 4–8 day-old females have an average of 14.2 mature eggs in their abdomen, similar to the maximum number of mature eggs observed per female throughout their reproductive life.
All insects were reared in a growth chamber (Conviron E15) at 24±1°C, 50±5 percent relative humidity, under a 16L:8D photoperiod.

2.2 Treatments
To determine if *T. podisi* females exhibit learning behaviour, the following four treatments were tested: (i) naïve parasitoid females foraging on *H. halys* traces; (ii) females with experience on *H. halys* traces and eggs, then tested on *H. halys* traces; (iii) naïve females foraging on *P. maculiventris* traces; and (iv) females with experience on *P. maculiventris* traces and eggs, then tested on *P. maculiventris* traces. The experiments were conducted from 10:00 to 14:00 at 24±1°C, 50±5 percent relative humidity, under a 16L:8D photoperiod. Between 39 to 43 replicates were conducted for each treatment.

2.3 Obtaining experienced females
Experienced parasitoid females were obtained in the following manner. A female of either *H. halys* or *P. maculiventris* in their pre-ovipositional phase (with a physogastric abdomen) was introduced in an experimental arena consisting of a Petri dish (5 cm diam., 1 cm height) placed upside-down on a filter sheath. The Petri dish cover had tissue mesh (0.01 cm holes) to prevent saturation of the atmosphere with volatiles released by the stink bug female. Females walked for 30 minutes on the filter paper to allow contamination with chemical traces. Females that occasionally walked on the Petri dish were discarded. Filter papers soiled by bug’s faeces were discarded. Once the stink bug female was removed, a small egg mass (5–6 eggs) of the same species was placed in the middle of the contaminated area. A naïve (i.e. without foraging and oviposition experience) *T. podisi* female was then introduced in the arena and continuously observed. Once she had oviposited the female was removed, isolated in a 1.5 mL tube for 1 h before being tested as an experienced parasitoid. Females that did not oviposit within 1 h were discarded.

2.4 Parasitoid female response to chemical cues
As previously described [38], bioassays were conducted on a large filter paper arena (20 x 20 cm) where parasitoid females could move freely on the surface. A 5 cm diam area at the centre was exposed to a female of *H. halys* or *P. maculiventris* in pre-ovipositional phase, as described above. For the assays, a *T. podisi* female was released in the middle of the contaminated area (without host eggs) and her behaviour recorded with a HDD video camera (Sony HDR-XR 500) placed 40 cm above the arena. The assay stopped when the wasp left the arena or after 10 minutes [38]. Individuals that flew away within 10 s after the release were excluded from the analysis (n = 6). Each arena was used to test 5 females.

We recorded the time spent by the female in the arena (total residence time) and the number of times the parasitoids went back to the contaminated area once left (number of re-encounters), indicative of a tortuous path associated with the searching behaviour of a parasitoid female [15, 39, 40].

2.5 Statistical analyses
Generalized linear models (GLMs with Gaussian distribution for time data or Poisson distribution for count data) were fitted to test the effects of host herbivore species (*H. halys* or *P. maculiventris*), parasitoid previous experience (experienced or naïve) and their interaction on total parasitoid residence time and number of re-encounters with the contaminated area. Residence time data were subjected to Box-Cox transformation for normalization before the
analyses. Significance of the model terms was evaluated by means of F test or Likelihood Ratio Test [41]. Significance of the different variable levels was assessed using the Tukey method for multiple comparisons procedure, adopting a significance level $\alpha = 0.05$. The potential influence of chemical residuals from a parasitoid female on the behaviour of the following female was evaluated as a random effect in mixed models. This influence was negligible and therefore models with only fixed effect were included. Analyses were conducted under R statistical environment [42].

3. Results

Total residence time of $T.\ podisi$ varied depending on the insect species footprint (Gaussian GLM: $F_{(1, 159)} = 53.78, P < 0.0001$, the previous experience ($F_{(1, 158)} = 16.83, P < 0.0001$) and the interaction of these two factors ($F_{(1, 157)} = 4.28, P = 0.04$). For the $T.\ podisi$—$P.\ maculiventris$ association, parasitoid females that had previously experienced the chemical traces left by their native host and had been rewarded with an oviposition did not have a greater residence time in the experimental arena than naïve females. In contrast, females with a rewarded experience on the exotic $H.\ halys$ stayed significantly longer in the arena than naïve wasps when tested on chemical footprints of $H.\ halys$ (Fig 1A). However, both naïve and experienced parasitoids displayed higher residence time on chemical traces of their coevolved host $P.\ maculiventris$ than those of the exotic $H.\ halys$ (Fig 1A).

The frequency of re-encounter with the area contaminated by chemical cues varied depending on the insect species footprint (Poisson GLM: $X^2 = 35.65, P < 0.0001$), the previous experience ($X^2 = 26.39, P < 0.0001$) and the interaction of these two factors ($X^2 = 12.3, P = 0.0005$). Experienced $T.\ podisi$ females re-entered the contaminated area more frequently than naïve females (Fig 1B). Naïve females tested on $H.\ halys$ footprints rarely returned to the contaminated area. However, following a rewarded experience on $H.\ halys$, the number of re-encounters with this species was similar to the number of re-encounters of naïve females tested on $P.\ maculiventris$ (Fig 1B). Both naïve and experienced $T.\ podisi$ females returned more frequently to a patch contaminated by $P.\ maculiventris$ than $H.\ halys$ (Fig 1B).

4. Discussion

Our findings indicate that $T.\ podisi$ females exhibit increased foraging behaviour following experience with chemical traces and oviposition in both its coevolved and novel host, probably due to associative learning [11, 43]. This capacity permits a female parasitoid to capture and retain information about host availability in the habitat and to adjust her foraging behaviour accordingly. However, the value of learning and its consequences on the reproductive success of $T.\ podisi$ are opposite when exploiting a suitable ($P.\ maculiventris$) vs. unsuitable ($H.\ halys$) host. Exploiting $H.\ halys$ eggs is maladaptive for $T.\ podisi$ because it incurs significant costs to foraging females and leads to a cul-de-sac for their progeny [27]. $Telenomus\ podisi$ females are not attracted to plants infested by $H.\ halys$ under laboratory conditions [44], whereas $T.\ podisi$ was the most common parasitoid sampled from $H.\ halys$ eggs under field conditions in Canada [33]. $Halyomorpha\ halys$ not only represents an egg sink for $T.\ podisi$, but also a ‘time sink’ (sensu [27]) since females increase time foraging in areas contaminated by the unsuitable host. The waste of time is further amplified when females protect the egg mass (patch guarding) from competitors and predators during several hours following oviposition [45].

Maladaptive learning has been reported in a number of social hymenopteran insects (bees and wasps) when copying the foraging decisions of conspecifics leads to the exploitation of already deprived food resources ([46] and references therein). It was also suggested [47] that new genetic combinations following hybridization in fishes and birds could negatively impact
Fig 1. (A) Residence time and (B) number of re-encounters with the host-contaminated arena of naive and experienced wasps. The four treatments were: *T. podisi* naïve females tested on *H. halys* traces (HH naï; N = 40); *T. podisi* females experienced on *H. halys* traces and eggs, then tested on *H. halys* traces (HH exp; N = 43); naïve *T. podisi* females tested on *P. maculiventris* traces (PM naï; N = 39); *T. podisi* females experienced on *P. maculiventris* traces and eggs, then tested on *P. maculiventris* traces (PM exp; N = 39). Different letters above bars indicate significant differences between treatments (p < 0.05; GLM followed by Tukey method for multiple comparison procedure).

https://doi.org/10.1371/journal.pone.0238336.g001
learning capacities, potentially leading to postzygotic reproductive isolation. Maladaptive learning has also been reported in parasitoid species used as biological control agents. When reared on alternative host species, artificial diets or artificial rearing units, parasitoids may partly lose their capacity to find and exploit the natural pest species [48, 49]. For example, it was shown [50] that prior experience of Exeristes roborator (Hymenoptera: Ichneumonidae) when reared in an artificial arena significantly altered the behavioural response of parasitoid females to their host, the European pine shoot moth, Rhyacionia buoliana (Lepidoptera: Tortricidae), when released in forests. The present study documents an original case of detrimental learning where a parasitoid learns to associate chemical cues from an unsuitable host, thereby re-enforcing a reproductive cul-de-sac (evolutionary trap).

Both naïve and experienced T. podisi females showed a higher response to chemical traces of P. maculiventris than of H. halys. This pattern was expected because derived stimuli from coevolved hosts are likely to evoke strong innate responses by naïve individuals; indeed the innate response can be stronger than the learned response in the location and acceptance of highly suitable hosts [51]. However, we cannot exclude an effect of the rearing host (P. maculiventris), as shown in other parasitoid species [52–54]. For instance, similar residence time between naïve vs. experienced wasps when exposed to P. maculiventris chemical traces could be partly explained by T. podisi females having already gained experience when developing in and emerging from P. maculiventris eggs.

Associative learning of cues from a novel but unsuitable host would also exacerbate the negative effects of the evolutionary trap on T. podisi populations. It may contribute to modify the community structure in areas invaded by H. halys through direct and indirect ecological effects [27, 55]. Recent exposure to H. halys may lead to an increase in T. podisi’s rate of parasitism on the invasive host (host switching), and a consequent decrease in parasitism of indigenous pentatomid species (apparent predation/parasitism; (+, −) type interaction). Additional research is required to determine the extent to which detrimental learning would affect the population dynamics of native stink bugs and parasitoids. We only tested females 1 h after their experience with host chemical cues and it would be important to determine how long they exhibit such learned behaviour under natural conditions, considering ecological factors such as the relative densities of native and exotic stink bugs and the persistence of the chemical cues in the footprints.

This original case of maladaptive learning arises from a situation where a native parasitoid encounters a new potential host species as a result of a biological invasion. On one hand, there is no operational ecological filter that stops host location and acceptance and, on the other hand, there is a strong physiological filter that prevents parasitoid development [27, 32]. Accordingly, a parasitoid could escape such an evolutionary trap by evolving (i) behavioural capacities to prevent acceptance of an unsuitable resource or (ii) physiological capacities to successfully reproduce in the novel host species [27, 56].

Supporting information
S1 File. R script. R scripts and supplementary figures.
(PDF)

S1 Data. T. podisi data.
(XLSX)

Acknowledgments
We thank Paul K. Abram, Jeremy N. McNeil and three anonymous reviewers for helpful comments and Josée Doyon for technical assistance.
**Author Contributions**

**Conceptualization:** Valeria Bertoldi, Ezio Peri, Eric Conti, Jacques Brodeur.

**Data curation:** Valeria Bertoldi, Gabriele Rondoni.

**Formal analysis:** Valeria Bertoldi, Gabriele Rondoni.

**Methodology:** Valeria Bertoldi, Eric Conti, Jacques Brodeur.

**Supervision:** Eric Conti, Jacques Brodeur.

**Validation:** Jacques Brodeur.

**Writing – original draft:** Valeria Bertoldi, Eric Conti, Jacques Brodeur.

**Writing – review & editing:** Jacques Brodeur.

**References**

1. Papaj D.R. & Lewis A.C. (1993) Insect learning: Ecology and evolutionary perspectives. London, UK: Chapman & Hall.
2. Vet L.E.M. & Dicke M. (1992) Ecology of inforchemical use by natural enemies in a tritrophic context. Annual Review of Entomology 37: 141–172. https://10.1146/annurev.en.37.010192.001041
3. Turlings T.C., Wäckers F.L., Vet L.E.M., Lewis W.J. & Tumlinson J.H. (1993) Learning of host-finding cues by hymenopterous parasitoids. In: Insect learning. Springer, pp 51–78. https://doi.org/10.1007/BF00994314 PMID: 24248945
4. Godfray H.C.J. (1994) Parasitoids: behavioral and evolutionary ecology. Princeton, USA: Princeton University Press.
5. Fatouros N.E., Dicke M., Mumm R., Meiners T. & Hilker M. (2008) Foraging behavior of egg parasitoids exploiting chemical information. Behavioral Ecology 19:677–689. https://doi.org/10.1038/beheco/arn011
6. Haverkamp A. & Smid H.M. (2020) A neuronal arms race: the role of learning in parasitoid-host interactions. Current Opinion in Insect Science 42: 47–54 https://doi.org/10.1016/j.cois.2020.09.003 PMID: 32947014
7. Arthur A.P. (1971) Associative learning by *Nemeritis canescens* (Hymenoptera: Ichneumonidae). The Canadian Entomologist 103: 1137–1141. https://doi.org/10.4039/ent1031137-8
8. Lewis W. & Tumlinson J.H. (1988) Host detection by chemically mediated associative learning in a parasitic wasp. Nature 331:257. http://doi.org/10.1038/331257a0
9. Vet L.E.M. & Groenewold A.W. (1990) Semiochemicals and learning in parasitoids. Journal of Chemical Ecology 16:3119–3135. https://doi.org/10.1007/BF00979615 PMID: 24263299
10. Dukas R. (2008) Evolutionary biology of insect learning. Annual Review of Entomology 53:145–160. https://doi.org/10.1146/annurev.ento.53.103106.093334 PMID: 17803459
11. Papaj D.R. & Prokopy R.J. (1989) Ecological and evolutionary aspects of learning in phytophagous insects. Annual Review of Entomology 34:315–350. https://doi.org/10.1146/annurev.en.34.010189.001531
12. Dukas R. & Duan J.J. (2000) Potential fitness consequences of associative learning in a parasitoid wasp. Behavioral Ecology 11:536–543. https://doi.org/10.1093/beheco/11.5.536
13. Nieberding C.M., Van Dyck H. & Chitika L. (2018) Adaptive learning in non-social insects: from theory to field work, and back. Current Opinion in Insect Science 27: 75–81. https://doi.org/10.1016/j.cois.2018.03.008 PMID: 30025638
14. Kruidhof H.M., Pashaïlou F.G., Fatouros N.E., Figueroa I.A., Vet L.E., Smid H.M. et al. (2012) Reward value determines memory consolidation in parasitic wasps. PLoS One 7:e39615. https://doi.org/10.1371/journal.pone.0039615 PMID: 22936971
15. Colazza S., Peri E., Salerno G. & Conti E. (2010) Host Searching by egg parasitoids: Exploitation of host chemical cues. In: Consoli FL, Parra JRP, Zucchi RA eds Egg parasitoids in agroecosystems with emphasis on *Trichogramma*. Springer Netherlands, Dordrecht, pp 97–147. https://doi.org/10.1007/978-1-4020-9110-0_4
16. Peri E., Salerno G., Slimani T., Frati F., Conti E., Colazza S. et al. (2016) The response of an egg parasitoid to substrate-borne semiochemicals is affected by previous experience. Scientific reports 6:27098. https://doi.org/10.1038/srep27098 PMID: 27250870
17. Abram P.K., Cusumano A. Abram K., Colazza S. & Peri E (2017). Testing the habituation assumption underlying models of parasitoid foraging behavior. PeerJ. 5, e3097. https://doi.org/10.7717/peerj.3097 PMID: 28321365

18. Schlaepfer M.A., Runge M.C. & Sherman P.W. (2002) Ecological and evolutionary traps. Trends in Ecology & Evolution 17:474–480. https://doi.org/10.1016/S0169-5347(02)02580-6

19. Berthon K. (2015) How do native species respond to invaders? Mechanistic and trait-based perspectives. Biological Invasions 17:2199–2211. https://doi.org/10.1007/s10530-014-0576-y

20. Cameron E.K., Vila M. & Cabeza M. (2016) Global meta-analysis of the impacts of terrestrial invertebrate invaders on species, communities and ecosystems. Glob. Ecol Biogeography 25: 596–606. https://doi.org/10.1111/geb.12436

21. Bradley B.A., Laginhas B.B., Whitlock R., Allen J.M., Bates A.E., Bernatchez G., et al. (2019) Disentangling the abundance-impact relationship for invasive species. Proceedings of the National Academy of Sciences 116:9919–9924. https://doi.org/10.1073/pnas.1818081116 PMID: 31036667

22. Hoogendoorn M. & Heimpel G.E. (2002) Indirect interactions between an introduced and native ladybird beetle species mediated by a shared parasitoid. Biological Control 25: 224–230. https://doi.org/10.1016/S1049-9644(02)00101-9

23. Schlaepfer M.A., Sherman P.W., Blossey B. & Runge M.C. (2005) Introduced species as evolutionary traps. Ecology Letters 8:241–246. https://doi.org/10.1111/j.1461-0248.2005.00730.x

24. Robertson B.A., Rehage J.S. & Sih A. 2013. Ecological novelty and the emergence of evolutionary traps. Trends Ecol Evol 28, 552–560. https://doi.org/10.1016/j.tree.2013.04.004 PMID: 23756104

25. Yeagan K.V. (1979) Parasitism and predation of stink bug eggs in soybean and alfalfa fields. Environmental Entomology 8: 715–719. https://doi.org/10.1093/ee/8.4.715

26. Koppel A.L., Hebert D.A., Kuhar T.P. & Kamminga K. (2009) Survey of stink bug (Hemiptera: Pentatomidae) egg parasitoids in wheat, soybean, and vegetable crops in southeast Virginia. Environmental Entomology 38: 375–379. https://doi.org/10.1603/022.038.0209 PMID: 19389285

27. Abram P.K., Garipey T.D., Boivin G. & Brodeur J. 2014. An invasive stink bug as an evolutionary trap for an indigenous egg parasitoid. Biological Invasions 16:1387–1395. https://doi.org/10.1007/s10530-013-0137-y

28. Costi E., Wong W., Costantine J., Acheampong S., Maistrello L., Haye T., et al. (2020) Variation in levels of acceptance, developmental success, and abortion of Halyomorpha halys eggs by native North American parasitoids. Biological Control https://doi.org/10.1016/j.biocontrol.2020.104351 PMID: 33144821

29. Cameron E.K., Vila M. & Cabeza M. (2016) Global meta-analysis of the impacts of terrestrial invertebrate invaders on species, communities and ecosystems. Glob. Ecol Biogeography 25: 596–606. https://doi.org/10.1111/geb.12436

30. Abram P.K., Cusumano A. Abram K., Colazza S. & Peri E (2017). Testing the habituation assumption underlying models of parasitoid foraging behavior. PeerJ. 5, e3097. https://doi.org/10.7717/peerj.3097 PMID: 28321365

31. Gariepy T.D., Bruin A., Konopka J., Scott-Dupree C., Fraser H., Bon M.-C. et al. (2019) Understanding the mismatch between underlying models of parasitoid foraging behavior. PeerJ. 5, e3097. https://doi.org/10.7717/peerj.3097 PMID: 28321365

32. Schlaepfer M.A., Runge M.C. & Sherman P.W. (2002) Ecological and evolutionary traps. Trends in Ecology & Evolution 17:474–480. https://doi.org/10.1016/S0169-5347(02)02580-6

33. Berthon K. (2015) How do native species respond to invaders? Mechanistic and trait-based perspectives. Biological Invasions 17:2199–2211. https://doi.org/10.1007/s10530-014-0576-y

34. Robertson B.A., Rehage J.S. & Sih A. 2013. Ecological novelty and the emergence of evolutionary traps. Trends Ecol Evol 28, 552–560. https://doi.org/10.1016/j.tree.2013.04.004 PMID: 23756104

35. Yeagan K.V. (1979) Parasitism and predation of stink bug eggs in soybean and alfalfa fields. Environmental Entomology 8: 715–719. https://doi.org/10.1093/ee/8.4.715

36. Koppel A.L., Hebert D.A., Kuhar T.P. & Kamminga K. (2009) Survey of stink bug (Hemiptera: Pentatomidae) egg parasitoids in wheat, soybean, and vegetable crops in southeast Virginia. Environmental Entomology 38: 375–379. https://doi.org/10.1603/022.038.0209 PMID: 19389285

37. Abram P.K., Garipey T.D., Boivin G. & Brodeur J. 2014. An invasive stink bug as an evolutionary trap for an indigenous egg parasitoid. Biological Invasions 16:1387–1395. https://doi.org/10.1007/s10530-013-0137-y

38. Costi E., Wong W., Costantine J., Acheampong S., Maistrello L., Haye T., et al. (2020) Variation in levels of acceptance, developmental success, and abortion of Halyomorpha halys eggs by native North American parasitoids. Biological Control https://doi.org/10.1016/j.biocontrol.2020.104351 PMID: 33144821

39. Cameron E.K., Vila M. & Cabeza M. (2016) Global meta-analysis of the impacts of terrestrial invertebrate invaders on species, communities and ecosystems. Glob. Ecol Biogeography 25: 596–606. https://doi.org/10.1111/geb.12436

40. Abram P.K., Cusumano A. Abram K., Colazza S. & Peri E (2017). Testing the habituation assumption underlying models of parasitoid foraging behavior. PeerJ. 5, e3097. https://doi.org/10.7717/peerj.3097 PMID: 28321365

41. Gariepy T.D., Bruin A., Konopka J., Scott-Dupree C., Fraser H., Bon M.-C. et al. (2019) Understanding the mismatch between underlying models of parasitoid foraging behavior. PeerJ. 5, e3097. https://doi.org/10.7717/peerj.3097 PMID: 28321365
42. R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

43. Smid H.M. & Vet L.E.M. (2016) The complexity of learning, memory and neural processes in an evolutionary ecological context. Current Opinion in Insect Science 15: 61–69. https://doi.org/10.1016/j.cois.2016.03.008 PMID: 27436733

44. Martorana L., Brodeur J. Foti M.C. Agro A., Colazza S. & Peri E. (2019) Egg parasitoid exploitation of plant volatiles induced by single or concurrent attack of a zoophytophagous predator and an invasive phytophagous pest. Scientific Reports 9: 18956. https://doi.org/10.1038/s41598-019-55396-0 PMID: 31831800

45. Guerra-Grenier E., Abram P.K. & Brodeur J. (2020) Asymmetries affecting structure and outcome of aggressive contests between solitary egg parasitoids: the effect of natal host species. Behavioral Ecology 31: 1391–1400 https://doi.org/10.1093/beheco/araa096

46. Leadbeater E. & Chitka L. (2009) Social information use in foraging insects. In Jarau S. & Hrncir M. (eds) Insect learning: Ecology and evolutionary perspectives. London, UK: Chapman & Hall. pp. 308–342.

47. Rice A.M. & McQuillan M.A. (2018) Maladaptive learning and memory in hybrids as a reproductive isolating barrier. Proceedings of the Royal Society of London B Proceedings of the Royal Society of London B 285:20180542. https://doi.org/10.1098/rspb.2018.0542 PMID: 29848649

48. Prokopy R.J. & Lewis W.J. (1993) Application of learning to pest management. In Papaj D.R. & Lewis A. C. (eds) Insect learning: Ecology and evolutionary perspectives. London, UK: Chapman & Hall. pp 308–342.

49. Leung K., Ras E., Ferguson K.B., Ariens S., Babendri er D., Bijma P., et al. (2020) Next generation biological control: the need for integrating genetics and genomics. Biological Reviews 95: 1838–1854. https://doi.org/10.1111/brv.12641 PMID: 32794644

50. Wardle A.R & Borden J.H. (1986) Detrimental effect of prior conditioning on host habitat location by Exeristes roborator. Naturwissenschaften 73: 559–560.

51. Vet L.E.M. (1995) Parasitoid foraging: the importance of variation in individual behaviour for population dynamics. In: Floyd R.B. (ed.) The Nicholson Centenary Frontiers of population ecology, CSIRO Publishing, Melbourne, Australia, pp 254–256.

52. König K., Krimmer E., Brose S., Gantert C., Buschlüter I., König C., et al. (2015) Does early learning drive ecological divergence during speciation processes in parasitoid wasps? Proceedings of the Royal Society B 282: 20141850. https://doi.org/10.1098/rspb.2014.1850 PMID: 25621331

53. Botch P.S., Delfosse E.S. (2018) Host-acceptance behavior of Trissolcus japonicus (Hymenoptera: Scelionidae) reared on the invasive Halyomorpha halys (Heteroptera: Pentatomidae) and nontarget species. Environmental Entomology 47:403–411. https://doi.org/10.1093/ee/myy014 PMID: 29506058

54. Boyle S.M., Weber D.C., Hough-Goldstein J. & Hoelmer K.A. (2020) Parental host species affects behavior and parasitism by the pentatomid egg parasitoid, Trissolcus japonicus (Hymenoptera: Scelionidae). Biological Control 149: 104324. https://doi.org/10.1016/j.biocontrol.2020.104324

55. Heimpel G., Neuhauser C. & Hoogendoorn M. (2003) Effects of parasitoid fecundity and host resistance on indirect interactions among hosts sharing a parasitoid. Ecology Letters 6:556–566. http://doi.org/10.1046/j.1461-0248.2003.00466.x

56. Robertson B.A. & Blumstein D.T. 2019. How to disarm an evolutionary trap. Conservation Science and Practice 1: e116. https://doi.org/10.1111/csp2.116