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Field collection of egg parasitoids of Pentatomidae and Scutelleridae in Northwest Italy and their efficacy in parasitizing *Halyomorpha halys* under laboratory conditions

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Abstract

The invasion of *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae) has caused severe economic damage in crops in North America and Europe, motivating research to identify its natural enemies, both in native and invaded areas. In its Asian native range, the main natural enemies are egg parasitoids, among which the most effective are *Trissolcus japonicus* (Ashmead) and *Trissolcus mitsukurii* (Ashmead) (Hymenoptera: Scelionidae) in China and Japan, respectively. In Europe, biology, host range, and impact of most native scelionid species are not well-known. The present study aimed to investigate (1) presence and abundance of scelionid species that parasitize native Pentatomidae and Scutelleridae eggs in Northwest Italy, and (2) their ability to develop on *H. halys* eggs. During 4-year field surveys, egg masses were collected and reared until bug nymph or adult parasitoid emergence. Then, the obtained scelionid females were tested for their ability to parasitize *H. halys* eggs in laboratory no-choice experiments. Egg masses of all collected bug species were parasitized, and *Telenomus* spp. (Hymenoptera: Scelionidae), *Trissolcus belenus* (Walker), and *Anastatus bifasciatus* (Geoffroy) (Hymenoptera: Eupelmidae) were the most common parasitoids. In the laboratory, *Trissolcus kozlovi* Rjachovskij was the only species to significantly produce offspring from fresh *H. halys* eggs, whereas all tested *Trissolcus* species significantly induced host egg abortion (non-reproductive effects). This study provides knowledge of the parasitoid species associated with native bugs, and represents a starting point to investigate the intricate interactions between native and exotic parasitoids recently found in northern Italy. These egg parasitoids could potentially be effective biocontrol agents of *H. halys*.

Introduction

The brown marmorated stink bug (BMSB), *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae), is an invasive pest of many crops, including pome and stone fruits, maize, and hazelnut (Rice et al., 2014; Maistrello et al., 2017; Bosco et al., 2018; Leskey & Nielsen, 2018). Introduced from Asia and now established in North America and Europe, both in native and invaded areas, research has been conducted to find predators and parasitoids of the pest (Lee et al., 2013; Abram et al., 2017; Zhang et al., 2017). In its native range, *H. halys* eggs are attacked by a complex of parasitoid species of the genera *Trissolcus*, *Telenomus* (Hymenoptera: Scelionidae), *Ooencyrtus* (Hymenoptera: Encyrtidae), and *Anastatus* (Hymenoptera: Eupelmidae), whereas nymphs and adults are rarely parasitized (Arakawa & Namura, 2002; Yang et al., 2009; Lee et al., 2013). In China, in the provinces Beijing and Hebei, *Trissolcus japonicus* (Ashmead) is the predominant egg parasitoid, showing parasitism rates ranging from 50 to 80%. Therefore, it is the most promising candidate for classical biological control (Yang et al., 2009, 2015; Zhang et al., 2017). In

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Japan, *Trissolcus mitsukurii* (Ashmead) is the main egg parasitoid of *H. halys* (Arakawa & Namura, 2002).

In North America and Europe, few native parasitoids can successfully develop on *H. halys* eggs (Abram et al., 2017; Costi et al., 2019; Konopka et al., 2019; Balusu et al., 2019a,b; Stahl et al., 2019a; Moraglio et al., 2020). The generalist *Anastatus bifasciatus* (Geoffroy) has emerged from both field-laid and sentinel *H. halys* egg masses in Italy and Switzerland (Haye et al., 2015; Roversi et al., 2016; Costi et al., 2019; Moraglio et al., 2020). Studies on its life history and host range revealed that this species could potentially be an effective biological control agent (Stahl et al., 2018, 2019a). However, although augmentative releases of *A. bifasciatus* increased parasitism of *H. halys* eggs in a 3-year field study in fruit orchards in Italy and Switzerland, the parasitism levels achieved were not high enough to effectively suppress the pest (Stahl et al., 2019b). The generalist *Ooencyrtus telenomicida* (Vassiliev) was obtained from frozen sentinel *H. halys* eggs in Central Italy, where the pest had not yet been reported (Roversi et al., 2016). Other native European egg parasitoids in the genera *Trissolcus* and *Telenomus* have been reported to oviposit in *H. halys* eggs, but may not be able to complete development in the exotic host (Abram et al., 2014; Haye et al., 2015; Konopka et al., 2017, 2019). Nevertheless, recently, novel species have been found emerging from field-collected *H. halys* eggs in northern Italy (Moraglio et al., 2020).

Distribution, biology, and host ranges of the European scelionid species have been poorly investigated, except for species whose hosts are harmful crop pests, such as *Trissolcus basalis* (Wollaston) on *Nezara viridula* (L.) (Hemiptera: Pentatomidae) (Colazza & Bin, 1995; Corrêa-Ferreira and Moscardi, 1996; Salerno et al., 2017), and *Trissolcus semistriatus* (Nees von Esenbeck) and *Trissolcus belenus* (Walker) [senior synonym of *Trissolcus grandis* (Thomson) (Tortorici et al., 2019)] on the sunn pest, *Eurygaster integriceps* Puton (Hemiptera: Scutelleridae) (Davari & Parker, 2018). Moreover, the systematics of these species needs to be thoroughly revised. The strong interest for egg parasitoids able to attack *H. halys* worldwide has stimulated taxonomic research. Recent studies have advanced the systematics of Palaearctic *Trissolcus* spp. and provided useful identification tools to facilitate their use as biocontrol agents (Talamas et al., 2017; Tortorici et al., 2019).

Knowledge of the European scelionid species has become even more important following the recent discovery of adventive populations of both *T. japonicus* and *T. mitsukurii* in Europe, egg parasitoids of *H. halys* in its native range (Sabbatini Peverieri et al., 2018; Stahl et al., 2019c; Moraglio et al., 2020). It is essential to assess interactions between exotic and native egg parasitoids, as well as their impact on native hosts and *H. halys*. The present study aims to investigate (1) the presence and abundance of scelionid species parasitizing eggs of native Pentatomidae and Scutelleridae in Northwest Italy, and (2) their ability to attack and develop on eggs of *H. halys* in no-choice laboratory tests.

Materials and methods

Field surveys of native egg parasitoids of native bugs

Field collection of egg masses and adults of native bugs. To determine which egg parasitoid species parasitize native Pentatomidae and Scutelleridae, naturally laid egg masses of various bug species were collected at 30 field sites in Piedmont (Northwest Italy) from 2016–2019 (Table 1). Crop and non-crop, herbaceous and arboreal plants were visually inspected for the presence of egg masses. Tree canopies were inspected at 1.5–2.5 m high from the ground using a four-step foldable aluminum ladder. All leaves with bug egg masses, as well as adult bugs seen during surveys, were collected and transferred to the laboratory.

Laboratory rearing of field-collected bugs and parasitoids. In the laboratory, all insects were reared in climate-controlled chambers at 24 ± 1 °C, 65 ± 5% r.h., and L16:D8 photoperiod. Field-collected egg masses were placed individually in plastic Petri dishes (6 cm diameter) until all bug nymphs or parasitoid adults had emerged. Emergence was recorded daily. Parasitoid adults were examined, separated according to taxa, and counted. Marking the egg mass of origin, specimens belonging to the family Scelionidae were transferred to glass tubes (12 cm long, 24 mm diameter) plugged with a cotton lid and fed with honey drops until use in *H. halys* egg parasitism tests as described below. Thereafter, parasitoids were stored in 99% ethanol until species identification as described below.

Field-collected adult bugs were first identified according to Derjanschi & Péricart (2005), Péricart (2010), and Ribes & Pagola-Carte (2013), and then were reared, separated by species, in polyester cages (BugDorm-4090 Insect Rearing Cage, 47.5 × 47.5 × 47.5 cm; MegaView Science, Taichung, Taiwan). Herbivorous pentatomids were fed with host plant shoots, *Vicia faba* L. (Fabaceae) seedlings, unshelled hazelnuts, *Corylus avellana* L. (Betulaceae), and apples, *Malus sylvestris* Mill (Rosaceae), which were periodically replaced. Diet for predatory pentatomids was complemented with adults and larvae of *Plodia interpunctella* Hübner (Lepidoptera: Pyralidae). Scutellerids collected on wheat, *Triticum aestivum* L. (Poaceae), were supplied with wheat ears and wet cotton, which were

Table 1 Sites in Northwest Italy where surveys for native Pentatomidae and Scutelleridae egg masses were conducted from 2016 to 2019

Id	Site (province)	Coordinates	Altitude (m a.s.l.)	2016	2017	2018	2019
1	Antignano (AT)	44°49'53.3"N, 8°08'14.2"E	206			x	
2	Avigliana (TO)	45°03'05.0"N, 7°23'49.0"E	361				x
3	Borgone di Susa (TO)	45°07'30.8"N, 7°14'43.2"E	490		x		x
4	Bosia (CN)	44°36'00.8"N, 8°09'13.7"E	604			x	
5	Bra (CN)	44°42'23.6"N, 7°50'31.9"E	286	x	x		x
6	Brozolo (TO)	45°06'55.7"N, 8°04'10.3"E	327	x	x		x
7	Buttigliera (TO)	45°04'13.6"N, 7°25'58.5"E	408		x		
8	Cameri (NO)	45°30'31.5"N, 8°39'41.6"E	165			x	x
9	Carrù (CN)	44°28'42.6"N, 7°52'37.2"E	363	x	x	x	x
10	Casale Monferrato (AL)	45°08'35.6"N, 8°26'47.4"E	117	x	x		x
11	Castellar (CN)	44°37'32.4"N, 7°26'37.8"E	337			x	x
12	Cavour (TO)	44°46'52.4"N, 7°22'59.2"E	295	x	x	x	x
13	Ceres (TO)	45°18'59.7"N, 7°23'34.6"E	661			x	
14	Ceva (CN)	44°25'26.5"N, 8°01'33.4"E	449				x
15	Cherasco (CN)	44°36'49.4"N, 7°52'19.7"E	299			x	x
16	Chieri (TO)	45°02'28.2"N, 7°50'03.9"E	335	x	x	x	x
17	Chivasso (TO)	45°11'42.8"N, 7°54'54.6"E	182	x	x		x
18	Frossasco (TO)	44°56'06.9"N, 7°24'43.9"E	289			x	
19	Grugliasco (TO)	45°03'51.5"N, 7°35'30.3"E	287	x	x	x	
20	Magliano Alfieri (CN)	44°45'46.8"N, 8°03'13.2"E	207	x	x	x	x
21	Montà d'Alba (CN)	44°49'31.6"N, 7°56'46.7"E	301			x	
22	Moretta (CN)	44°46'01.8"N, 7°32'13.7"E	253	x	x	x	x
23	Orbassano (TO)	44°59'57.3"N, 7°33'01.4"E	266	x	x	x	x
24	Pinerolo (TO)	44°53'16.8"N, 7°20'06.1"E	370	x	x		x
25	Pino Torinese (TO)	45°03'34.4"N, 7°47'03.0"E	546				x
26	Prunetto (CN)	44°29'35.5"N, 8°08'41.2"E	729				x
27	Rivalta (TO)	45°01'51.7"N, 7°30'53.2"E	288				x
28	Stupinigi (TO)	44°59'44.2"N, 7°35'48.3"E	243				x
29	Trezzo Tinella (CN)	44°39'20.6"N, 8°06'25.2"E	561			x	x
30	Trofarello (TO)	44°58'48.6"N, 7°45'08.7"E	243	x	x		

periodically replaced. Freshly laid egg masses were collected daily, and were compared with the field-collected ones to ensure their correct identification.

At the end of the season, all field-collected egg masses were inspected under a Leica stereo microscope S6D (Leica Microsystems, Buccinasco, Milano, Italy) at up to 40× magnification to assess egg fate, especially useful if the eggs were already empty when collected. Following Moraglio et al. (2020), with some adjustments, the following egg fate categories were assigned to individual eggs within each egg mass: (1) hatched – a bug nymph had emerged, and at least one of the following was seen: attached open lid, egg buster, or incision line of the lid (Javahery, 1994); (2) parasitized – a parasitoid had emerged, leaving a hole with irregular margins, and sometimes a different coloration was seen; (3) preyed – the egg was empty due to the attack of a sucking or chewing predator; and (4) unhatched – a direct cause of mortality could not be determined.

Parasitoid identification and characterization. Specimens stored in ethanol were dried and glued on card points for morphological analyses. A Leitz large-field stereo microscope TS (Leica Microsystems) with up to 160× magnification and a spotlight Leica CLS 150X (Leica Microsystems) were used for morphological diagnosis. A semi-transparent light shield was used to reduce glare and diffuse the light. Published keys and descriptions were used to identify specimens of Eupelmidae (Askew & Nieves-Aldrey, 2004) and Pteromalidae (Grissell & Smith, 2006; Sabbatini Peverieri et al., 2019). For Scelionidae specimens, species of the genus *Trissolcus* were identified according to Talamas et al. (2017) and Tortorici et al. (2019). Some species of the genus *Telenomus* were identified by comparison with images of the primary types of *Telenomus turesis* Walker (kindly provided by Dr. Elijah Talamas), and others were indicated as *Telenomus* spp., pending a thorough revision of this genus. Specimens used for morphological analysis are deposited in the Dipartimento di Scienze Agrarie, Forestali e Alimentari (DISAFA), Italy.

Laboratory evaluation of parasitism on *Halyomorpha halys* by native egg parasitoids

To ensure the egg masses necessary for laboratory trials, colonies of *H. halys* were reared as described above for the native bug species. Fresh egg masses were obtained daily. After emergence, scelionid adults, both females and males from the same egg mass, were kept in the glass tubes described above for 24 h to allow mating. Within a week, females were used in the experiments after discriminating them by the clavate antennae. When too few parasitoid females of a species emerged from field-collected egg masses, they were offered laboratory-reared egg masses of their host species to obtain additional offspring, and females of new generations were used in the experiments.

Parasitism ability was evaluated in no-choice experiments. Each parasitoid female, tested only once, was offered a single *H. halys* egg mass in a glass tube for 24 h. The exposed egg masses were removed from the test tubes and individually reared in new glass tubes. Egg hatch and adult parasitoid emergence were evaluated daily. At least 20 fresh (laid within 24 h) and 20 frozen (freshly laid and kept at –20 °C for at least 24 h) *H. halys* egg masses were used for each scelionid species. An additional 30 fresh *H. halys* egg masses were reared in similar conditions, but not exposed to a parasitoid female (control). The following parameters were recorded for each egg mass: (1) number of eggs from which a *H. halys* nymph emerged, (2) number of eggs from which an adult parasitoid emerged, and (3) number of unhatched eggs.

Mean proportions of parasitized, hatched, and unhatched eggs (only for fresh egg masses) within each egg mass, exposed to parasitoid species or unexposed, were compared separately for fresh and frozen egg masses. Means were compared using the general linear model (GLM) procedure of IBM SPSS Statistics v.25 (IBM, Armonk, NY, USA) with a binomial distribution model and a logit link function, and separated by the Bonferroni test under the GLM procedure ($\alpha = 0.05$).

Results

Field surveys of native parasitoids

Field collection of egg masses and adults of native bugs. During surveys carried out from 2016 to 2019, we identified pentatomid egg masses to eight species and one genus (*Carpocoris*), and scutellerid egg masses to one genus (*Eurygaster*). For *Carpocoris* and *Eurygaster*, the genus was considered, and not the species, as adults of sibling species – for example, *Carpocoris mediterraneus* Tamanini and *Carpocoris purpureipennis* (De Geer); *Eurygaster maura* (L.) and *Eurygaster austriaca* (Schrank) – were found at the same time, and egg masses were not easily distinguishable. Only one predatory species was found, *Arma custos* (Fabricius), whereas the other taxa were herbivorous. Overall, 480 pentatomid and 127 scutellerid egg masses (11 800 and 1 635 eggs, respectively) were collected, on various host plants (Tables 2 and 3). In many cases, eggs of different bug taxa were found at the same sites and on the same plants. For example, egg masses of *Eurygaster* spp. and *Carpocoris* spp. were collected together on *T. aestivum* in 2016–2017. Egg masses of *N. viridula* were all collected where egg masses of *Palomena prasina* L., *Rhaphigaster nebulosa* Poda, or *A. custos* were also found. Almost all species, except *Pentatoma rufipes* L. and *Eurygaster* spp., were present on the same host plants and at the same time as *H. halys* eggs, as evaluated in simultaneous field surveys from 2016 to 2018 (Moraglio et al., 2020).

Egg fate and parasitism rate. Parasitoids emerged from field-collected egg masses of all identified bug taxa, although in different amounts (Table 3, Figure 1). Overall, the highest egg parasitism rates (>40%) were observed in *A. custos*, *Eurydema ventralis* Kolenati, *P. prasina*, and *Eurygaster* spp. (all Pentatomidae), whereas the lowest rates (about 7%) were observed in *N. viridula*. *Carpocoris* spp. and *R. nebulosa* showed intermediate values. Egg masses of *Dolycoris baccarum* L., *P. rufipes*, and *Peribalus strictus* (Fabricius) (all Pentatomidae) were collected in low numbers and only in 1 year, so parasitism rates were not considered to be representative (Table 3, Figure 1). Parasitism rates of host species at the same sites and on the same host plants (e.g., *Eurygaster* spp. and *Carpocoris* spp. at site 6 on wheat) were not similar and depended more on the bug species than on the site (Tables 2 and 3). By contrast, the predation rate was generally low for *Carpocoris* spp., *E. ventralis*, and *P. rufipes* (Table 3, Figure 1).

Parasitoid species composition and abundance. In the laboratory, a total of 437, 884, 546, and 401 hymenopteran adults emerged in 2016, 2017, 2018, and 2019, respectively. Among them, *Telenomus* spp., *A. bifasciatus*, and *T. belenus* were the most common taxa, emerging from 5 to 6 host taxa (Tables 3 and 4). They were also the most widespread parasitoids, emerging from egg masses collected at 16, 11, and 9 sites, respectively. *Telenomus* spp. (893 adults) was the most abundant taxon, emerging from eggs of five bug taxa. *Anastatus bifasciatus* (670 adults) was the second parasitoid species and *Trissolcus belenus* (291

Table 2 Numbers of egg masses of each native bug taxon collected in Northwest Italy from 2016 to 2019, collection period and sites, and host plants on which they were found

Family	Species	Year	No. egg masses	Period	Site Id[1]	Host plants
Pentatomidae	*Arma custos*	2016	4	1–18 Aug	12	*Acer* spp.
		2017	20	14 Jun–3 Aug	12	*Acer* spp., *Fraxinus* spp., *Tilia* spp.
		2018	4	19 Jul–22 Aug	12	*Acer* spp., *Fraxinus* spp., *Tilia* spp.
		2019	4	24 Jul–21 Aug	8, 9, 23, 27	*Acer* spp., *Fraxinus* spp., *Prunus persica* (L.) Stokes
	Carpocoris spp.	2016	28	18 May–13 Jun	6	*Triticum aestivum* L.
		2017	16	23–29 May	6	*T. aestivum*, *Acer* spp.
		2018	1	24 May	18	*T. aestivum*
		2019	35	13 May–19 Aug	6, 9, 15	*Corylus avellana* L., *T. aestivum*
	Dolycoris baccarum	2019	13	16 May–20 Aug	9, 15, 16, 25, 27, 29	*C. avellana*, *Fraxinus* spp., *Salvia pratensis* L., *Viburnum lantana* L.
	Eurydema ventralis	2017	24	10 May	3	*Brassica oleracea* L.
		2019	7	31 May–25 Aug	3, 16, 24	*Capparis spinosa* L., *C. avellana*
	Nezara viridula	2016	1	2 Jun	22	*Solanum lycopersicum* L.
		2017	11	25 May–29 Aug	5, 7, 12, 16, 17, 19	*Acer* spp., *Sambucus nigra* L., *Solanum melongena* L., *Tilia* spp.,
		2018	5	25 Jul–28 Aug	11, 16	*C. avellana*
		2019	22	19 Jun–23 Aug	9, 10, 15, 16, 17, 23, 27, 28	*Acer* spp., *Ailanthus altissima* (Miller) Swingle, *C. avellana*, *Diospyros kaki* L. fil., *Fraxinus* spp.
	Palomena prasina	2016	3	16–22 Jul	16, 20	*C. avellana*
		2017	40	12 May–3 Aug	5, 7, 12, 16, 17, 19, 20, 24, 30	*Acer* spp., *C. avellana*, *Prunus avium* (L.) L., *S. lycopersicum*, *Tilia* spp.
		2018	118	11 May–4 Aug	1, 4, 11, 13, 16, 20, 21, 29	*A. altissima*, *C. avellana*, *Cornus sanguinea* L., *Juglans regia* L., *P. avium*, *Pyrus communis* L., *Rosa* spp.
		2019	39	16 May–20 Sep	2, 9, 14, 15, 16, 20, 28, 29	*Acer* spp., *Alnus glutinosa* (L.) Gaertn., *C. avellana*, *D. kaki*, *P. avium*, *Quercus robur* L.
	Peribalus strictus	2019	31	6–23 Aug	2, 9, 15, 16, 28	*Acer* spp., *C. avellana*, *C. sanguinea*, *Hibiscus syriacus* L.
	Pentatoma rufipes	2019	4	20 Sep–2 Oct	2, 26	*Acer* spp.
	Rhaphigaster nebulosa	2017	24	9 May–14 Sep	5, 9, 12, 19, 20, 23, 30	*Acer* spp., *C. avellana*, *Tilia* spp.
		2018	19	31 May–27 Jul	4, 8, 11, 16, 18, 19, 20	*Acer* spp., *C. avellana*, *C. sanguinea*, *Platanus* spp.
		2019	7	22 May–19 Aug	9	*C. avellana*, *C. sanguinea*
Scutelleridae	*Eurygaster* spp.	2016	38	18 May–13 Jun	6	*T. aestivum*
		2017	69	23–29 May	6	*T. aestivum*
		2019	20	13–29 May	6	*T. aestivum*

[1]Site Ids correspond to Table 1.

adults) was the third species, both emerging from six bug taxa (Table 4).

All other *Trissolcus* spp. emerged in lower amounts from fewer (1-5) host species and sites. *Trissolcus viktorovi* Kozlov emerged from three host taxa, *Trissolcus cultratus* (Mayr), *Trissolcus kozlovi* Rjachovskij, and *T. semistriatus* emerged from two host taxa, and *T. basalis* and *Trissolcus colemani* (Crawford) each emerged from one host species, *N. viridula* and *E. ventralis*, respectively. As many as five of the eight scelionid species emerged from egg masses collected at a single site. Furthermore, the hyperparasitoid *Acroclisoides sinicus* (Huang & Liao) (Hymenoptera:

Table 3 Numbers of egg masses and eggs of each native bug taxon collected in Northwest Italy from 2016 to 2019, percentage of parasitized (parasitoid adult emergence), hatched (bug nymph emergence), unhatched (for unknown reasons), and preyed (sucked or chewed by predators) eggs, and numbers and species of egg parasitoids that emerged from the collected egg masses when reared in the laboratory

			Egg masses		Eggs					
Family	Species	Year	No.	No. parasitized	No.	% parasitized	% hatched	% unhatched	% preyed	No. and species of parasitoids
Pentatomidae	*Arma custos*	2016	4	4	72	50.0	20.83	29.17	0.0	15 *Anastatus bifasciatus*, 14 *Trissolcus kozlovi*, 6 *Trissolcus belenus*, 1 *Acroclisoides sinicus*
		2017	20	18	400	60.75	12.0	27.0	0.25	121 *A. bifasciatus*, 13 *T. kozlovi*, 24 *Ac. sinicus*
		2018	4	2	72	44.44	40.28	15.28	0.0	
		2019	4	2	68	30.88	33.82	29.41	5.88	4 *A. bifasciatus*
	Carpocoris spp.	2016	28	8	398	22.11	64.57	13.32	0.0	35 *Trissolcus semistriatus*, 53 *Telenomus* spp.[1]
		2017	16	5	214	19.63	72.43	7.94	0.0	6 *A. bifasciatus*, 13 *T. kozlovi*, 5 *T. semistriatus*, 1 *Trissolcus viktorovi*
		2018	1	0	14	0.0	92.86	7.14	0.0	
		2019	35	5	507	13.21	77.32	9.47	0.0	27 *T. semistriatus*, 31 *Telenomus* spp.[1]
	Dolycoris baccarum	2019	13	3	321	15.89	70.40	8.10	5.61	23 *T. belenus*
	Eurydema ventralis	2017	24	24	343	54.23	29.15	16.62	0.0	95 *T. viktorovi*
		2019	7	4	82	21.95	50.0	28.05	0.0	5 *A. bifasciatus*, 4 *Trissolcus colemani*, 9 *T. viktorovi*
	Nezara viridula	2016	1	0	81	0.0	100.0	0.0	0.0	
		2017	11	1	921	14.55	63.52	21.93	0.0	47 *A. bifasciatus*, 2 *Trissolcus basalis*
		2018	5	2	459	13.51	74.29	12.20	0.0	
		2019	22	3	1941	2.16	67.13	15.77	14.94	30 *A. bifasciatus*
	Palomena prasina	2016	3	2	83	53.01	15.66	31.33	0.0	8 *A. bifasciatus* 27 *T. belenus*
		2017	40	29	844	39.34	18.01	33.53	9.12	83 *A. bifasciatus*, 7 *Trissolcus cultratus*, 128 *Telenomus* spp.[1], 2 *Ac. sinicus*
		2018	118	97	2830	53.07	14.20	29.40	3.32	200 *A. bifasciatus*, 99 *T. belenus*, 27 *T. cultratus*, 162 *Telenomus* spp.[1], 21 *Ac. sinicus*
		2019	39	19	1003	33.70	23.93	13.26	29.11	110 *A. bifasciatus*, 51 *T. belenus*, 56 *T. cultratus*, 1 *Telenomus* sp.[1]

Table 3 Continued

Family	Species	Year	Egg masses No.	Egg masses No. parasitized	Eggs No.	% parasitized	% hatched	% unhatched	% preyed	No. and species of parasitoids
	Peribalus strictus	2019	31	1	421	0.71	89.79	5.94	3.56	3 *Telenomus* spp.[1]
	Pentatoma rufipes	2019	4	3	84	48.81	17.86	33.33	0.0	18 *T. belenus*, 24 *T. cultratus*
	Rhaphigaster nebulosa	2017	24	10	325	20.92	40.92	29.85	8.31	15 *A. bifasciatus*
		2018	19	13	262	27.10	13.36	56.11	3.44	26 *A. bifasciatus*, 1 *T. belenus*, 10 *Telenomus* spp.[1]
		2019	7	3	98	34.96	31.36	27.55	6.12	2 *Telenomus* spp.[1]
Scutelleridae	*Eurygaster* spp.	2016	38	28	486	58.23	23.87	17.90	0.0	46 *T. belenus*, 10 *T. semistriatus*, 222 *Telenomus* spp.[1]
		2017	69	66	875	71.43	4.23	23.66	0.69	21 *T. semistriatus*, 20 *T. belenus*, 3 *T. viktorovi*, 278 *Telenomus* spp.[1]
		2019	20	2	274	2.55	70.07	25.18	2.19	5 *Telenomus* spp.[1]

[1]*Telenomus* spp. includes *Te. turesis*.

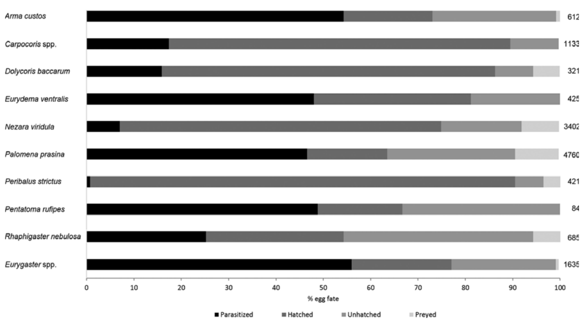

Figure 1 Fate of eggs of pentatomids and scutellerids native to Italy. Percentages of parasitized (parasitoid adult emergence), hatched (bug nymph emergence), unhatched (for unknown reasons), and preyed (sucked or chewed by predators) eggs collected for each bug taxon in Northwest Italy from 2016 to 2019. The total number of eggs is indicated on the right.

Pteromalidae) emerged from eggs of *A. custos* (12.6%) and *P. prasina* (2.3%) collected at four sites (Tables 3 and 4).

Parasitism in no-choice tests

In no-choice experiments, females of all *Trissolcus* spp. obtained in the laboratory were tested for parasitism of *H. halys* eggs, except females of *T. colemani*, because of the low number of emerged adults and the failure to produce additional offspring. Among *Telenomus* spp., only females of *Te. turesis* emerged from *Eurygaster* spp. eggs were used. Females of all seven species showed oviposition behavior on *H. halys* eggs, but only *T. kozlovi* was able to successfully parasitize fresh *H. halys* eggs in higher proportions than the other species, for which average emergence was lower than 2% (Table 5). However, all of the *Trissolcus* spp. reduced nymph emergence compared to the control. The highest reductions were observed for *T. kozlovi* and *T. basalis*, which consequently resulted in a significant increase of unhatched eggs. On the contrary, *Te. turesis* did not affect the proportion of either nymph emergence or unhatched eggs compared to the control (Table 5).

From frozen eggs, higher proportions of offspring emerged for most of the tested parasitoid species relative to fresh eggs. The highest parasitism rates were observed for *T. kozlovi* and *T. basalis*, followed by *T. belenus* and *T. cultratus*, whereas *T. semistriatus* and *T. viktorovi* were not able to produce any offspring from either fresh or frozen *H. halys* eggs (Table 5).

Discussion

Field surveys of native parasitoids

This study contributes to the knowledge of the parasitoid species complexes associated with Pentatomidae and Scutelleridae native to Italy. Literature is abundant for egg parasitoids of the agricultural pests *N. viridula* and

Table 4 Percentage of parasitoid species emerged in the laboratory from the egg masses of each native pentatomid and scutellerid bug taxon collected in Northwest Italy from 2016 to 2019

	Bug species									
Parasitoid species	*Arma custos*	*Carpocoris* spp.	*Dolycoris baccarum*	*Eurydema ventralis*	*Nezara viridula*	*Palomena prasina*	*Peribalus strictus*	*Pentatoma rufipes*	*Rhaphigaster nebulosa*	*Eurygaster* spp.
Anastatus bifasciatus	70.71	3.51		4.42	79.38	40.84			78.85	
Trissolcus basalis					20.62					
Trissolcus belenus	3.03		100.0			18.02		42.86	1.92	10.89
Trissolcus colemani				3.54						
Trissolcus cultratus						9.16		57.14		
Trissolcus kozlovi	13.64	7.60								
Trissolcus semistriatus		39.18								5.28
Trissolcus viktorovi		0.58		92.04						0.50
Telenomus turesis		49.12				29.63	100.0		19.23	83.33
Acroclisoides sinicus	12.63					2.34				
Total no.	198	171	23	113	97	982	3	42	52	606

Eurygaster spp., whereas few studies are available on field parasitism of other bugs.

Parasitoids of *N. viridula*, be it naturally occurring or through augmentative releases, are potentially effective biocontrol agents (Colazza & Bin, 1995; Corrêa-Ferreira & Moscardi, 1996). Recent research has focused on chemical ecology, that is, the emission by plants of volatile compounds in response to herbivory and egg deposition, which could affect the behavior of natural enemies, just as (volatile) compounds from herbivores themselves. A particular focus has been the interaction between *N. viridula* and *T. basalis* (Colazza et al., 2004, 2007; Salerno et al., 2006, 2019). In our study in Northwest Italy, *T. basalis* was the only scelionid species associated with *N. viridula*, consistent with observations from central Italy (Colazza & Bin, 1995), whereas other parasitoid species emerged from field-collected eggs in other areas (Jones, 1988; Corrêa-Ferreira & Moscardi, 1996). Despite its broad host range, *T. basalis* appears to be quite specialized in Italy, probably because of its selective response to host chemical cues (Salerno et al., 2006). However, its impact on *N. viridula* was low in some agro-ecosystems, and *A. bifasciatus*, another egg parasitoid of this species, may be more effective (Colazza & Bin, 1995; Stahl et al., 2018). In our study, the successful emergence of *A. bifasciatus* from *N. viridula* eggs was probably due to the host plants on which the egg masses were collected. *Anastatus bifasciatus* emerged from egg masses collected mainly on bushes and trees, such as *C. avellana*, maple (*Acer* spp.), *Ailanthus altissima* (Mill.), *Fraxinus* spp., and *Tilia* spp. In contrast, the species never emerged from *N. viridula* egg masses collected in soybean, *Glycine max* (L.) Merr. (Colazza & Bin, 1995). Similarly, *A. bifasciatus* emerged from *Carpocoris* spp. egg masses collected in maple, but never from those in wheat, suggesting a preference and/or increased performance in arboreal environments.

Most data of *Eurygaster* spp. on parasitism rates in the field are available for the sunn pest, *E. integriceps*. *Trissolcus belenus* and *T. semistriatus* have been reported as the main biocontrol agents of *E. integriceps* (Davari & Parker, 2018). However, it was not until recently that these species could be identified reliably (Tortorici et al., 2019), and all available data about their biology, host range, and impact cannot be attributed to one species or the other (Kivan & Kilic, 2002, 2006; Allahyari et al., 2004; Shirazi, 2006; İslamoğlu, 2012). In our study, both *T. belenus* and *T. semistriatus* were obtained from the eggs of *Eurygaster* spp. found on wheat. *Trissolcus semistriatus* emerged from eggs

Table 5 No-choice laboratory tests on the ability of parasitoids native to Northwest Italy to parasitize eggs of the invasive pest *Halyomorpha halys*. Mean (± SE) numbers of eggs per egg mass, and percentages of parasitoid emergence, bug nymph emergence, and unhatched eggs for fresh and frozen egg masses singly exposed to a female parasitoid for 24 h, or not exposed (control)

	Fresh egg masses					Frozen egg masses		
Species	No.	No. eggs per egg mass	% emerged parasitoid	% emerged nymphs	% unhatched eggs	No.	No. eggs per egg mass	% emerged parasitoids
Trissolcus basalis	20	22.35 ± 1.44	0.53 ± 0.37b	55.43 ± 8.06c	44.04 ± 8.05a	20	26.05 ± 0.81	28.88 ± 6.61ab
Trissolcus belenus	32	25.81 ± 0.65	0.82 ± 0.61b	71.07 ± 4.98b	28.17 ± 4.74b	22	27.23 ± 0.46	23.50 ± 6.88b
Trissolcus cultratus	21	26.05 ± 0.95	1.61 ± 1.07b	71.12 ± 5.80b	27.27 ± 5.77b	20	28.15 ± 0.48	11.03 ± 2.99c
Trissolcus kozlovi	26	24.58 ± 0.99	22.00 ± 5.10a	49.39 ± 6.77c	28.62 ± 4.58b	25	26.68 ± 0.56	34.62 ± 5.15a
Trissolcus semistriatus	30	25.47 ± 0.70	0b	67.35 ± 5.85b	32.65 ± 5.85b	20	27.35 ± 1.21	0e
Trissolcus viktorovi	20	25.00 ± 1.29	0b	75.88 ± 5.07b	24.12 ± 5.07b	20	27.95 ± 0.005	0e
Telenomus turesis	30	27.07 ± 0.43	0.12 ± 0.12b	92.13 ± 2.22a	7.75 ± 2.20c	25	26.28 ± 0.52	3.16 ± 1.25d
Control	30	26.80 ± 1.11	0	90.28 ± 2.01a	9.72 ± 2.01c			
GLM	Wald χ^2		174.426	383.645	276.386			199.553
	df		5	7	7			4
	P		<0.001	<0.001	<0.001			<0.001

Means within a column followed by the same letter are not significantly different [Bonferroni test: P<0.05, under general linear model (GLM) procedure with binomial distribution and logit link].

(both *Eurygaster* spp. and *Carpocoris* spp.) collected only on wheat, whereas *T. belenus* was more widespread and appeared to have a wider host range, associated with more host plants. However, *Telenomus* spp. had the highest impact on *Eurygaster* spp., and represented >80% of the parasitoids that emerged from these hosts. As performed for Palaearctic *Trissolcus* spp. (Talamas et al., 2017; Tortorici et al., 2019), a systematic revision of the genus *Telenomus* is needed to accurately ascribe parasitism to different hosts and environments.

Additional data on the presence of egg parasitoids in the field are available for *Carpocoris* spp., *D. baccarum*, and *Eurydema ornatum* (L.) in Iran and Turkey (Ghahari et al., 2011; İslamoğlu & Kornoşor, 2016), and for *D. baccarum* in China and Japan (Mahmoud & Lim, 2008; Zhang et al., 2017). Overall, egg parasitoids and their host associations should be further investigated, especially now that the Palaearctic species can reliably be identified. In our study in Italy, seven native *Trissolcus* spp. were obtained from field-collected egg masses of native pentatomids and scutellerids. These species are sympatric with regard to habitat and overlap in host choice (Haye et al., 2015), with the exception of *T. basalis*, which has a narrow host range in Europe, unlike in North America, and of *T. semistriatus*, which was particularly associated with wheat.

Parasitism in no-choice tests

All tested scelionid species performed oviposition behavior toward *H. halys* eggs, but generally, no offspring emerged from fresh eggs. Offspring did emerge from frozen eggs, but not for all species, corroborating results of a previous study (Haye et al., 2015). Only *T. kozlovi* was able to produce offspring in significant amounts from fresh viable eggs, consistent with field surveys in Northwest Italy, where it was the only scelionid species that emerged from *H. halys* field-laid egg masses for three consecutive years (Moraglio et al., 2020). However, *T. kozlovi* seems not to be widespread, as it was only found at one site, where it was first recorded in Italy (Moraglio et al., 2020). Little information is available about its distribution and host range, except for records of its emergence in Moldova and Russia from eggs of *P. rufipes* and *P. prasina* (Hymenoptera Online; http://hol.osu.edu). Further studies on distribution and biology of *T. kozlovi* are needed to evaluate its impact on both native bugs and *H. halys*, especially after the finding of adventive populations of *T. japonicus* in northern Italy (Sabbatini Peverieri et al., 2018; Moraglio et al., 2020), because the two species share similarities (Talamas et al., 2017).

Besides mortality, parasitoids can also cause detrimental non-reproductive effects and induce host egg abortion (Abram et al., 2016, 2019; Kaser et al., 2018). All tested *Trissolcus* spp., including *T. kozlovi*, were able to induce *H. halys* egg abortion compared with the control (eggs not exposed to parasitoids). The presence of *H. halys* egg masses at the same sites where native Pentatomidae egg masses parasitized by native *Trissolcus* spp. were found, demonstrates that *Trissolcus* spp. could encounter eggs of the exotic pest in their environment. The fact that high numbers of unhatched *H. halys* eggs were observed in the field in Italy (Moraglio et al., 2020) could possibly be contributed to non-reproductive effects caused by *Trissolcus* spp. and, in this case, *H. halys* eggs could act as an evolutionary trap for these parasitoids (Abram et al., 2014). This hypothesis should still be verified with molecular diagnoses, but seems not to be specific for Italy, as it was demonstrated in Canada, Switzerland, and China (Gariepy et al., 2014, 2019; Konopka et al., 2019).

Unhatched eggs were also found in the field-collected egg masses of native Pentatomidae and Scutelleridae. Therefore, a similar non-reproductive effect could occur, which was indeed observed for Canadian species (Gariepy et al., 2019). Also in this case, molecular diagnosis could clarify the interaction between host and parasitoid species. This aspect acquires even more importance considering that *T. japonicus* can attack eggs of the native bugs and has demonstrated non-reproductive effects on *N. viridula* eggs (Haye et al., 2020). Whereas *T. mitsukurii* is reported as a major solitary egg parasitoid of *N. viridula* in Japan (Arakawa et al., 2004), its impact on European bugs is currently unknown. The two exotic *Trissolcus* spp. recently recorded in Italy could simultaneously provide an invasional lifeline for native parasitoids, as observed for *T. cultratus*, which can act as facultative hyperparasitoid of *T. japonicus* (Konopka et al., 2017). The data provided in this study can be built upon to investigate the interactions between native and exotic *Trissolcus* spp., as well as the trophic interactions with different hosts.

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Conflict of interest

The authors declare that they have no conflict of interest.

Author contribution statement

LT, STM, and MGP conceived and designed the research. DG, STM, MGP, and SV conducted the research. FT identified the parasitoids. STM, FT, and LT wrote the manuscript. All authors read and approved the final manuscript.

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