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Study of the overwintering ecology of the hazelnut pest, *Palomena prasina* (L.) (Hemiptera: Pentatomidae) in a perspective of Integrated Pest Management

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Abstract

Palomena prasina, the green shield bug (GSB), is widely distributed in the Eurosiberian region. In the Southwest of France, it is considered as a serious pest of hazelnuts, its feeding punctures lead to blank hazelnuts and kernel necrosis, causing heavy losses in commercial orchards. To date, no Integrated Pest Management strategy is available to control *P. prasina*. Control strategies often focus on the pests' spring–summer ecology, when they are in the field or in the vicinity of crops. However, the abundance of pest populations in crops is also related to their autumn–winter ecology. The present work focussed on the autumn–winter ecology of *P. prasina* to identify new opportunities for this pest suppression. We investigate (i) where *P. prasina* overwinters, (ii) if it aggregates in its overwintering sites and (iii) if it mates while overwintering. Samples were collected over a 2-year period in different ecosystems (forests, hedges, orchards), in human-made structures and habitats (litter, bushes/trees, dead trees). The reproductive status of GSB individuals was monitored in winter, and in spring when they emerged from overwintering sites. Our results show that 97% *P. prasina* adults overwinter in the leaf litter of orchards and natural ecosystems and that 70% overwinter individually. The abundance of GSB in those sites is negatively correlated with litter temperature and positively correlated with humidity levels. Furthermore, adults only mate after leaving their overwintering site. Finally, unexpectedly, there was an important number of overwintering adults hosting endoparasitoids (32%). The fact that GSB overwinters alone in the leaf litter means controlling its populations by destroying the overwintering sites is not a solution. All the same, our results point out some promising lines of research for developing methods to control *P. prasina*. First, the emergence traps, in particular the cone traps, proved efficient for collecting emerging adults and could be considered for monitoring. Moreover, our observations suggest the existence of long-range mating signals that could be exploited for trapping. Last but not least, the important number of overwintering parasitised adults is a potential biocontrol avenue.

KEYWORDS

abiotic conditions, green shield bug, overwintering behaviour, overwintering habitat, reproductive status

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1 | INTRODUCTION

Understanding the ecology and evolution of insect herbivores is key to designing efficient Integrated Pest Management programmes (Peterson et al., 2018; Sentis et al., 2022). However, existing pest control strategies often focus on the spring–early summer ecology of pests, when the pests are in the field or in the vicinity of crops. To reduce pest pressure on the crop, we need to better account for the overall temporal and landscape ecological dynamics of pests (Schellhorn et al., 2015).

In temperate regions, insects spend a large proportion of their lifetime in diapause in the autumn–winter season (Delinger, 2022). Although diapause is an adaptive advantage for surviving this critical period (Hahn & Denlinger, 2007), it still has an important impact on the life history of insects, and strongly influences their population dynamics (Delinger, 2022). As such, some pest control strategies do account for the overwintering ecology of insect herbivores.

Trapping strategies based on knowledge of overwintering behaviour, for instance, have been tested with success for the control of *Eucryptorrhynchus scrobiculatus* (Motschulsky) and *E. brandti* (Harold) (Coleoptera: Curculionidae), which attack *Alianthus altissima* (Simaroubaceae). Late in the season, adults of these pests crawl down their host trees to overwinter in the soil nearby (Guo et al., 2021). Based on this knowledge, Yang and Wen (2021) designed bottle traps they buried in the soil close to the host trees that efficiently reduced the density of the pests in the orchard. Another strategy based on overwintering trap plants was developed to control the cotton pest *Lygus lineolaris* (Palisot de Beauvois) (Hemiptera: Miridae) (Dumont & Provost, 2022). The adults of this species overwinter in different plants (Hanny et al., 1977; Villavaso & Snodgrass, 2004) and *Verbascum thapsus* L. (Scrophulariaceae) was used to attract the bugs, as they tend to converge on it. In the following winter, these plants are sprayed with insecticides (Dumont & Provost, 2022). Overwintering aggregation may also occur independently of the spatial distribution of resources and could be used to develop control strategies. Indeed, to increase their survival rate, some species aggregate during diapause, a strategy thought to contribute to their thermoregulation (Schowalter, 1986), as protection against predators (Delinger, 2022; Wolda & Denlinger, 1984), to improve the metabolic rate (Szejner-Sigal & Williams, 2022; Tanaka et al., 1988) or is part of species' mating systems (Susset et al., 2018). Thus, for species with overwintering aggregation behaviour, control strategies could target the aggregation sites and hence a large number of insects simultaneously (Kenis et al., 2008; Lee et al., 2014).

Palomena prasina (L.) (Hemiptera: Pentatomidae), the green shield bug (GSB), is a widely distributed species in the Eurosiberian region (Lupoli & Dusoulier, 2015). The feeding punctures of this polyphagous stink bug lead to kernel necrosis or to empty hazelnuts (Romero et al., 2009) with type of damage depending on the feeding period (Hamidi et al., 2022). As a consequence, *P. prasina* causes heavy crop losses in commercial orchards in Europe (e.g. Saruhan et al., 2023; Ateş & Kaçar, 2021, for Turkey, and Bosco et al., 2018, for Italy). In southern France, *P. prasina* is a major pest of hazelnuts

(Hamidi et al., 2022) and a minor pest of other crops including apples and kiwis (Blanc, 1988).

Pyrethroid insecticides are applied to the crop in summer when the hazelnuts are most vulnerable to *P. prasina* attacks, but with limited success and with negative environmental impacts (Ceuppens et al., 2015; Liu et al., 2012). Although biological control strategies using entomopathogenic fungus (Ozdemir et al., 2021), bacteria (Ozsahin et al., 2014) or parasitoids are under study (Ozdemir et al., 2023), to date, no comprehensive IPM strategy for the control of *P. prasina* is available. There is thus a need to advance our knowledge of the overall temporal and landscape ecology of the GSB.

In the present study, we focussed on the overwintering ecology of *P. prasina*. In Southern Europe, GSB is univoltine and, at the adult stage, it enters obligate diapause in the autumn–winter season, which lasts between 3 and 4 months (Musolin & Saulich, 1996; Saulich & Musolin, 2014). However, its overwintering ecology remains mostly unknown. The information available on the pentatomid family is scattered but suggests a diversity of overwintering behaviours (Table 1), and this knowledge has been used to design control strategies for some pests. For instance, traps based on aggregation pheromones (Leskey et al., 2015) or particular building materials (Lee et al., 2013) are used to attract the overwintering brown marmorated stink bug, *Halyomorpha halys* (Stal) to help monitor its populations and have also been considered as possible trap-and-kill devices (Weber et al., 2017). Moreover, the potential of entomopathogenic fungi and parasites as biocontrol agents of overwintering individuals of this species has been evaluated (Chen et al., 2020; Hajek et al., 2023).

The aim of this study was to advance our knowledge of the overwintering ecology of *P. prasina* to identify new opportunities for pest management. We focused on the following questions: (i) where does *P. prasina* overwinter, that is, in which ecosystems, specific habitats and abiotic conditions? (ii) does it aggregate in the overwintering sites? (iii) does it mate while overwintering? The answers to these questions are discussed both from an ecological and an IPM perspective.

2 | MATERIALS AND METHODS

2.1 | Characterisation of overwintering sites

A field study was conducted in a zone with a radius of 20 km around the city of Cancon, France (44°32'09.7" N, 0°37'30.1" E, 160 m a.s.l.) from December to February (10 weeks), both in 2021 and 2022.

In 2021, three different types of ecosystems were studied: hazelnut orchards, linear hedges and woods. The hazelnut orchards were over 20 years old, at least 1 ha in size, and most of them were planted with the Pautet cultivar, which is sensitive to *P. prasina*. They were all commercial orchards with no cultural practices or pesticide spraying during the study period (the last management practices before that period correspond to pesticide spraying in July). The linear hedges were lines of trees and bushes that separated two

TABLE 1 Diapause characteristics and overwintering sites of Pentatomidae.

Tribe	Species	Diapause program	Diapause stage	Aggregation behaviour	Overwintering site	Studied region/country	References
Aeliini	<i>Aelia rostrata</i> Boheman	Obligatory	Adult	?	Leaf litter	Turkey	Memişoğlu et al. (1996); Cakmak et al. (2008)
Atestiini	<i>Plautia stali</i> Scott	Facultative	Adult	?		Asia	Kotaki and Yagi (1989)
Cappaeini	<i>Halyomorpha halys</i> (Stål)	Facultative	Adult	Present	Bark of trees; Human-made structures	North America and Asia	Toyama et al. (2006); Inkley (2012); Leskey et al. (2012); Lee et al. (2014); Hancock et al. (2019)
Carpocorini	<i>Dolycoris baccarum</i> (L.)	Facultative	Adult	?	Leaf litter; bark of trees	Asia et Europe	Jung and Lee (2018); Mutlu et al. (2018); Sabuncu et al. (2021)
Graphosomatini	<i>Graphosoma lineatum</i> (L.)		Adult	?	Leaf litter	Europe	Tullberg et al. (2008)
Halyini	<i>Erthesina fullo</i> (Thunberg)	Facultative	Adult	Present	Human-made structures; bark of tree; leaf litter	Northern Asia	Mi et al. (2020)
Pentatomini	<i>Euschistus heros</i> (Fabricius)	Facultative	Adult	?	Leaf litter	South America	Panizzi and Niva (1994); Mourão and Panizzi (2000)
	<i>Oebalus poecilus</i> (Dallas)	Facultative	Adult	?	Leaf litter	South America	Albuquerque (1993); Santos et al. (2003, 2007)
	<i>Oebalus pugnax</i> (Fabricius)	Facultative	Adult	?	Grasses	South America	Nilakhe (1976)
	<i>Oebalus mexicana</i> Sailer	Unknown	Adult	Present	Leaf litter	South America	Cortez-Madrigal et al. (2022)
	<i>Pentatoma rufipes</i> (L.)	Obligate	Nymphal	?	Bark of trees	Europe	Powell (2020)
Piezodorini	<i>Piezodorus guildinii</i> (Westwood)	Facultative	Adult	?	Leaf litter, alfalfa, pittosporum	South America	Zerbino et al. (2020)
	<i>Piezodorus hybneri</i> (Gmelin)	Facultative	Adult	?	?	Asia	Higuchi (1994)
	<i>Piezodorus lituratus</i> (Fabricius)	Unknown	Adult	?	Leaf litter; bushes	Europe	Mutlu et al. (2018); Laterza et al. (2023)
Strachiini	<i>Bagrada hilaris</i> (Burmeister)	Unknown	Adult	?	Soil	North America	Reed et al. (2013)
Rhynchocorini	<i>Biprorulus bibax</i> (Breddin)	Facultative	Adult	Present	?	Europe	James (1990)
Menidini	<i>Menida disjecta</i> (Puton) (=M. scotti)	Obligate	Adult	Present	?	Asia	Koshiyama et al. (1994)
Nezarini	<i>Palomena prasina</i> (L.)	Obligate	Adult	?	?	Northern Europe	Musolin and Saulich (1996)
	<i>Nezara viridula</i> (L.)	Facultative	Adult	?	Leaf litter; bark of trees; human-made structures	North America and Australia	Jones and Sullivan (1981); Coombs (2000); Ehler (2002); Laterza et al. (2023)

Abbreviation: ?, no information available.

fields and were more than 116 m in length. The woods were at least 0.68 ha in size. The hedges and the woods were mainly composed of local deciduous trees, different species of oak, chestnut, hornbeam, checker tree and some shrubs including dogwood and hawthorn; evergreen bushes included wild blackberry, butcher's broom and wild madder (Badeau et al., 2017; Bonneaud, 2014). In 2022, apple orchards were added to the above-mentioned ecosystems. The apple orchards were at least 3.36 ha in size. All the orchards were managed conventionally and most were surrounded by crops, mainly hazelnut, plum and apple orchards. Ten sites representing each ecosystem, located at least 8 km apart, were selected for the study. Each week, one site of each ecosystem type was prospected (i.e. each site was prospected only once per year).

Three main types of habitats were sampled in each ecosystem: leaf litter, the bark of trees and the foliage of evergreen bushes. Five samples were collected at 10-m intervals along a 50 m transect in the hedges and at the edges of orchards and woods starting at 0 m and continuing to 40 m. A further five samples were collected at the centre of the orchards and woods, at a distance of between 10 and 50 m from the edge.

A total of 600 leaf litter samples were collected, of 1 m² each (250 and 350 samples were collected in 2021 and 2022 respectively). For each sample, four abiotic parameters were recorded at the surface of the litter using a TR-74Ui Series data logger (TandD corporation, Japan): temperature, relative humidity, illuminance and UV. The depth of the leaf litter was also measured. After the measurements were complete, the leaf litter covering each 1 m² area was collected separately, placed in a black plastic bag and transported to the laboratory. The contents of each bag were placed under a photo-elector trap (Soil photo-elector Ø1 m², ecoTech Umwelt-Meßsysteme GmbH, Germany) for 24 h at 25°C under constant light (Philips Master TDL 18W/840 Cool white), after which the presence of insects was checked in each trap. At the end of the 24-h period, the photo-elector traps were removed, and leaf litter was carefully inspected for any remaining insects.

We then defined an area with a radius of 2 metres around each leaf litter sampling area. In this area, the bark of one dead or standing

tree was inspected visually for 2 minutes, and one evergreen bush was prospected for 10 seconds using a beating tray.

Finally, during the same monitoring period, a survey was conducted of potential overwintering sites in human-made structures (buildings and houses) based on a call for witnesses broadcast by radio, on Internet, and using flyers. Witnesses were asked to take photos of stink bugs present in their houses and buildings and to send them to the laboratory by email together with information on the general geographical location, plus the exact place and date of collection. Thirty-seven volunteers in the Cancon region responded to the call.

All the individuals belonging to the Pentatomoidea collected in the above-mentioned samples were identified to species level.

The abundance of *P. prasina* in the 600 leaf litter samples was analysed. We fitted a gGeneralised linear mixed model (GLMM) with a Poisson error distribution and the following fixed effects: type of ecosystem (categorical factors: hedge, woods, apple and hazelnut orchards), zone (categorical factors: interface and centre; interface corresponds to samples collected in the hedges and edges of woods and orchards), abiotic parameters of the leaf litter (continuous factors: litter depth, temperature, humidity, light and UV), study year (categorical factors: 2021 and 2022). To consider the spatial autocorrelation, we added the sampling site as a random effect (Table 2).

The goodness of fit was evaluated through the randomised quantile residuals calculated using the DHARMA package (version 0.4.6; (Hartig, 2022)). The GLMM was performed with the HLfit function of the spaMM package (version 3.13.0; Rousset & Ferdy, 2014) using R software version: 4.1.2.; (R Developmental Core Team, 2021). P-values were calculated using the type II log likelihood ratio test (hereafter L.R.). We started with a model including all the double interactions between the zone and the other seven independent variables and removed them when they were not significant. This first model is called 'Full model'.

The same statistical procedure was applied to two partial models focused on *P. prasina* abundance in the 250 samples collected in the centre of woods and orchards (called the 'Centre model') and in

TABLE 2 Description of the variables used in the overwintering site characterisation models.

Variable name	Description of the variable	Scale	Code
Abundance of <i>Palomena prasina</i>	Absence or presence of <i>P. prasina</i> in a m ² of leaf litter	0–5	Ab
Ecosystem type	Woods, hedges, apple and hazelnut orchards		Eco
Zone	Sampling area	Interface and Centre	Zone
Litter depth	Depth of the leaf litter (cm)	0.5–9	D
Temperature	Surface temperature (°C) of leaf litter	-2 to -17	Ts
Humidity	Relative humidity (%) inside the leaf litter	70–100	HR
Light intensity	Light above the leaf litter (Lux)	369–94,361	L
UV	UV (mW/cm ²) above the leaf litter	0.019–0.99	UV
Years	Study years	2021 and 2022	Year
Study sites	All the sampling sites	10 sites	Site

the 350 samples collected at the edge of woods and orchards and in the hedges (called the 'Interface model'). The effect 'zone' was removed from each of those GLMM and the remaining fixed and random effects were tested. Using the two final partial models and the 'predict' function in R, we calculated the predicted number of *P. prasina* individuals. We computed predictions and their 95% confidence intervals according to each type of ecosystem and for the year in which the largest number of individuals was recorded, except the apple orchard ecosystem which was only sampled in 2022. Furthermore, the quantitative predictive variables with no significant effect were set to their average value and the random effect was not included in the calculation.

Next, a qualitative variable with two categories corresponding to high and low values of the parameter was created for the quantitative abiotic parameters which showed a significant effect in the partial models. The threshold for defining these categories was determined by selecting a value that minimised the P-value of the effect associated with this new qualitative variable in the partial model. In simple terms, this threshold represents a value above which the number of *P. prasina* individuals in our leaf litter samples changed significantly.

2.2 | Reproductive status

The reproductive status of *P. prasina* was assessed for the overwintering adults collected in the leaf litter, as described in the previous section, plus adults emerging from overwintering sites at the end of the hibernation period, captured as described below. The study was performed in 2021–2022.

From the end of February to the end of April 2022, adults of *P. prasina* newly emerged from overwintering sites were collected in two ecosystems: a 2.3 ha hazelnut orchard surrounded by lakes and other hazelnut orchards, located near the village of Moulinet (44°31'23.9" N, 0°36'00.5" E, 117 m a.s.l.), and a 2.25 ha wood surrounded by buildings, crop fields and hazelnut orchards, located close to the city of Cancon (44°32'34.6" N, 0°35'34.2" E, 97 m a.s.l.). As no information was available concerning the most efficient traps to catch *P. prasina* emerging from overwintering sites, we used two different kinds of traps. The first was a homemade Cone trap (Raney, 1969) adapted from a pop-up mosquito transparent net tent measuring 1.8 m × 2 m × 1.5 m (LxWxH, @GLKEBY). The adaptation consisted of cutting off the floor of each tent and placing a plastic cone collector, with a 1.5 cm Ø entrance at the top of the tent. The tent was kept in place by a 1.50 m wooden pole inserted into the ground at the centre of the tent. The second trap was a homemade trap based on the Circle trap design (Mulder Jr et al., 2012), modified and adapted for *P. prasina* by enlarging the opening at the top of the trap top from Ø 0.80 cm to 1.50 cm, and by reducing the width of the trap from 81 cm to 66 cm so it fitted the circumference of the tree trunks better.

Ten cone traps and 20 Circle traps were installed at each site. The cone traps were spaced about 20 m apart and the Circle traps were

fixed to trees growing about 10 m apart. The presence of *P. prasina* in the traps was checked three times every day in the morning (at 9 am, at noon and at 5 pm), to avoid leaving emerging individuals together which could bias the evaluation of mating status (see below).

We checked the sexual maturity of both male and female *P. prasina* collected weekly in the overwintering sites between December and February, in 2020–21 and 2021–22, and in the cone and Circle traps between the end of February and the end of April 2022. All parasitised individuals were excluded from the analyses, as they could interfere with reproductive status (De Salles, 1992). First, we observed the colour of the individuals, which is considered as a proxy for reproductive status in the close species *Nezara viridula* (L.) and *Plautia stali* Scott (Kotaki & Yagi, 1989; Musolin & Numata, 2003): russet or reddish brown during the winter reproductive diapause and green during the period of active reproduction. The insects were then killed by freezing at -20°C for 2 min, dissected and the sexual organs extracted in distilled water under a stereo microscope (Nikon, SMZ1270). Ovarian development was assessed using a scale starting at 0 (previtellogenic females) and going up to 4 (post-reproductive females) (Kiritani, 1963; Nielsen et al., 2017). The mated status of females was evaluated by the presence of spermatozooids in the spermatheca (Golec & Hu, 2015; Hamidi et al., 2021) observed under the microscope. In males, sexual maturity was assessed through the presence of living (i.e. moving) spermatozooids in the testes.

3 | RESULTS

3.1 | Characterisation of overwintering sites

Table 3 lists the results of sampling Pentatomoidea in overwintering sites. A total of 471 individuals belonging to five Pentatomoidae families were collected during the two-year survey: Pentatomidae (87%), Coreidae (12%), Acanthosomatidae (0.4%), Scutelleridae (0.4%) and Reduviidae (0.2%). The three most abundant species belonging to the Pentatomidae family were *P. prasina* (38.1%), *N. viridula* (26.2%) and *H. halys* (9.2%). Coreidae were mainly represented by *Gonocerus acuteangulatus* (Goez) (86%). With 159 individuals, *P. prasina* was the most abundant true bug found among the samples.

No GSB were found in human-made structures as it is the case for *G. acuteangulatus* and in contrast to *H. halys* or *N. viridula* which were only found in human-made structures (Table 3). In natural ecosystems, *P. prasina* is extremely rare in apple orchards but is consistently present in hazelnut orchards, hedges and woods. Ninety-seven percent of *P. prasina* individuals were found in the leaf litter, while the remaining 3% were present in evergreen foliage. No individuals were found overwintering in the bark of trees. Henceforth, our analysis focuses on the litter samples.

The 'Full model' (Table 4) reveals significant interactions between zone and temperature and between zone and light. However, the p-values and estimates obtained from the partial models show

TABLE 3 Total and relative abundance (%) of the Pentatomoidea species collected in the different ecosystems and habitats during the 2-year study.

Taxon	Species	Relative abundance (%)												Total abundance			
		Apple orch.			Hazelnut orch.			Hedge			Wood						
		L.I	T.	i.	L.I	T.	i.	B.	L.I	T.	B.	L.I	T.		Human-made structures		
Acanthosomatidae:	<i>Acanthosoma</i>																
Acanthosomatinae	<i>haemorrhoidale</i>																2
Coreidae: Coreinae																	
Anisoscellini	<i>Leptoglossus</i> sp.															25	2
Coreini	<i>Coreus marginatus</i>			3.2								11.8	2.9	1.1			6
Gonocerini	<i>Gonocerus acuteangulatus</i>					2				40				21.7	24.5		49
Pentatomidae:																	
Pentatominae																	
Aelini	<i>Aelia acuminata</i>			6.5		10				3.6				8.7	8.5		23
Cappaeini	<i>Halyomorpha halys</i>															22.3	37
Carpocorini	<i>Chlorochroa pinicola</i>														1.4		1
	<i>Carpocoris purpureipennis</i>			3.2		2				3.6							4
	<i>Dolycoris baccarum</i>			6.5		4				3.6			11.8	12.5	2.9	4.3	14
	<i>Peribalus strictus</i>			12.9		8				10.7				4.3	5.3		19
Nezarini	<i>Palomena prasina</i>	100	100	61.3		74				50			11.8	37.5	46.4	52.1	159
	<i>Nezara viridula</i>															63.9	106
Pentatomini	<i>Rhaphigaster nebulosa</i>												5.9		1.4	12	25
Piezodorini	<i>Piezodorus lituratus</i>			3.2						28.6			17.6		7.2	2.1	19
Strachiini	<i>Eurydema</i> sp.			3.2											1.1		2
Scutelleridae: Eurygastrinae	<i>Eurygaster maura</i>													1.4		0.6	2
Reduviidae: Harpactorinae	<i>Nagusta goedelii</i>															0.6	1
Total abundance		1	2	31		50			5	28		17	8	69	94	166	471

Abbreviations: B, bushes; c, centre; i, interface; L, leaf litter; orch., orchard; T, tree.

TABLE 4 Results of the three best fitting models (GLMM) used to test the effect of the type of ecosystem, zone and abiotic parameters on the abundance of *Palomena prasina* in leaf litter.

Model/variable	Loglike- ratio	Df	p value
1) Full model			
D	5.45	1	0.020
Eco	2.27	3	0.518
HR	2.25	1	0.134
L	0.45	1	0.500
Ts	1.71	1	0.192
UV	3.35	1	0.067
Year	0.82	1	0.364
Zone	0.07	1	0.795
Zone: Ts	4.50	1	<0.050
Zone: L	4.52	1	<0.050
2) Interface			
D	2.32	1	0.128
Eco	1.06	3	0.788
HR	6.41	1	<0.050
L	1.92	1	0.165
Ts	0.10	1	0.754
UV	1.42	1	0.233
Year	0.00	1	0.977
3) Centre			
D	2.14	1	0.144
Eco	1.08	2	0.581
HR	0.42	1	0.515
L	3.17	1	0.075
Ts	9.34	1	<0.010
UV	1.42	1	0.233
Year	0.00	1	0.977

that these effects are not significant within each zone and exhibit inconsistency between zones (Table 4). No other effect was significant. The two partial models, 'Interface' and 'Centre', used to analyse the two zones separately, show that the abundance of *P. prasina* in the samples is explained by relative humidity and temperature: the 'Interface' model reveals a positive effect of the relative humidity of the leaf litter on *P. prasina* abundance (Table 4, Figure 1), whereas the 'Centre' model shows a negative effect of the temperature at the litter surface on the abundance of *P. prasina* (Table 4, Figure 2).

The relative humidity threshold above which the majority of *P. prasina* were observed in the 'Interface' zone was 69% and the temperature threshold under which the most *P. prasina* were observed in the 'Centre' zone was 7.5°C.

Concerning aggregation during overwintering, 70% of the leaf litter samples in which *P. prasina* were found contained only one individual, and a maximum of five individuals were present in less than 1% of the samples (Figure 3).

3.2 | Reproductive status

A total of 72 *P. prasina* were collected in the overwintering sites, 53 in Cone traps and 42 in Circle traps. There were, 2.7 and 1.1 individuals per cone and Circle trap respectively (Figure 4). There was a significant difference between the total abundance collected in the two types of traps ($\chi^2 = 3.69$, $p < 0.05$, $df = 2$) as well as in the abundance at the two different sites ($\chi^2 = 5.24$, $p < 0.05$, $df = 1$) (Figure 4).

Twenty-nine adults collected in the overwintering sites and 24 adults collected in the emergence traps hosted endoparasitoids, that is, a total of 32% overwintering individuals were parasitised. Analyses of the reproductive status were performed exclusively on non-parasitised individuals, that is, 23 females and 20 males collected in the overwintering sites and 22 females and 13 males collected during the following emergence period. From December to the end of March, all the females presented an ovarian development in rank zero (Figure 5) and none was fecundated (Figure 6). During the emergence period, although more than 65% of the females still presented an ovarian development rank of 0, some were already at a more advanced stage of ovarian development (rank 1 or 3) and also had spermatozooids in the spermatheca (Figures 5 and 6). In contrast, the testes of all the males were full of living spermatozooids in both the overwintering and the spring emergence periods.

Almost all the overwintering *P. prasina* collected, whether male or female, were brown, with less than 20% remaining green (Figure 7). In contrast, more than 80% of the emerging male and female *P. prasina* collected were green (Figure 7).

4 | DISCUSSION

Overwintering is an important driver of arthropod population dynamics (Lawton et al., 2022) and may be pivotal to developing alternative management programmes for insect pests. In this study, we investigated the almost unknown overwintering ecology of *P. prasina*, to explore new avenues for the development of IPM strategies against this important hazelnut pest.

Our results show that *P. prasina* overwintered almost exclusively in the leaf litter in all the natural ecosystems studied. Leaf litter is often used as an overwintering habitat by Pentatomidae species (McPherson et al., 2018; Table 1), but apparently varies between populations of the same species. For instance, *N. viridula*, a species phylogenetically close to *P. prasina* (Roca-Cusachs et al., 2022) which shares the same habitat in spring- and summer (wild plants and hazelnut trees, personal observ.), in the present study was only found in human-made structures, as also reported by other authors (Musolin, 2012), although Jones and Sullivan (1982) and Laterza et al. (2023) observed this stink bug overwintering in leaf litter.

Leaf litter is a common overwintering habitat for insects because it helps them survive the harsh winter season in several ways (Danks, 2006; Lee, 1989), such as by protecting them against natural enemies, but also against cold temperatures by improving their supercooling capacity (Wagner et al., 2012), or preventing marked

FIGURE 1 Prediction of the abundance of *Palomena prasina* in leaf litter in the Interface zone of the four ecosystem types, according to relative humidity. Dashed line: CI; solid line: prediction curve; ◇ 2021; ▲ 2022.

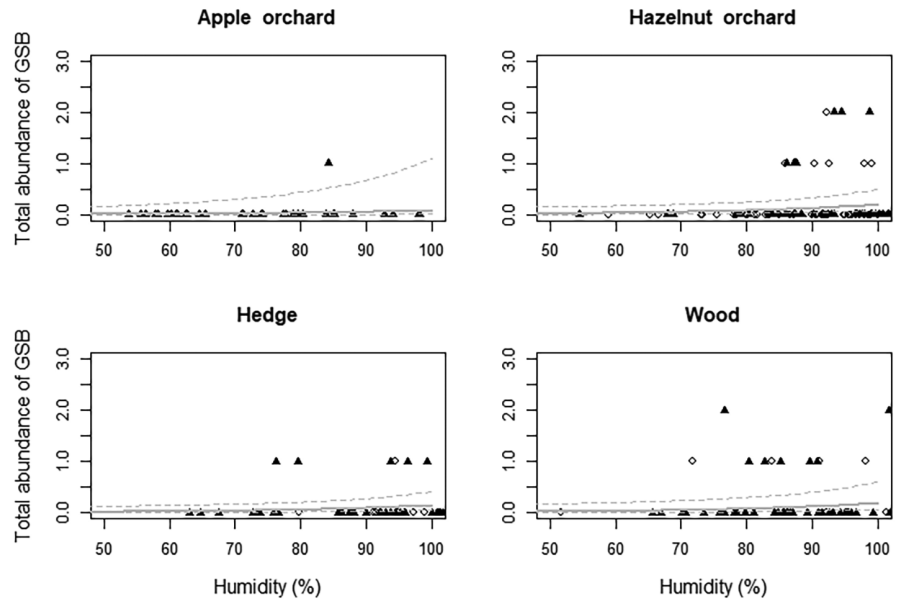
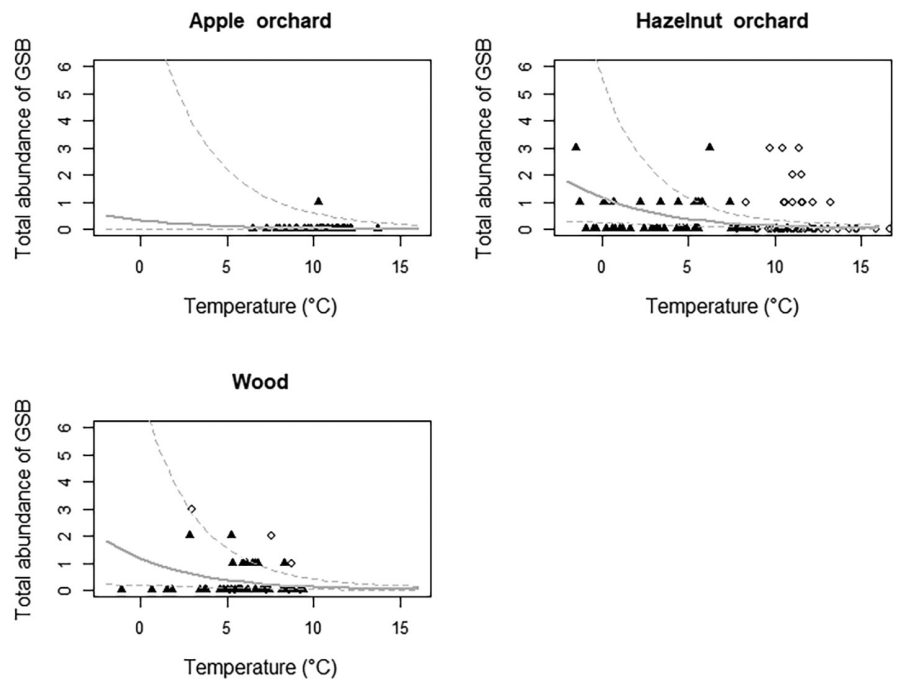


FIGURE 2 Prediction of the abundance of *Palomena prasina* in the leaf litter at the Centre zone of three ecosystem types, according to temperature. Dashed line: CI; solid line: prediction curve; ◇ 2021; ▲ 2022.



temperature variations (Parajulee et al., 1996) Thus, abiotic parameters play an essential role for insects that overwinter in leaf litter. This is also the case for *P. prasina*: our results show that GSB prefers humidity levels above 69% and temperatures below 7.5°C, which broadly corresponds to the climate characteristics of woods, the natural environment of hazelnut trees (Al-Khayri et al., 2019) and to which they are therefore more adapted.

Our study, based on a large sample, shows that *P. prasina* does not aggregate in the overwintering sites. Adults of several pentatomid species aggregate at different periods of their cycle (Musolin & Saulich, 2018), including during diapause (e.g. Table 1). Aggregation behaviour may be related to mating, as is the case of the pentatomid species *Menida disjuncta* (Ulher), where mating was observed within

overwintering aggregations (Koshiyama et al., 1994). However, aggregation is more generally considered to be a defence strategy (Gamberale & Tullberg, 1996; Parrish & Edelman-Keshet, 1999), for instance, in the Spined citrus bug *Biprorulus bibax* (Breddin), whose winter aggregations form a prickly mass hypothesised to repel predators (Panizzi et al., 2000). In contrast, the overwintering defence strategy of *P. prasina* may rely on hiding and being camouflaged by the leaf litter, as our results show that overwintering individuals were brown and difficult to spot in the leaf litter, whereas they turned green after the diapause period. Cryptic coloration in winter is often used by insects to avoid predation. In the genus *Chrysoperla*, lacewings living in deciduous forests change colour from green to yellowish in autumn, while those living in coniferous forests remain green, in each case to blend

in with the corresponding forest foliage and thereby avoid predation (Duelli et al., 2014; Macleod, 1967). Winter defence strategies based on colour changes have also been demonstrated in Pentatomidae. For instance, *Graphosoma lineatum* (L.) is a usually red-striated species in spring and summer whereas in late summer, individuals become pale-brown striated and overwinter among dried grasses on the ground (Tullberg et al., 2008). Johansen et al. (2010) showed that avian predators of *G. lineatum* need longer to find the pale-brown adults in the dried grasses than the red ones. Colour changes during the winter

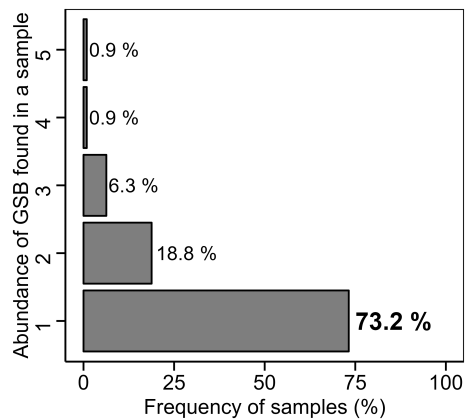


FIGURE 3 Percentage of leaf litter samples hosting 1 to 5 *Palomena prasina* individuals ($n=600$).

diapause have also been observed in *N. viridula*, where, in autumn, prior to overwintering, adults turn from green to reddish brown, become brown in winter and become green again at the beginning of spring (Musolin, 2012; Musolin & Numata, 2003).

In the case of *P. prasina*, not only winter aggregation behaviour is absent, but mating does not occur before the adults leave the overwintering sites in early spring. Indeed, although males of *P. prasina* have active spermatozooids in their testes during the overwintering period, the females remain sexually immature and do not mate during that period. In many adult insects, diapause corresponds to the arrested development of ovaries, testes, accessory glands and reproductive structures, and mating behaviour is absent (Delinger, 2022). The reproductive status of pentatomid species in winter and once they emerge from their winter habitats, differs between species. Although *Oeobalus poecilus* (Dallas) and *N. viridula* behave in a similar way to *P. prasina* (Santos et al., 2003), that is, do not mate in the overwintering sites, species such as *M. disjuncta* do mate just before emergence (Koshiyama et al., 1993, 1994).

Colour changes during the winter often match diapause. This is the case for *N. viridula* (Musolin & Numata, 2003) but also, for instance, for *Lygus Hesperus* Knight (Hemiptera: Miridae) (Brent, 2012). In our study, the changes in colour by *P. prasina* from green to brown also correspond to diapause in females. Concerning males, although active spermatozooids were present throughout the sampling period, they could have been produced in autumn before the beginning of

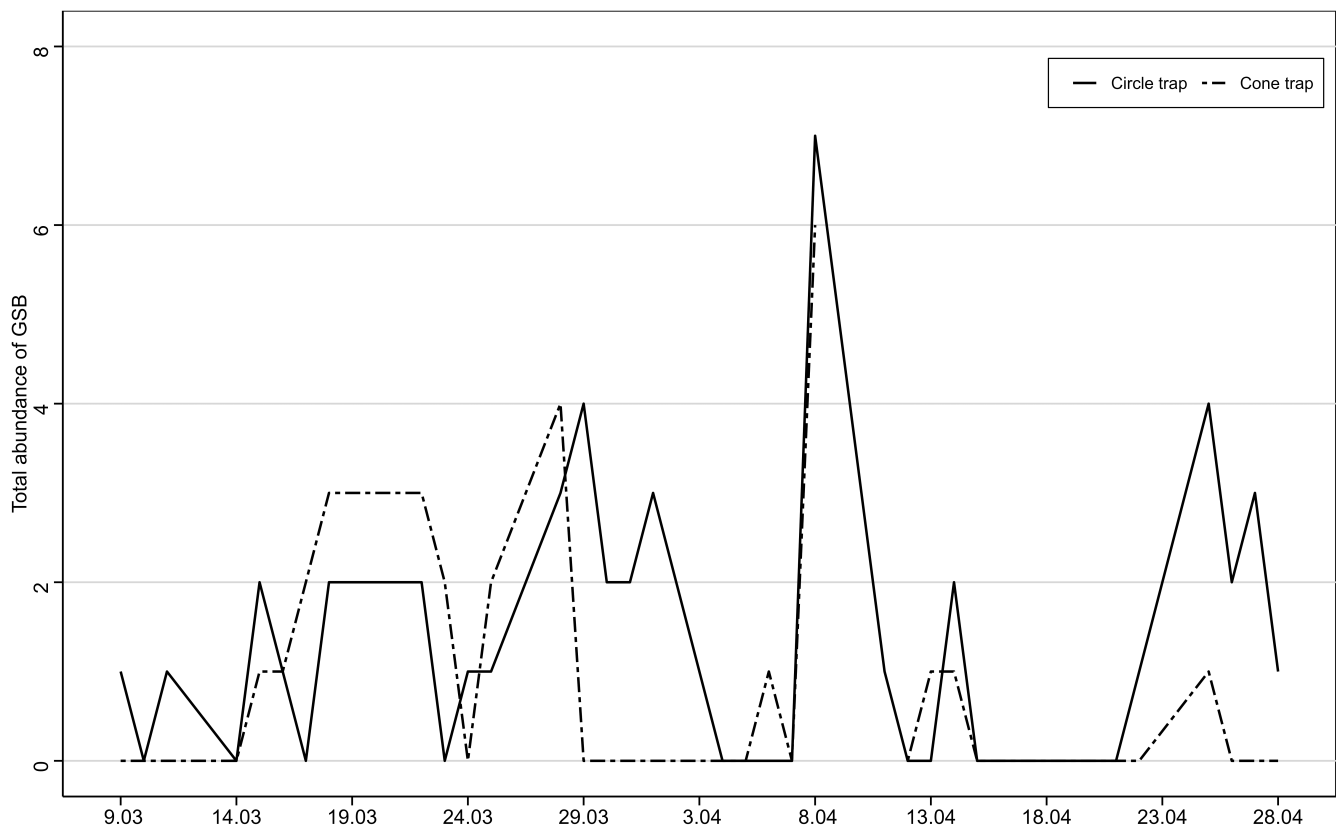


FIGURE 4 Abundance of *Palomena prasina* adults emerging from the leaf litter that were collected in the cone traps (20) and the Circle traps (20) at both sites, (a wood and a hazelnut orchard).

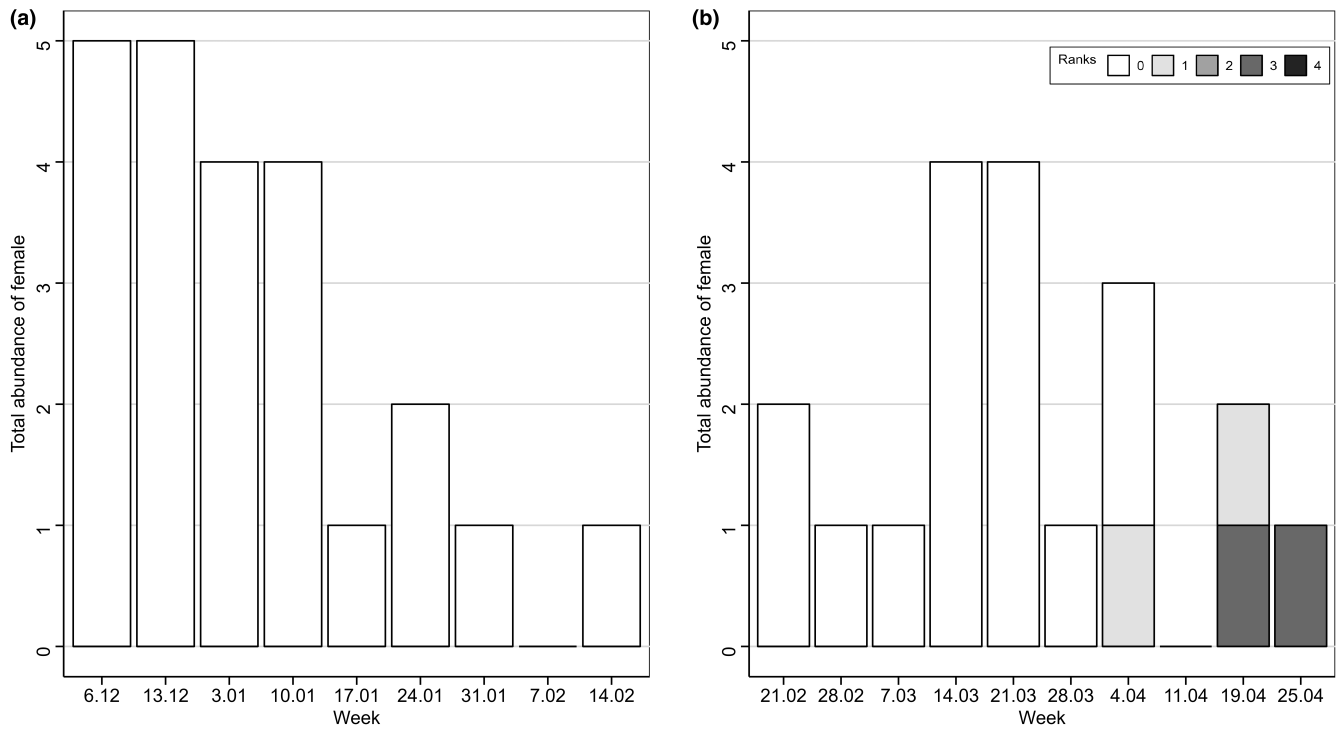


FIGURE 5 Stage of ovarian development (ranked 0 to 4) of *Palomena prasina* females collected weekly (a) at the overwintering sites, and (b) in the cone and Circle traps.

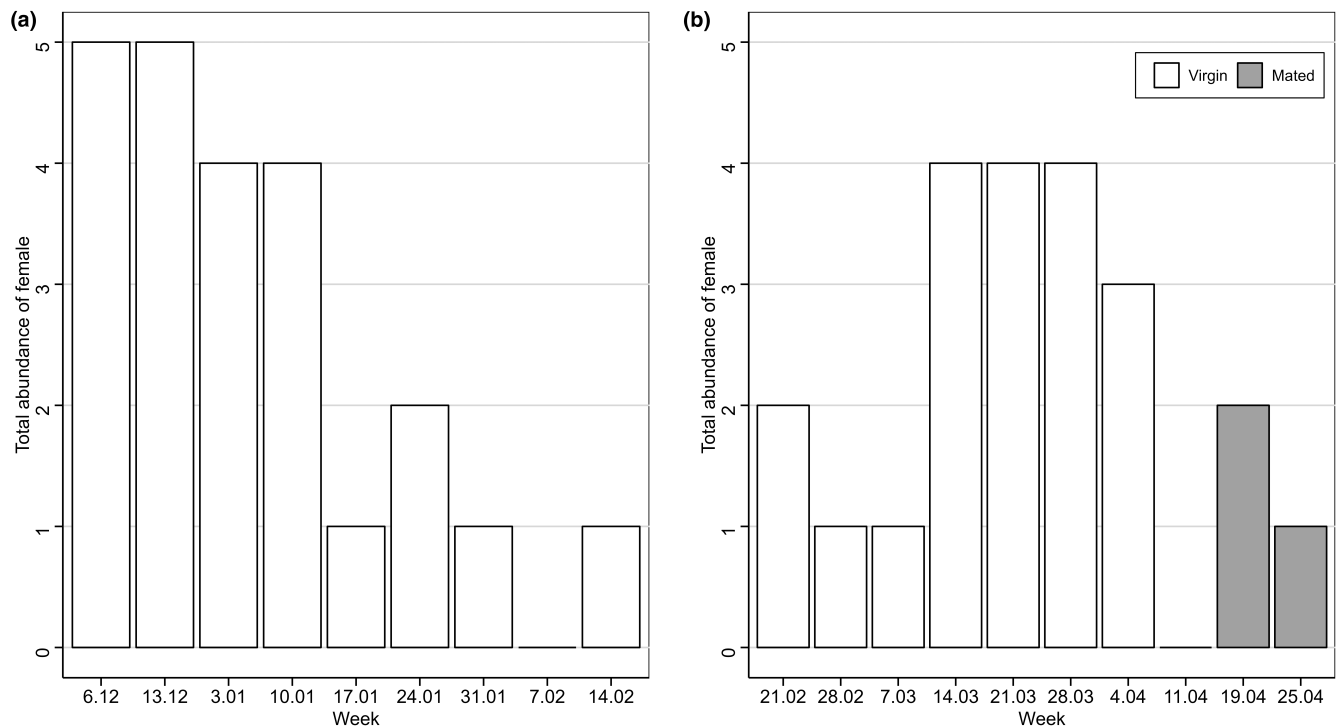


FIGURE 6 Number of virgin and mated *Palomena prasina* females collected weekly (a) at the overwintering sites, and (b) in the cone and Circle traps.

diapause, meaning we were unable to resolve the diapause status of males in our study.

The main objective of the present work was to exploit the knowledge gathered on the overwintering ecology of *P. prasina*, in order to

design new pest management strategies. The fact that GSB overwinters in the leaf litter of several different ecosystems and that, in addition, individuals overwinter alone, means controlling its populations by destroying the overwintering sites is not a solution, in contrast

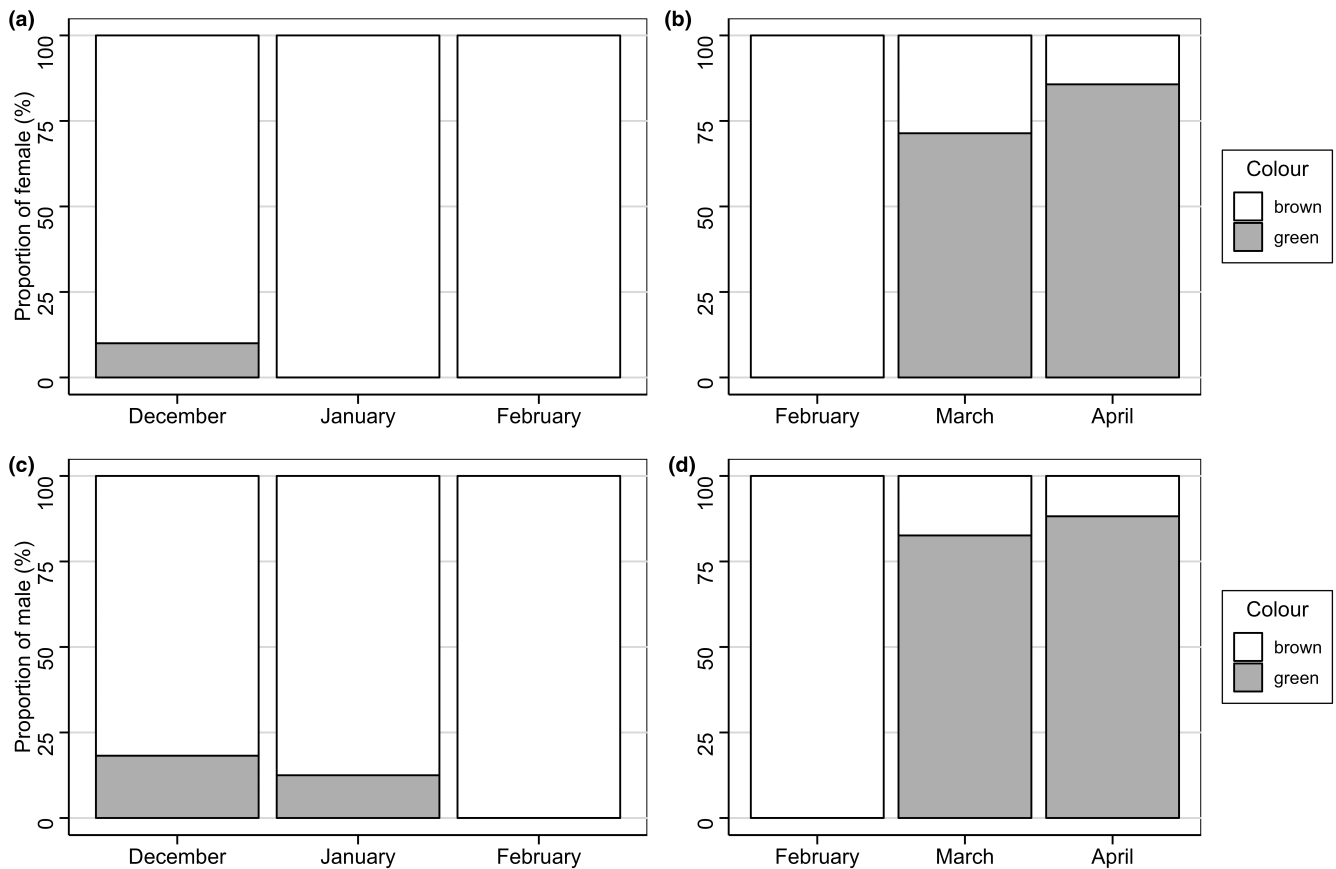


FIGURE 7 Proportion of brown and green *Palomena prasina* collected (a) at the overwintering sites, and (b) in the cone and Circle traps.

to other species (e.g. Seiter et al., 2013). All the same, our results do open new perspectives for the control of *P. prasina*. In particular, the fact that no mating was found to take place in the overwintering sites strongly suggests that mating takes place after overwintering and thereby raises the question of how individuals that emerge singly from their overwintering site manage to find each other. Beyond the framework of the present study, in several years, we observed from April to May many large aggregations of post-overwintering *P. prasina* individuals on the bark of willow and black poplar trees growing next to one of our sampling sites. Many mating events were taking place in these aggregations, which could mean sex pheromones are involved in the attraction of partners. Sex pheromones have been identified in several pentatomid species (Weber et al., 2017) and have for instance been used for monitoring *Euschistus heros* (F.) (Borges et al., 2011). However, group mating communication in pentatomid species is generally multimodal, involving both long and short-range signals (Čokl et al., 2019). Although short-range vibrational signals have been reported for *P. prasina* (Polajnar et al., 2013), long-range communication with chemical signals still requires investigation for this species.

It is also noteworthy that both cone and Circle traps succeeded in collecting post-overwintering individuals, and cone traps proved to be particularly efficient. As such, cone traps could be used to establish a Biofix, either for the first emerging individuals or for the time they consistently emerge from diapause (Pak et al., 2022). This

could then be used to construct degree-day models to predict the future presence of GBS at particular developmental stages in the crop, as suggested for *H. halys* (Bergh et al., 2017).

Finally, unexpectedly, we found a large number of parasitised individuals in the overwintering sites, corresponding to 32% of all the individuals collected. Identification of these natural enemies of *P. prasina* is still ongoing, but strategies to favour the presence of parasitoids close to overwintering sites to enhance biological control of pests is a promising option which now requires further study.

To conclude, our work on the overwintering ecology of *P. prasina* points out three promising lines of research for developing methods to control this pest, in particular the use of emergence traps for monitoring, the identification of long-range mating signals as attractants for traps, and the study of winter endoparasitoids as potential biocontrol agents.

AUTHOR CONTRIBUTIONS

Laetitia Driss: Conceptualization; methodology; investigation; writing – original draft; visualization; formal analysis; data curation. **Rachid Hamidi:** Conceptualization; methodology; project administration; supervision; writing – review and editing. **Christophe Andalo:** Formal analysis; methodology; visualization; writing – review and editing. **Alexandra Magro:** Conceptualization; methodology; supervision; project administration; validation; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

All the co-authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Raw data are available on the following link: <https://doi.org/10.5061/dryad.zcrjdfnjt>.

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REFERENCES

- Albuquerque, G. S. (1993). Planting time as a tactic to manage the small rice stink bug, *Oebalus poecilus* (Hemiptera, Pentatomidae), in Rio Grande do Sul, Brazil. *Crop Protection*, 12, 627–630. [https://doi.org/10.1016/0261-2194\(93\)90128-6](https://doi.org/10.1016/0261-2194(93)90128-6)
- Al-Khayri, J. M., Jain, S. M., & Johnson, D. V. (2019). *Advances in plant breeding strategies: Nut and beverage crops*. Springer International Publishing Springer.
- Ateş, S., & Kaçar, G. (2021). Population dynamics of green shield bug (*Palomena prasina* L.) and nut weevil (*curculio nucum* L.) in Sakarya province of Turkey. *Journal of Agriculture and Nature*, 24, 362–371. <https://doi.org/10.18016/ksutarimdogva.vi.746253>
- Badeau, V., Bonhomme, M., Bonne, F., Carré, J., Cecchini, S., Chuine, I., Ducatillon, C., Jean, F., & Lebourgeois, F. (2017). *Les plantes au rythme des saisons: Guide d'observation phénologique*. Biotope.
- Bergh, J. C., Morrison, W. R., Joseph, S. V., & Leskey, T. C. (2017). Characterizing spring emergence of adult *Halyomorpha halys* using experimental overwintering shelters and commercial pheromone traps. *Entomologia Experimentalis et Applicata*, 162, 1–10. <https://doi.org/10.1111/eea.12539>
- Blanc, M. (1988). *Guide de protection raisonnée: pommier, poirier*. Association de coordination technique agricole.
- Bonneaud, F. (2014). Atlas des paysages de Lot-et-Garonne, *La forêt*. [Text Article]. <https://atlaspaysages.lotetgaronne.fr/spip.php?article38>
- Borges, M., Moraes, M. C. B., Peixoto, M. F., Pires, C. S. S., Sujii, E. R., & Laumann, R. A. (2011). Monitoring the neotropical brown stink bug *Euschistus heros* (F.) (Hemiptera: Pentatomidae) with pheromone-baited traps in soybean fields: Pheromone traps to stink bug monitoring. *Journal of Applied Entomology*, 135, 68–80. <https://doi.org/10.1111/j.1439-0418.2010.01507.x>
- Bosco, L., Moraglio, S. T., & Tavella, L. (2018). *Halyomorpha halys*, a serious threat for hazelnut in newly invaded areas. *Journal of Pest Science*, 91, 661–670. <https://doi.org/10.1007/s10340-017-0937-x>
- Brent, C. S. (2012). Classification of diapause status by color phenotype in *Lygus hesperus*. *Journal of Insect Science*, 12, 1–14. <https://doi.org/10.1673/031.012.13601>
- Cakmak, O., Bashan, M., & Kocak, E. (2008). The influence of life-cycle on phospholipid and triacylglycerol fatty acid profiles of *Aelia rostrata* Boheman (Heteroptera: Pentatomidae). *Journal of the Kansas Entomological Society*, 81, 261–275. <https://doi.org/10.2317/JKES-709.11.1>
- Ceuppens, B., Eeraerts, M., Vleugels, T., Cnops, G., Roldan-Ruiz, I., & Smaghe, G. (2015). Effects of dietary lambda-cyhalothrin exposure on bumblebee survival, reproduction, and foraging behavior in laboratory and greenhouse. *Journal of Pest Science*, 88, 777–783. <https://doi.org/10.1007/s10340-015-0676-9>
- Chen, J., Li, W., Mi, Q., Zhang, F., Shi, S., & Zhang, J. (2020). A newly reported parasitoid, *Pentatomophaga latifascia* (Diptera: Tachinidae), of adult *Halyomorpha halys* in Beijing, China. *Insects*, 11, 1–8. <https://doi.org/10.3390/insects11100666>
- Čokl, A., Blassioli-Moraes, M. C., Laumann, R. A., Žunič, A., & Borges, M. (2019). Stinkbugs: Multisensory communication with chemical and vibratory signals transmitted through different media. In P. Hill, R. Lakes-Harlan, V. Mazzoni, P. Narins, M. Virant-Doberlet, & A. Wessel (Eds.), *Biotremology: Studying vibrational behavior* (pp. 91–122). Springer. https://doi.org/10.1007/978-3-030-22293-2_7
- Coombs, M. T. (2000). Seasonal phenology, parasitism, and evaluation of mowing as a control measure for *Nezara viridula* (Hemiptera: Pentatomidae) in Australian pecans. *BioOne*, 29, 1027–1033. <https://doi.org/10.1603/0046-225X-29.5.1027>
- Cortez-Madrigal, H., Montores-Ramírez, J., Cárdenas-Ochoa, C., & Ochoa-Echegollen, M. (2022). Epizootics of entomopathogenic fungi at overwintering sites of *Oebalus mexicana* Sailer (Hemiptera: Pentatomidae) from Western Mexico. *Egyptian Journal of Biological Pest Control*, 32, 11. <https://doi.org/10.1186/s41938-022-00509-7>
- Danks, H. V. (2006). Insect adaptations to cold and changing environments. *The Canadian Entomologist*, 138, 1–23. <https://doi.org/10.4039/n05-802>
- De Salles, L. A. (1992). Effect of *Trichopoda pennipes* parasitization on *Nezara viridula*. *Pesquisa Agropecuária Brasileira*, 27, 981–986.
- Delinger, D. L. (2022). *Insect diapause*. Cambridge University Press.
- Duelli, P., Johnson, J. B., Waldburger, M., & Henry, C. S. (2014). A new look at adaptive body coloration and color change in “common green lacewings” of the genus *Chrysoperla* (Neuroptera: Chrysopidae). *Annals of the Entomological Society of America*, 107, 382–388. <https://doi.org/10.1603/AN13139>
- Dumont, F., & Provost, C. (2022). Using autumnal trap crops to manage tarnished plant bugs (*Lygus lineolaris*). *Insects*, 13, 441. <https://doi.org/10.3390/insects13050441>
- Ehler, L. E. (2002). An evaluation of some natural enemies of *Nezara viridula* in northern California. *BioControl*, 47, 309–325. <https://doi.org/10.1023/A:1014895028451>
- Gamberale, G., & Tullberg, B. S. (1996). Evidence for a more effective signal in aggregated aposematic prey. *Animal Behaviour*, 52, 597–601. <https://doi.org/10.1098/rspb.1998.0374>
- Golec, J. R., & Hu, X. P. (2015). Preoverwintering copulation and female ratio bias: Life history characteristics contributing to the invasiveness and rapid spread of *Megacopta cribraria* (Heteroptera: Plataspidae). *Environmental Entomology*, 44, 411–417. <https://doi.org/10.1093/ee/nvv014>
- Guo, W., Qin, Y., & Wen, J. (2021). Reproductive dormancy in overwintering adult *Eucryptorrhynchus brandti* (Coleoptera: Curculionidae). *Environmental Entomology*, 50, 1166–1172. <https://doi.org/10.1093/ee/nvab078>
- Hahn, D. A., & Denlinger, D. L. (2007). Meeting the energetic demands of insect diapause: Nutrient storage and utilization. *Journal of Insect Physiology*, 53, 760–773. <https://doi.org/10.1016/j.jinsphys.2007.03.018>

- Hajek, A. E., Brandt, S. N., González, J. B., & Bergh, J. C. (2023). Entomopathogens infecting brown marmorated stink bugs before, during, and after overwintering. *Journal of Insect Science*, 23, 1–8. <https://doi.org/10.1093/jisesa/iead033>
- Hamidi, R., Calvy, M., Valentie, E., Driss, L., Guignet, J., Thomas, M., & Tavella, L. (2022). Symptoms resulting from the feeding of true bugs on growing hazelnuts. *Entomologia Experimentalis et Applicata*, 170, 477–487. <https://doi.org/10.1111/eea.13165>
- Hamidi, R., Taupin, P., & Frérot, B. (2021). Physiological synchrony of the broad bean weevil, *Bruchus rufimanus* Boh., to the host plant phenology, *Vicia faba* L. *Frontiers in Insect Science*, 1, 1–10. <https://doi.org/10.3389/finsc.2021.707323>
- Hancock, T. J., Lee, D., Bergh, J. C., Morrison, W. R., & Leskey, T. C. (2019). Presence of the invasive brown marmorated stink bug *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae) on home exteriors during the autumn dispersal period: Results generated by citizen scientists. *Agricultural and Forest Entomology*, 21, 99–108. <https://doi.org/10.1111/afe.12312>
- Hanny, B. W., Cleveland, T. C., & Meredith, W. R. (1977). Effects of tarnished plant bug, (*Lygus lineolaris*), infestation on presquaring cotton (*Gossypium hirsutum*). *Environmental Entomology*, 6, 460–462. <https://doi.org/10.1093/ee/6.3.460>
- Hartig, F. (2022). DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models. [Text article]. <https://cran.r-project.org/web/packages/DHARMA/vignettes/DHARMA.html>
- Higuchi, H. (1994). Photoperiodic induction of diapause, hibernation and voltinism in *Piezodorus hybneri* (Heteroptera: Pentatomidae). *Applied Entomology and Zoology*, 29, 585–592. <https://doi.org/10.1303/aez.29.585>
- Inkley, D. B. (2012). Characteristics of home invasion by the brown marmorated stink bug (Hemiptera: Pentatomidae). *Journal of Entomological Science*, 47, 125–130. <https://doi.org/10.18474/0749-8004-47.2.125>
- James, D. G. (1990). Energy reserves, reproductive status and population biology of overwintering *Biprorulus bibax* (Hemiptera, Pentatomidae) in southern new-South-Wales citrus groves. *Australian Journal of Zoology*, 38, 415–422. <https://doi.org/10.1071/zo9900415>
- Johansen, A. I., Exnerova, A., Hoyova, S., Katerin, A., Štys, P., Gamberale-Stille, G., & Tullberg, B. S. (2010). Adaptive change in protective coloration in adult striated shieldbugs *Graphosoma lineatum* (Heteroptera: Pentatomidae): Test of detectability of two colour forms by avian predators. *Ecological Entomology*, 35, 602–610. <https://doi.org/10.1111/j.1365-2311.2010.01219.x>
- Jones, W. A., & Sullivan, M. J. (1981). Overwintering, habitats, spring emergence patterns, and winter mortality of some South Carolina Hemiptera. *Environmental Entomology*, 10, 409–414.
- Jones, W. A., & Sullivan, M. J. (1982). Role of host plants in population dynamics of stink bug pests of soybean in South Carolina. *Environmental Entomology*, 11, 867–875.
- Jung, M., & Lee, D.-H. (2018). Characterization of overwintering behaviors and sites of bean bug, *Riptortus pedestris* (Hemiptera: Alydidae), under laboratory and field conditions. *Environmental Entomology*, 47, 1280–1286. <https://doi.org/10.1093/ee/nvy123>
- Kenis, M., Roy, H. E., Zindel, R., & Majerus, M. E. N. (2008). Current and potential management strategies against *Harmonia axyridis*. *BioControl*, 53, 235–252. <https://doi.org/10.1007/s10526-007-9136-7>
- Kiritani, K. (1963). The change in reproductive system of the southern green stink bug, *Nezara viridula*, and its application to forecasting of the seasonal history. *Japanese Journal of Applied Entomology and Zoology*, 7, 327–337.
- Koshiyama, Y., Fujisaki, K., & Nakasuji, F. (1994). Mating and diapause in hibernating adults of *Menida scotti* Puton (Heteroptera: Pentatomidae). *Population Ecology*, 36, 87–92. <https://doi.org/10.1007/BF02515089>
- Koshiyama, Y., Tsumuki, H., Muraji, M., Fujisaki, K., & Nakasuji, F. (1993). Transfer of male secretions to females through copulation in *Menida scotti* (Heteroptera: Pentatomidae). *Applied Entomology and Zoology*, 28, 325–332. <https://doi.org/10.1303/aez.28.325>
- Kotaki, T., & Yagi, S. (1989). Hormonal control of adult diapause in the brown-winged green bug, *Plautia stali* Scott (Heteroptera: Pentatomidae). *Applied Entomology and Zoology*, 24, 42–51. <https://doi.org/10.1303/aez.24.42>
- Laterza, I., Dioli, P., & Tamburini, G. (2023). Semi-natural habitats support populations of stink bug pests in agricultural landscapes. *Applied Entomology and Zoology*, 342, 108223. <https://doi.org/10.1016/j.agee.2022.108223>
- Lawton, D., Huseeth, A. S., Kennedy, G. G., Morey, A. C., Hutchison, W. D., Reising, D. D., Dorman, S. J., Dillard, D., Venette, R. C., Groves, R. L., Adamczyk, J. J., Barbosa Dos Santos, I., Baute, T., Brown, S., Burkness, E., Dean, A., Dively, G. P., Doughty, H. B., Fleischer, S. J., ... Zuefle, M. (2022). Pest population dynamics are related to a continental overwintering gradient. *Proceedings of the National Academy of Sciences*, 119, e2203230119. <https://doi.org/10.1073/pnas.2203230119>
- Lee, D.-H., Cullum, J. P., Anderson, J. L., Daugherty, J. L., Beckett, L. M., & Leskey, T. C. (2014). Characterization of overwintering sites of the invasive brown marmorated stink bug in natural landscapes using human surveyors and detector canines. *PLoS One*, 9, e91575. <https://doi.org/10.1371/journal.pone.0091575>
- Lee, D.-H., Short, B. D., Joseph, S. V., Bergh, J. C., & Leskey, T. C. (2013). Review of the biology, ecology, and management of *Halyomorpha halys* (Hemiptera: Pentatomidae) in China, Japan, and the Republic of Korea. *Environmental Entomology*, 42, 627–641. <https://doi.org/10.1603/EN13006>
- Lee, R. E. (1989). Insect cold-hardiness: To freeze or not to freeze. *Biosciences*, 39, 308–313.
- Leskey, T. C., Agnello, A., Bergh, J. C., Dively, G. P., Hamilton, G. C., Jentsch, P., Khrimian, A., Krawczyk, G., Kuhar, T. P., Lee, D.-H., Morrison, W. R., Polk, D. F., Rodriguez-Saona, C., Shearer, P. W., Short, B. D., Shrewsbury, P. M., Walgenbach, J. F., Weber, D. C., Welty, C., ... Zaman, F. (2015). Attraction of the invasive *Halyomorpha halys* (Hemiptera: Pentatomidae) to traps baited with semiochemical stimuli across the United States. *Environmental Entomology*, 44, 746–756. <https://doi.org/10.1093/ee/nvv049>
- Leskey, T. C., Hamilton, G. C., Nielsen, A. L., Polk, D. F., Rodriguez-Saona, C., Bergh, J. C., Herbert, D. A., Kuhar, T. P., Pfeiffer, D., Dively, G. P., Hooks, C. R. R., Raupp, M. J., Shrewsbury, P. M., Krawczyk, G., Shearer, P. W., Whalen, J., Koplinka-Loehr, C., Myers, E., Inkley, D., ... Wright, S. E. (2012). Pest status of the brown marmorated stink bug, *Halyomorpha halys* in the USA. *Outlooks on Pest Management*, 23, 218–226. <https://doi.org/10.1564/23oct07>
- Liu, X., Zhan, Y., Luo, Y., Zhang, M., Geng, S., & Xu, J. (2012). Almond organophosphate and pyrethroid use in the San Joaquin Valley and their associated environmental risk. *Journal of Soils and Sediments*, 12, 1066–1078. <https://doi.org/10.1007/s11368-012-0519-8>
- Lupoli, R., & Dusoulier, F. (2015). *Les punaises Pentatomidae de France*. Éditions Ancyrosoma.
- Macleod, E. G. (1967). Experimental induction and elimination of adult diapause and autumnal coloration in *Chrysopa carnea* (Neuroptera). *Journal of Insect Physiology*, 13, 1343–1349. [https://doi.org/10.1016/0022-1910\(67\)90136-9](https://doi.org/10.1016/0022-1910(67)90136-9)
- McPherson, J. E., Bundy, C. S., & Wheeler, G., Jr. (2018). Overview of the superfamily Pentatomidae. In J. McPherson (Ed.), *Invasive stink bugs and related species: Biology, higher systematics, semiochemistry, and management* (pp. 3–20). CRC Press.
- Memişoğlu, H., Melan, K., Özkan, M., Kiliç, A., & Dörtbudak, Y. (1996). Investigations on the hibernation and migration of *Aelia rostrata* Boh. in the Central Anatolia. *Plant Protection Bulletin*, 36, 115–142.

- Mi, Q., Zhang, J., Gould, E., Chen, J., Sun, Z., & Zhang, F. (2020). Biology, ecology, and management of *Erthesina fullo* (Hemiptera: Pentatomidae): A review. *Insects*, 11, 1–18. <https://doi.org/10.3390/insects11060346>
- Mourão, A. P. M., & Panizzi, A. R. (2000). Diapause and different seasonal morphs of *Euschistus heros* (Fabr.) (Hemiptera: Pentatomidae) in northern Paraná state. *Anais da Sociedade Entomológica do Brasil*, 29, 205–218. <https://doi.org/10.1590/S0301-8059200000200002>
- Mulder, P. G., Jr., Harris, M. K., & Grantham, R. A. (2012). Biology and management of the pecan weevil (Coleoptera: Curculionidae). *Journal of Integrated Pest Management*, 3, A1–A9. <https://doi.org/10.1603/IPM10027>
- Musolin, D. L. (2012). Surviving winter: Diapause syndrome in the southern green stink bug *Nezara viridula* in the laboratory, in the field, and under climate change conditions. *Physiological Entomology*, 37, 309–322. <https://doi.org/10.1111/j.1365-3032.2012.00846.x>
- Musolin, D. L., & Numata, H. (2003). Photoperiodic and temperature control of diapause induction and colour change in the southern green stink bug *Nezara viridula*. *Physiological Entomology*, 28, 65–74. <https://doi.org/10.1046/j.1365-3032.2003.00307.x>
- Musolin, D. L., & Saulich, A. K. (1996). Photoperiodic control of seasonal development in bugs (Heteroptera). *Entomological Review*, 76, 849–864.
- Musolin, D. L., & Saulich, A. K. (2018). Diapause in Pentatomoidea. In J. McPherson (Ed.), *Invasive stink bugs and related species: Biology, higher systematics, semiochemistry, and management* (pp. 497–555). CRC Press.
- Mutlu, C., Buyuk, M., Eren, S., Karaca, V., Duman, M., & Bayram, Y. (2018). Management of the stink bugs *Dolycoris baccarum* (L.) and *Piezodorus lituratus* (F.) (Hemiptera: Pentatomidae), and chalky spot damage on red lentil in Southeast Anatolia region, Turkey. *Journal of the Kansas Entomological Society*, 91, 40–50. <https://doi.org/10.2317/0022-8567-91.1.40>
- Nielsen, A. L., Fleischer, S., Hamilton, G. C., Hancock, T., Krawczyk, G., Lee, J. C., Ogburn, E., Pote, J. M., Raudenbush, A., Rucker, A., Saunders, M., Skillman, V. P., Sullivan, J., Timer, J., Walgenbach, J., Wiman, N. G., & Leskey, T. C. (2017). Phenology of brown marmorated stink bug described using female reproductive development. *Ecology and Evolution*, 7, 6680–6690. <https://doi.org/10.1002/ece3.3125>
- Nilakhe, S. S. (1976). Overwintering, survival, fecundity, and mating behavior of the rice stink bug. *Annals of the Entomological Society of America*, 69, 717–720. <https://doi.org/10.1093/aesa/69.4.717>
- Ozdemir, I. O., Tuncer, C., & Ozer, G. (2021). Molecular characterisation and efficacy of entomopathogenic fungi against the green shield bug *Palomena prasina* (L.) (Hemiptera: Pentatomidae) under laboratory conditions. *Biocontrol Science and Technology*, 31, 1298–1313. <https://doi.org/10.1080/09583157.2021.1944608>
- Ozdemir, I. O., Tuncer, C., Tortorici, F., & Ozer, G. (2023). Egg parasitoids of green shield bug, *Palomena prasina* L. (Hemiptera: Pentatomidae) in hazelnut orchards of Turkey. *Biocontrol Science and Technology*, 33, 61–75. <https://doi.org/10.1080/09583157.2022.2158308>
- Ozsahin, E., Sezen, K., Demir, I., & Demirbag, Z. (2014). Bacterial isolates from *Palomena prasina* (Hemiptera: Pentatomidae) include potential microbial control agents. *Biocontrol Science and Technology*, 24, 1039–1051. <https://doi.org/10.1080/09583157.2014.918584>
- Pak, D., Carran, S., Biddinger, D., Nelson, B., & Bjørnstad, O. N. (2022). Incorporating diapause to predict the interannual dynamics of an important agricultural pest. *Population Ecology*, 64, 267–279. <https://doi.org/10.1002/1438-390X.12117>
- Panizzi, A. R., McPherson, J. E., James, D. G., Javahery, M., & McPherson, R. M. (2000). Stink bugs, (Pentatomidae). In C. W. Schaefer & A. R. Panizzi (Eds.), *Heteroptera of economic importance* (pp. 421–474). CRC Press.
- Panizzi, A. R., & Niva, C. C. (1994). Overwintering strategy of the brown stink bug in northern Paraná. *Pesquisa Agropecuária Brasileira*, 29, 509–511.
- Parajulee, M. N., Wilson, L. T., Rummel, D. R., Carroll, S. C., & Trichilo, P. J. (1996). Climatic data-based analysis of boll weevil (Coleoptera: Curculionidae) overwintering survival and spring emergence. *Environmental Entomology*, 25, 882–894. <https://doi.org/10.1093/ee/25.5.882>
- Parrish, J. K., & Edelman-Keshet, L. (1999). Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science*, 284, 99–101. <https://doi.org/10.1126/science.284.5411.99>
- Peterson, R. K. D., Higley, L. G., & Pedigo, L. P. (2018). Whatever happened to IPM? *American Entomologist*, 64, 146–150. <https://doi.org/10.1093/ae/tmy049>
- Polajnar, J., Kavčič, A., Kosi, A., & Čokl, A. (2013). *Palomena prasina* (Hemiptera: Pentatomidae) vibratory signals and their tuning with plant substrates. *Open Life Sciences*, 8, 670–680. <https://doi.org/10.2478/s11535-013-0188-z>
- Powell, G. (2020). The biology and control of an emerging shield bug pest, *Pentatoma rufipes* (L.) (Hemiptera: Pentatomidae). *Agricultural and Forest Entomology*, 22, 298–308. <https://doi.org/10.1111/afe.12408>
- Raney, H. G. (1969). *Flight habits of the pecan weevil, Curculio caryae* (horn), (Coleoptera: Curculionidae) (Doctoral dissertation). Oklahoma State University.
- R Developmental Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from <https://www.R-project.org/>
- Reed, D. A., Palumbo, J. C., Perring, T. M., & May, C. (2013). *Bagrada hilaris* (Hemiptera: Pentatomidae), an invasive stink bug attacking Cole crops in the southwestern United States. *Journal of Integrated Pest Management*, 4, C1–C7. <https://doi.org/10.1603/IPM13007>
- Roca-Cusachs, M., Schwertner, C. F., Kim, J., Eger, J., Grazia, J., & Jung, S. (2022). Opening Pandora's box: Molecular phylogeny of the stink bugs (Hemiptera: Heteroptera: Pentatomidae) reveals great incongruences in the current classification. *Systematic Entomology*, 47, 36–51.
- Romero, A., Tous, J., & Martí, E. (2009). White spots in hazelnut kernel: Symptoms, causes and quality loss. *Acta Horticulturae*, 845, 607–612. <https://doi.org/10.17660/ActaHortic.2009.845.95>
- Rousset, F., & Ferdy, J.-B. (2014). Testing environmental and genetic effects in the presence of spatial autocorrelation. *Ecography*, 37, 781–790. <https://doi.org/10.1111/ecog.00566>
- Sabuncu, Y., Mamay, M., & Özgen, İ. (2021). Overwintering insect (Arthropoda: Insecta) biodiversity in pistachio orchards of the middle Euphrates Valley, Turkey. *Harran Tarım ve Gıda Bilimleri Dergisi*, 25, 185–192. <https://doi.org/10.29050/harranziraat.884529>
- Santos, R. S. S., Redaelli, L., Diefenbach, L., Romanowski, H., Prando, H., & Antochewis, R. (2007). Distribuição espacial de *Oeobalus poecilus* (Dallas, 1851) (Hemiptera: Pentatomidae) durante a hibernação. *Entomotropica*, 19, 91–100.
- Santos, R. S. S., Redaelli, L. R., Diefenbach, L. M. G., Romanowski, H. P., & Prando, H. F. (2003). Characterization of the imaginal reproductive diapause of *Oeobalus poecilus* (Dallas) (Hemiptera: Pentatomidae). *Brazilian Journal of Biology*, 63, 695–703. <https://doi.org/10.1590/S1519-69842003000400017>
- Saruhan, İ., Tunçer, M. K., & Tunçer, C. (2023). Economic damage levels of the green shield bug (*Palomena prasina*, Hemiptera: Pentatomidae) in Türkiye hazelnut orchards. *Black Sea Journal of Agriculture*, 6, 183–189. <https://doi.org/10.47115/bsagriculture.122428>
- Saulich, A. K., & Musolin, D. L. (2014). Seasonal cycles in stink bugs (Heteroptera, Pentatomidae) from the temperate zone: Diversity and control. *Entomological Review*, 94, 785–814.
- Schellhorn, N. A., Parry, H. R., Macfadyen, S., Wang, Y., & Zalucki, M. P. (2015). Connecting scales: Achieving in-field pest control from areawide and landscape ecology studies. *Insect Science*, 22, 35–51. <https://doi.org/10.1111/1744-7917.12161>

- Schowalter, T. D. (1986). Overwintering aggregation of *Boisea rubrolin-eatus* (Heteroptera: Rhopalidae) in Western Oregon. *Environmental Entomology*, 15, 1055–1056. <https://doi.org/10.1093/ee/15.5.1055>
- Seiter, N. J., Benson, E. P., Reay-Jones, F. P. F., Greene, J. K., & Zungoli, P. A. (2013). Residual efficacy of insecticides applied to exterior building material surfaces for control of nuisance infestations of *Megacocta cribraria* (Hemiptera: Plataspidae). *Journal of Economic Entomology*, 106, 2448–2456. <https://doi.org/10.1603/EC13309>
- Sentis, A., Hemptinne, J. L., Magro, A., & Outreman, Y. (2022). Biological control needs evolutionary perspectives of ecological interactions. *Evolutionary Applications*, 15, 1537–1554. <https://doi.org/10.1111/eva.13457>
- Susset, E. C., Hemptinne, J. L., Danchin, E., & Magro, A. (2018). Overwintering aggregations are part of *Hippodamia undecimnotata*'s (Coleoptera: Coccinellidae) mating system. *PLoS One*, 13, e0197108. <https://doi.org/10.1371/journal.pone.0197108>
- Szejner-Sigal, A., & Williams, C. M. (2022). Aggregations reduce winter metabolic rates in the diapausing ladybeetle *Hippodamia convergens*. *Journal of Insect Physiology*, 137, 104357. <https://doi.org/10.1016/j.jinsphys.2022.104357>
- Tanaka, S., Wolda, H., & Denlinger, D. L. (1988). Group size affects the metabolic rate of a tropical beetle. *Physiological Entomology*, 13, 239–241. <https://doi.org/10.1111/j.1365-3032.1988.tb00928.x>
- Toyama, M., Ihara, F., & Yaginuma, K. (2006). Formation of aggregations in adults of the brown marmorated stink bug, *Halyomorpha halys* (Stål) (Heteroptera: Pentatomidae): The role of antennae in short-range locations. *Applied Entomology and Zoology*, 41, 309–315. <https://doi.org/10.1303/aez.2006.309>
- Tullberg, B. S., Gamberale-Stille, G., Bohlin, T., & Merilaita, S. (2008). Seasonal ontogenetic colour plasticity in the adult striated shield bug *Graphosoma lineatum* (Heteroptera) and its effect on detectability. *Behavioral Ecology and Sociobiology*, 62, 1389–1396. <https://doi.org/10.1007/s00265-008-0567-7>
- Villavaso, E. J., & Snodgrass, G. L. (2004). Diapause in tarnished plant bug (Heteroptera: Miridae) reared in dynamic photoperiod environmental cabinets. *Journal of Agricultural and Urban Entomology*, 21, 87–97.
- Wagner, D., Doak, P., Sformo, T., Steiner, P. M., & Carlson, B. (2012). Overwintering physiology and microhabitat use of *Phyllocnistis populiella* (Lepidoptera: Gracillariidae) in interior Alaska. *Environmental Entomology*, 41, 180–187. <https://doi.org/10.1603/EN11193>
- Weber, D. C., Khirman, A., Blassioli-Moraes, M. C., & Millar, J. G. (2017). Semiochemistry of Pentatomoidea. In J. E. McPherson (Ed.), *Invasive stink bugs and related species: Biology, higher systematics, semiochemistry, and management* (pp. 677–726). CRC Press.
- Wolda, H., & Denlinger, D. L. (1984). Diapause in a large aggregation of a tropical beetle. *Ecological Entomology*, 9, 217–230. <https://doi.org/10.1111/j.1365-2311.1984.tb00717.x>
- Yang, K., & Wen, J. (2021). Developing traps for the overwintering tree-of-heaven weevils *Eucryptorrhynchus scrobiculatus* and *E. brandti* (Coleoptera: Curculionidae). *Pest Management Science*, 77, 2766–2772. <https://doi.org/10.1002/ps.6305>
- Zerbino, M. S., Miguel, L., Altier, N. A., & Panizzi, A. R. (2020). Overwintering of *Piezodorus guildinii* (Heteroptera, Pentatomidae) populations. *Neotropical Entomology*, 49, 179–190. <https://doi.org/10.1007/s13744-019-00743-z>

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