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ORIGINAL PAPER

Vibrational calling signals improve the efficacy of pheromone traps to capture the brown marmorated stink bug

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Abstract

Halyomorpha halys (Stål, 1855), the brown marmorated stink bug (BMSB), is an invasive species that has become a key agricultural pest in its invaded range. Commercial traps available for BMSB monitoring rely on male produced aggregation pheromones as lure, with two possible shortcomings: trap spillover and low detection precision. In this study, we assessed if vibrational signals can increase the attractiveness of pheromone traps by testing the optimized vibration-based lure (Female Song 2, FS2) associated with a specifically designed trap (i.e., the vibrotrap). We evaluated the efficacy of this bimodal trap (i.e., pheromones + vibrations) on females, males and nymphs in controlled conditions (greenhouse) and in the field, in two sites at the margin of two commercial vineyards. In the field, bimodal vibrotraps were compared to three unimodal (i.e., only pheromone) trap types. Both experiments showed that the vibrotrap is highly attractive for BMSB, and the optimized FS2 signal significantly improved its effectiveness. Even though FS2 was selected to target males, the number of trapped females increased as well. Overall, the presented findings show a feasible improvement to future commercial BMSB traps through the synergic use of semiophysicals and semiochemicals. Further research is needed to evaluate the effectiveness of vibrotraps for both early detection and mass trapping.

Keywords Behavioral manipulation · Pest control · Applied biotremology · Hemiptera · Pentatomidae · Halyomorpha halys

Key messages

- Vibrational signals increase the captures of pheromone-baited traps for *H. halys*
- The vibrational signal Female Song 2 attracts both *H. halys* males and females
- The synergic use of vibrations and pheromones can increase the efficacy of insect traps

Introduction

Behavioral manipulation is a technique of pest control largely used worldwide to protect many crops from different insect species (Čokl and Millar 2009; Agarwal and Sunil 2020; Mazzoni and Anfora 2021). In most cases, it relies on the use of volatile compounds (i.e., semiochemicals) that aim at disrupting, inhibiting or promoting target behaviors, which in turn prevent or reduce crop losses (Foster and Harris 1997). Besides semiochemicals, a new term, semiophysicals, has been recently coined (Nieri et al. 2021) to indicate the use of physical stimuli (e.g., lights, sounds, and vibrations) to interfere with pest behaviors. In particular, the use of substrate-borne vibrations for behavioral manipulation has been the object of conspicuous investigation in the last decade (e.g., Eriksson et al. 2012; Laumann et al. 2018; Krugner and Gordon 2018; Gordon et al 2019; Mazzoni et al. 2019; Dias et al. 2021). Thanks to such studies,

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the potential for pest insect control methods employing this communication modality is becoming evident (Polajnar et al. 2015).

An application of behavioral manipulation with substrate-borne vibrations is the use of artificial signals as lures to attract insect pests into trapping devices. By mimicking the sexual calling signal of a gender, it would be possible to capture the mating partner by triggering searching behavior (Foster and Harris 1997; Strauss et al. 2021). Given the high specificity of vibrational signals, such a trap would be highly selective but with limited active space, being confined to the surface in contact with the vibration emitter (Polajnar et al. 2016a). Examples of use of vibrational signals to attract insects are reported for psyllids (Mankin 2019) and stinkbugs (Laumann et al. 2017). In particular, the stinkbug (Hemiptera and Pentatomidae) strategy for pair formation is bimodal, being based on the release of semiochemicals (i.e., pheromones) for long-range aggregation followed by the emission of semiophysicals (i.e., vibrational signals) for short-range mating communication (Virant-Doberlet and Cokl 2004). However, commercial traps currently available to catch noxious stink bugs are based exclusively on the use of pheromones as a lure (Laumann et al. 2017), thus missing the vibrational component which is crucial, in natural conditions, to accomplish the location of mating partners.

This means that pheromone traps can attract stink bugs from far away, but then they are not likewise effective in capturing individuals that in part remain out of the trap and/or in the nearby vegetation ("trap spillover"), where they may cause damage (Sargent et al. 2014; Morrison et al. 2016). This is the case of the brown marmorated stink bug (BMSB), *Halyomorpha halys* (Stål, 1855), an Asian species that has become a key agricultural pest in both America and Europe. Due to "trap spillover," farmers prefer placing the monitoring traps out of the orchards to avoid infesting their own plants (Akotsen-Mensah et al. 2018). However, this strategy is controversial; because of the wide host plant range, the presence of BMSB in the nearby vegetation can be abundant and must be considered as a risk factor, but it does not necessarily imply immediate crop infestation (Maistrello et al. 2017; Bergh et al. 2021). Overall, low capture efficacy and the tendency to place the traps outside the orchards can be solved by increasing the trap effectiveness. Previous studies focused on integrating semiochemicals and semiophysicals to increase trap attractiveness, testing the combination of light traps with restricted light wavelengths together with pheromones (e.g., Rice et al. 2017). In this view, several authors advocate the synergic use of pheromones combined with vibrations (Laumann et al. 2017; Leskey and Nielsen 2018).

As other stink bugs, BMSB communication is characterized by a repertoire of male and female vibrational signals that mediate the mating behavior (Polajnar et al. 2016b). Females are the calling sex and a signal in particular, the Female Song 2 (FS2), has proved to trigger directional movements in males to the source of emission on different experimental arenas (Mazzoni et al. 2017). Further research provided more details about the spectral and temporal parameters of FS2 that best trigger the male searching behavior (Caorsi et al. 2021).

In this study, we tested for the first time the use of this optimized FS2 vibrational signal in combination with pheromones in a bimodal trap for BMSB. First, we studied in controlled conditions (greenhouse) whether the vibrational signal could increase the number of BMSB entering the trap, assessing males, females and nymphs separately. Second, to evaluate the performance of the bimodal trap in the field, we tested it together with other BMSB commercial traps.

Materials and methods

Vibrotrap description

The vibrotraps (CBC Europe S.r.l.) consisted of a transparent collection container attached to a black coroplast pyramid 100-cm tall (Fig. 1). The top of the lid of the

Fig. 1 Vibrotrap used in both control conditions and field assessments

collection container was fitted with a solar panel on the outer side, while in contact with the inner side was a custom-made transducer, associated with a microchip to which the attractive signal had been loaded. The signal used was the FS2 previously tested in Caorsi et al. (2021). To characterize the signal spread through the trap and ensure that the signal amplitude was over the optimal basal threshold (> 100 μm/s), we measured signal amplitude and frequency from two points on each trap (on the pyramid panel and at the entrance of the plastic container) by means of two accelerometers (model 352A24, PCB Piezotronics, sensitivity 100 mV/g) connected to a computer through a multichannel LAN-XI data acquisition hardware (Brüel and Kjær Sound & Vibration A/S). The recordings were digitized with a 48 kHz sample rate and 16-bit depth. Lures (Dual Lure; Trécé Inc., Adair, OK) were positioned externally, at the junction between container and pyramid, next to the entrance. Stink bug individuals could access the collection container only from its basal part.

Trap assessment in controlled conditions

During June and July 2021, a greenhouse experiment was conducted to assess the efficacy of vibrotraps in catching BMSB (i) males, (ii) females, and (iii) nymphs (i.e., third to fifth stage). Each category was tested separately by placing ten individuals inside an insect rearing cage (BugDorm-6M1010 for adults and BugDorm-4F4590 for nymphs). A vibrotrap lured with pheromones (Dual Lure; Trécé Inc.) was placed in the middle of each cage. In the treatment cage, the vibrotrap was turned on thus emitting FS2 (VON, vibration on), whereas in the control cage, the vibrotrap did not vibrate (VOFF, vibration off). The intensity of vibrations on both VOFF and VON traps was monitored using the same protocol described before, to ensure that the FS2 was not detectable on VOFF traps.

A total of 15 replicates per category ($n = 3$) and per treatment ($n = 2$) were carried out over a seven-week period. The number of individuals inside the collection container was counted every 20 min for one hour (three observations per replicate). Insects were not used for more than one trial per day, and they were never used more than once for the same treatment. Since repetitions were performed on different days, one treatment and one control were always performed simultaneously. Temperature and relative humidity during the experimental time were constant, 26 ± 3 °C and 60 ± 10% RH, respectively.

Field trap assessment

All experiments were conducted at the hedgerow located near two commercial vineyards in Fondazione Edmund Mach, S. Michele all'Adige (TN), Italy (46.192903 N—11.135488 E). This hedgerow was divided in two sectors (S1 and S2), where the traps were positioned to compare their performance in different conditions of natural shade (Online Resource 1). The two sectors were used in different and consecutive periods: S1 from 21/05 to 14/06/21; S2 from 16/06 to 09/07/21.

Four types of traps were tested: 1) VON trap lured with Trécé Inc. Dual Lure; 2) VOFF trap (i.e., transducer turned off) lured with Trécé Inc. Dual Lure; 3) Rescue trap (Sterling International, Inc., Spokane, WA, USA) lured with Rescue Stink Bug Attractant (RR); 4) Rescue trap lured with Trécé Inc. Dual Lure (RT). Three traps of each type were randomly deployed along the hedgerow in each sector (total number of traps per site = 12), at least 25 m apart (Online Resource 1), the distance that prevents interference, according to manufacturer's label instructions. Rescue traps (RR, RT) were hung at approximately 1.5 m, on branches of trees and shrubs in the wood edge, while VON and VOFF were placed on the ground. The traps were emptied three times a week, between 7:30 and 10:00 AM, with 11 sessions (i.e., trap checks) per sector (Online Resource 2). The number of BMSB males, females and nymphs (divided in two subgroups, II-III and IV-V instars) captured were recorded. Climatic conditions (Online Resource 3 and 4) were recorded by a weather station located in Fondazione Edmund Mach.

Data analysis

Data exploration followed the protocol described in Zuur et al. (2010), all analyses were performed with R version 4.0.3 (R Core Team, 2020) and RStudio (RStudio Team, 2021). All plots were produced using ggplot2 (Wickham 2016). Since data were not normally distributed, statistical significance was assessed with nonparametric tests: Wilcoxon test for paired data to compare the number of individuals inside the collection container at each observation time (controlled conditions) and Dunn's test with Bonferroni correction to compare the number of individuals in each trap (field conditions).

To model the performance of the different trap types in field conditions, considering that each trap was checked several times (Online Resource 2), generalized mixed models (GLMMs) in which trap ID was used as a random factor were applied, using the glmmTMB function (Brooks et al. 2017). First, for each sector (S1 and S2, the latter considering adults and nymphs separately), to test the effect of the interaction between trap type and sex (for adults) and trap type and stage (for nymphs), a GLMM was fitted with the number of collected individuals as the response variable. For adults in S1, the analyses revealed that the data suffered from overdispersion and zero inflation, thus, a zero inflated negative binomial GLMM with a log-link function was used. For adults in S2 and for nymphs in S2, Poisson GLMMs with a log-link function were used.

Second, after verifying the correlation among the different variables and factors, we built a set of GLMMs including sex/stage, trap type, date and climatic conditions.

Model assumptions were verified following the protocol presented by Zuur and Ieno (2016), plotting residuals versus fitted values, versus each covariate in the model and versus each covariate not in the model. The residuals were assessed for spatial dependency with variograms (Zuur and Ieno 2016). Akaike Information Criterion (AIC) was used for model selection, marginal R^2 values for fixed effects alone and conditional R^2 for both fixed and random effects were also assessed (Lüdecke et al. 2021). Predictor effect plots (Fox and Weisberg 2018) were used to visualize the fitted coefficients.

Results

The signal amplitude was over the optimal basal threshold for all the vibrotraps used in the study. At 80 Hz, the dominant frequency of the FS2, the mean intensity of the signal (± SD) on the pyramid panel and at the entrance of the plastic container were 203.86 ± 127.52 µm/s and 2855.33 ± 1629.61 µm/s, respectively.

Trap assessment in controlled conditions

Overall, VON traps captured a significantly higher number of males ($p < 0.001$) and females ($p < 0.001$) than VOFF traps. Furthermore, for males this prevalence of VON over VOFF was significant for each observation time (Table 1; Fig. 2). As for females, in the first observation time (20 min from the beginning of the trial), there was no difference between VON and VOFF. However, both in the second (40 min) and third (60 min) observation time, the number of females inside the VON trap was significantly higher (Table 1; Fig. 2). On the contrary, the number of captured nymphs did not significantly differ between the two tested traps for all the observation periods.

Field trap assessment

The two sectors (S1 and S2), which corresponded to consecutive periods, showed a different abundance of BMSB adults and nymphs (Table 2). In fact, 2,928 and 494 adults were captured in S1 and S2, respectively, with a capture peak on the 04/06/21 (Fig. 3). Nymphs were caught only in S2 ($n = 4{,}097$), 96% of them in the II and III nymphal instars. The lowest catches were associated with important rainfall events (Fig. 3 and Online Resource 4), while we observed a progressive decline with the passing of time, especially during the final sessions for each sector.

In general, VON traps captured a significantly higher number of individuals than the other trap types, while the performances of VOFF and RT were similar (Fig. 4a–b). The performance of VON, VOFF and RT for nymphs did not show significant differences (Fig. 4c).

While the sex ratio (F/M) was almost equal for RR and RT in the two sectors (48–55% of females), more females than males were caught by VON and VOFF traps (59–69%) (Table 2), especially in S1 where this difference was significant ($p < 0.05$) (Fig. 4d).

Model validation, including spatial dependency (Online Resource 5), indicated no problems. The GLMM results showed that VON traps captured a significantly higher number of adults than the other trap types in both S1 and S2 (Fig. 5a–b). The interaction between sex and trap type was significant (with a negative effect) only for males and for both VON and VOFF traps: GLMMs results confirmed that these traps were more attractive for females. For nymphs, the number of caught individuals of VON, VOFF and RT was similar (Fig. 5c), slightly higher for VOFF for nymphs in II-III stage. A significant negative effect of date (as day since start) was also detected for both nymphs and adults (Online Resource 6 and 7). With respect to climatic variables, we observed a minor positive effect of maximum temperature for both adults and nymphs, and a minor negative effect of maximum humidity for nymphs.

Discussion

Increasing trap efficacy is a critical element for the development of new devices to monitor and manage BMSB. An unfortunate shortcoming of traps relying only on BMSB

Table 1 Wilcoxon test comparing the number of *Halyomorpha halys* individuals inside the two tested traps (VOFF and VON) for each group (males, females and nymphs) at each observation time (20, 40 and 60 min)

	20 min		40 min		60 min	
	W	*P*-value	*W*	*P*-value	*W*	*P*-value
Males	58.5	0.012	10	< 0.001	0	< 0.001
Females	87	0.197	42.5	0.002	36	0.001
Nymphs (III-V)	80	0.140	72	0.079	73	0.091

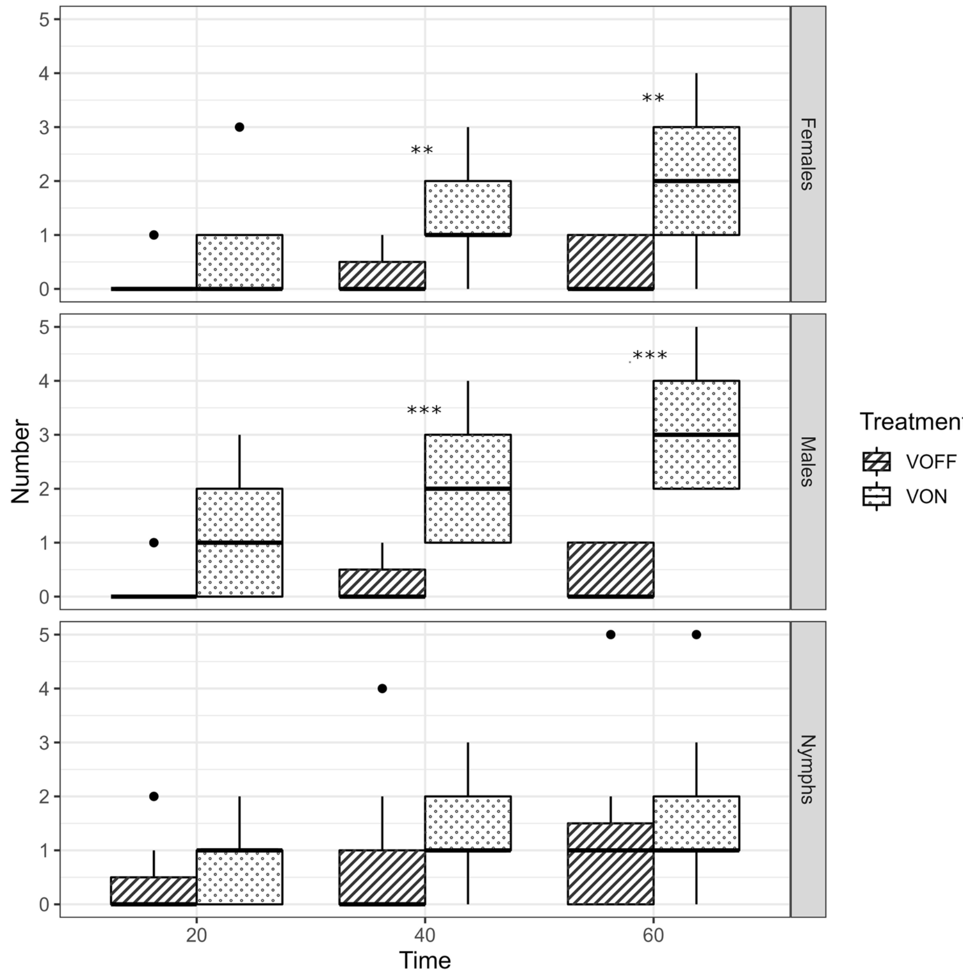


Fig. 2 Boxplot for the trap capture data from the control (VOFF) and vibrotrap (VON) for *Halyomorpha halys* males, females and nymphs. Significant differences among traps were assessed using Wilcoxon test between the two treatments at each time (* $p<0.05$; ** $p<0.01$; *** $p<0.001$)

Table 2 Number of collected individuals of *Halyomorpha halys* in the two sectors (S1 and S2) with the different traps: Total (sum of collected individuals); Mean (average number of collected individuals per trap per day); Std. Dev. (standard deviation of the average number of collected individuals per trap per day)

		RR		RT		VOFF		VON		
		Total	Mean (Std. Dev)	Total	Mean (Std. Dev)	Total	Mean (Std. Dev)	Total	Mean (Std. Dev)	Total
S1	Females	181	5.5 (6.2)	363	11.0 (7.9)	466	14.1 (9.6)	618	18.7 (9.9)	1628
	Males	199	6.0 (6.2)	400	12.1 (8.7)	270	8.2 (7.9)	431	13.1 (7.9)	1300
	Total	380		763		736		1049		2928
S2	Female	13	0.39 (0.86)	72	2.2 (3.5)	68	2.1 (2.9)	134	4.1 (4.1)	287
	Male	12	0.36 (0.96)	59	1.8 (2.7)	47	1.4 (1.9)	89	2.7 (3.0)	207
	Juv. II-III	84	2.55 (3.56)	1097	32.2 (34.5)	1598	48.4 (84.1)	1157	35.1 (54.0)	3936
	Juv. IV-V	8	0.27 (0.64)	49	1.6 (3.1)	44	1.4 (2.6)	60	2.0 (2.7)	161
	Total	117		1277		1757		1440		4591

aggregation pheromones is that the individuals tend to arrest nearby the source (within 2.5 m) regardless of its concentration (Morrison et al. 2016). Our results demonstrate that the FS2 signal can improve the performance of pheromone traps, both in controlled conditions and in the field.

In controlled conditions, its effect increased with time, showing a significantly higher number of trapped individuals after 20 min of exposure to the signal for males, and after 40 min for females. In field conditions, GLMMs analysis supports that the attraction effect of the optimized FS2 was positive for both sexes. While hanging traps (RR

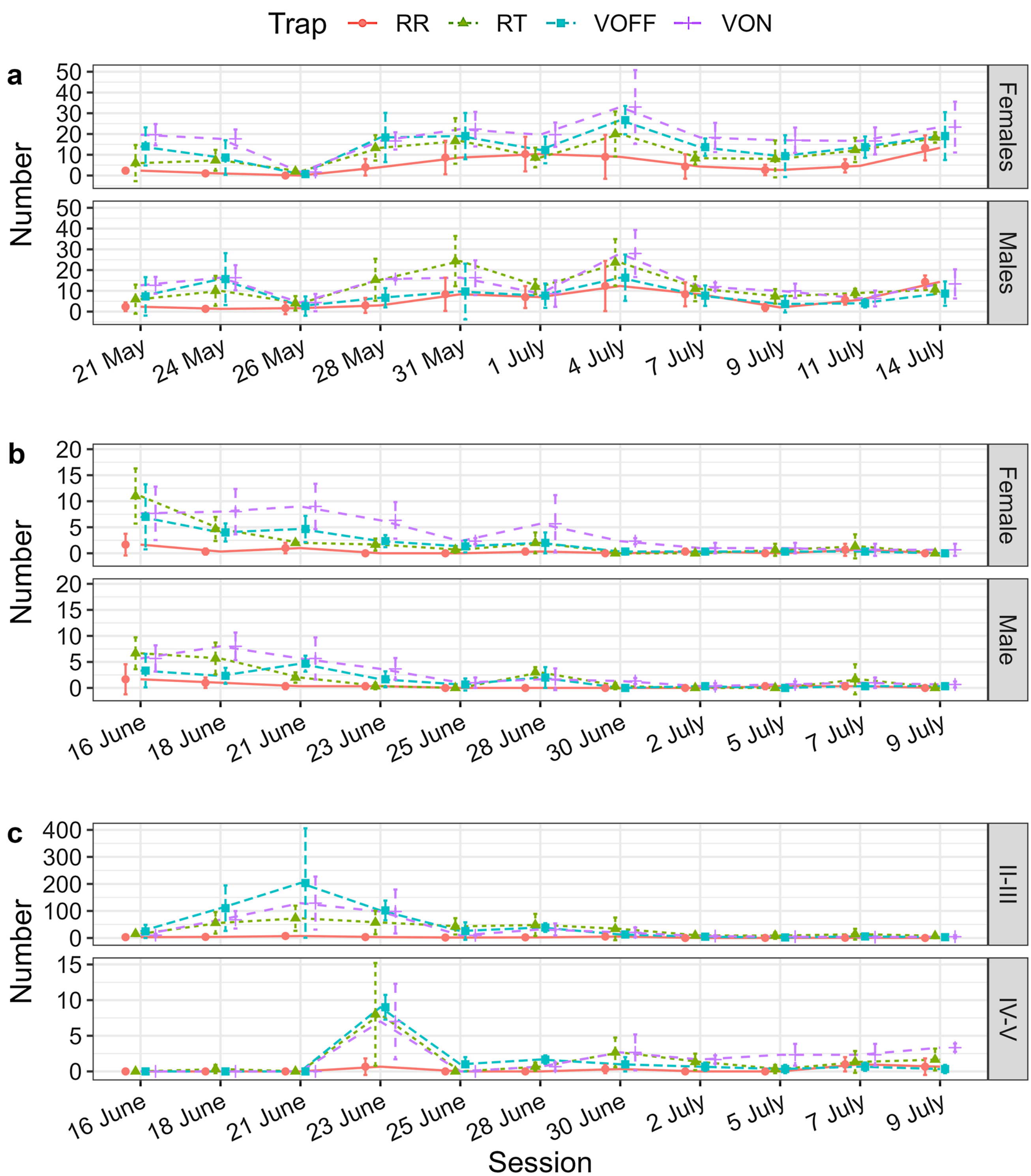


Fig. 3 Trends (mean and standard deviation) in the captures of *Halyomorpha halys* adults (a—Sector 1 and b—Sector 2) and nymphs (Sector 2). Data pooled per trap type for each session

and RT) showed a balanced sex ratio, significantly more females were caught with ground traps (VOFF and VON). Previous studies on field experiments using pheromone traps pooled adult capture data together (e.g., Rice et al. 2017; Hadden et al. 2021); thus, this is the first observation of unbalanced BMSB sex ratio related to trap design.

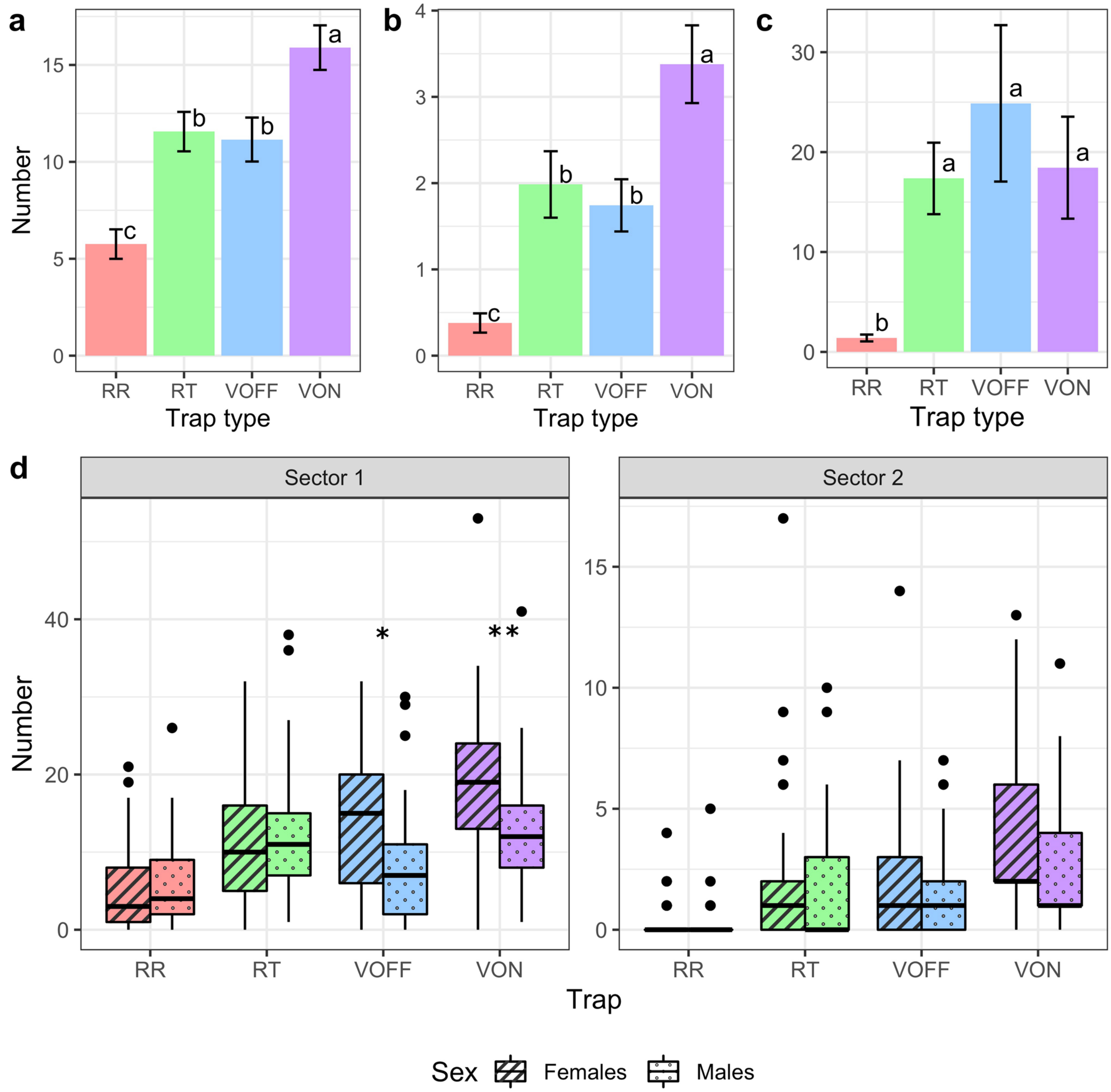
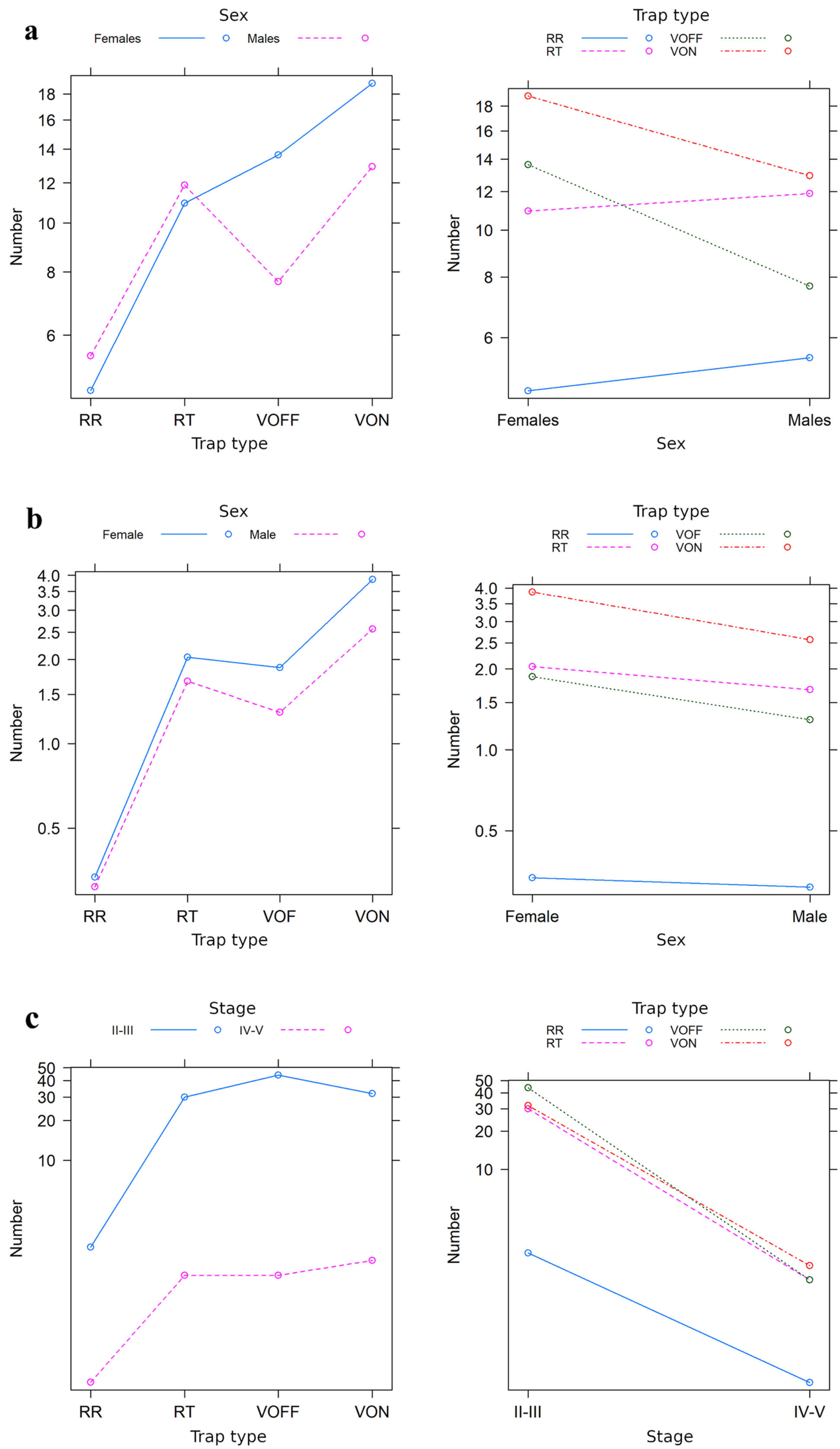


Fig. 4 Trap capture data for *Halyomorpha halys* from the two sectors, barplot showing mean and standard deviation for the four trap types, letters indicate significant differences ($p < 0.05$) after Dunn's test: **a** S1: adults, **b** S2: adults and **c** S2: nymphs; **d** boxplot showing the number of males and females per trap in each sector (*$p < 0.05$; **$p < 0.01$)

A possible hypothesis is that females are more attracted by traps on the ground; however, further experiments are needed to clarify this finding.

The two tested lures performed differently, with higher catches observed with Trécé Inc. Dual Lure. Both lures contained methyl (2E,4E,6Z)-2,4,6-decatrienoate (MDT), the aggregation pheromone of *Plautia stali* Scott, which is attractant for BMSB both in Asia (Lee et al. 2002) and in its invaded range (Aldrich et al. 2007). In the Trécé Inc. Dual Lure, MDT is used together with the two-component aggregation pheromone specific to BMSB (3S,6S,7R,10S)-10,11-epoxy-1-bisabolen-3-ol and (3R,6S,7R,10S)-10,11-epoxy-1-bisabolen 3-ol (PHER) (Khrimian et al. 2014), since MDT is known to act as a synergist when employed together with PHER (Weber et al. 2014). As experimented by Morrison et al. (2015) in apple orchards, large coroplast pyramid traps (having a wider access area) tend to be more effective in trapping BMSB adults and

Fig. 5 Effect plots for the variables included in the GLMMs, for the three models testing the effect of the interaction between trap type and sex (for adults) and trap type and stage (for nymphs): **a** number of *Halyomorpha halys* adults (Sector S1), **b** number *H. halys* of adults (Sector S2), **c** number of *H. halys* nymphs (Sector S2)



nymphs compared to smaller pyramids and hanging traps. Furthermore, lures positioned outside the traps should increase plume propagation, maximizing their effect, compared to pheromones confined in collection containers (Rice et al. 2018). Interestingly, we observed that for adult BMSB, when using the same pheromone (commercial MDT + PHER), neither the size of the access area (larger in VON/VOFF than in RR/RT) nor the reach of the pheromone plume (pheromones outside the trap for VON/VOFF and confined in the trap container for RR/RT), affected the trap performance, which was similar for RT and pyramids without vibration (VOFF). Conversely, our findings suggest that FS2 vibrational signal is the key element responsible for the higher number of adults captured with VON traps. For nymphs, the performance of the three traps using MDT plus PHER was similar. However, the results of the trials in controlled conditions indicate that nymphs were not repelled by FS2, and thus the use of vibrational signals did not negatively affect the general trap effectiveness.

The attractiveness of FS2 for males was expected from previous studies (Polajnar et al. 2016b), while the positive response of females was unexpected. Even though the intraspecific communication of stink bugs has been widely investigated, the behavioral ecology of females is extremely unclear (Čokl et al. 2021). Males are supposed to be the active sex that promotes the emission of vibrational signals in stationary females by releasing pheromones and then uses the vibrational cues to locate them on the plant. For this reason, studies tend to focus on male searching behavior, while female behavior is generally overlooked. Polajnar et al. (2016b) reported that females alone and in pairs did not emit spontaneous calls, except for two individuals. However, they did not test the response of females to a female playback signal or the combination of a male together with more than one female. In other species of stink bugs, it has been found that females respond to females' signals with a complex rivalry behavior (Čokl et al. 2017). It is possible that BMSB females also use intrasexual communication, which has not been described yet. These questions remain open and should be further investigated. It is possible that with more specific studies targeting female communication, new evidences will arise.

In northern Italy, BMSB has two generations/year, with egg masses laid from mid-May and increased mortality of the overwintering generation observed from mid-July (Costi et al. 2017). The observed negative effect of time passing on trap catches is thus in accordance with the species' phenology and year fluctuations, with an observed decrease in the abundance of overwintering adults starting from mid-June (i.e., end of S1). Likewise, nymphs were captured only in S2 (i.e., from 16/06 for II-III stage and from 18/06 for IV-V stage). The number of trapped nymphs in II-III stage was more than 20-fold higher than those in IV–V stage, which is in agreement with the high nymphal mortality (93%) observed in the field (Stahl et al. 2021). Further experiments should be conducted in the second part of the summer and even in fall, when individuals are looking for overwintering sites (Leskey and Nielsen 2018). Bedoya et al. (2020) observed in controlled conditions that during pre-diapause aggregations, only males called and the signals did not trigger any clustering. In this context, when mating is no more a priority, it is likely that vibrotraps performance might not differ from non-vibrated traps.

Finally, in the field experiment, we observed a minor positive effect of maximum temperature (range: 6.0–33.7 °C) and maximum humidity (range: 16.3–97.7%) on both adults and nymphs. It has been suggested that a decline in adult and nymph captures in summer may be related to high temperatures (> 36 °C), responsible for mortality/lowered activity (Ingels and Daane 2018). Our findings confirm that when temperatures are below such threshold, they do not seem to affect BMSB captures.

A number of conclusions of this study may have a significant relevance to BMSB management. Vibrotraps could be effective for post-overwintering early detection, when individuals are at low densities but searching for mating and also for mass trapping. However, the assessment of the effectiveness of this device for both these applications requires further investigation. A bimodal device, with the addition of vibrations to pheromones, regardless of trap design, represents the way forward for future monitoring strategies, improving the timing of IPM strategies implementation and surveillance programs, for example in countries that aim to prevent BMSB arrival and settlement. More generally, we expect that in the near future, the synergic use of semiophysicals and semiochemicals may be applied to increase the efficacy of insect traps.

Author contributions

All authors contributed to the study conception and design. LZ, VM, RN and VZC conducted experiments. LZ analyzed data, with advising from all other authors. LZ, RN, VZC and VM wrote the manuscript. NMP revised the manuscript. All authors read and approved the manuscript.

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Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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