Effect of vibrational mating disruption on flight activity and oviposition to control the grapevine pest, *Scaphoideus titanus*

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ABSTRACT

The increasing demand for safe and sustainably produced food is leading to the development of strategies of pest control alternative to chemicals. One innovative method is Vibrational Mating Disruption (VMD) to disrupt insect communication in plants. VMD was proven effective in preventing mating of the grapevine pest *Scaphoideus titanus*, vector of flavescence dorée. However, the stress induced by VMD on the target species has the potential to influence other crucial aspects of the insect biology and ethology. Therefore, the goal of this study was to understand side effects of VMD on the flight activity and oviposition of *S. titanus*. The results of our experiments conducted in the greenhouse showed that in the presence of a receptive female, males fly more if exposed to vibrations than in the silent control but not differently from singles males in silence. Surprisingly, we found that also females subjected to VMD fly more than in the silence. Regarding oviposition, we found that mated females exposed to vibrations and single females (unmated) laid significantly fewer eggs than mated females in silence. In conclusion, this study shows the potential of VMD to interfere, besides with mating, with other important biological aspects of the pest species.

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1. Introduction

The increasing demand for safe and sustainably produced food is one of the tough challenges of the next decades. One issue of particular concern is the reduction of external inputs required for pest control, which currently mainly relies on pesticides (Isman, 2019). For example, in order to meet production standards, pest management in viticulture requires a massive recourse to external inputs including conventional pesticides, which are considered a treacherous but inevitable tool (Pertot et al., 2017). For this reason, alternative methods to control insect pests are needed to minimize risks associated to both environment and human health.

Behavioural manipulation is one of the most promising strategies to reduce the environmental impact of pest management in agriculture. It interferes with the cues used by a pest to detect and colonize its host plant, or with the signals used for inter-and intraspecific communication (Foster and Harris, 1997). Behavioural manipulation for pest control can involve the use of natural and/or artificial signals, such as pheromones, kairomones, sounds, and vibrations, to interfere with fundamental behaviours, such as feeding and mating (Agarwal and Sunil, 2020; Čokl and Millar, 2009; Nieri et al., 2021). Sexual pheromones are largely used in the field worldwide to control several crop pests (Koul et al., 2008; Welter et al., 2005). They negatively affect not only mating behaviour, but also other behaviours of the target insect, such as flight activity and oviposition (Gibbs et al., 2010; Harari et al., 2015). For instance, Harari et al. (2015) reported a reduction in eggs laid in the European grapevine moth, *Lobesia botrana*, exposed to mating-disruption pheromones. Meanwhile, Gibbs et al. (2010) did not find a decrease in the number of eggs in the speckled wood butterfly, *Pararge aegeria*, but they found a delay on the laying process and a decrease in egg size. Furthermore, they reported an increase in flight activity with a possible allocation of energy from other behaviours. Based on these findings, they suggested that the reduction of insects due to pheromone strategies could be related not

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only to diminished mating but also to an effect on the investment of the energetic resources for other vital activities.

The use of substrate-borne vibrations as a strategy of behavioural manipulation is still in its infancy, but the first results are encouraging (Caorsi et al., 2021; Eriksson et al., 2012; Mazzoni et al., 2019; Polajnar et al., 2016). Since, in many insect species, vibrational signals are essential to accomplish crucial activities, such as feeding and mating (Cocroft and Rodriguez, 2005; Polajnar et al., 2014; Strauß et al., 2021), the use of vibrations specifically designed to disrupt such behaviours seems to be promising (e.g., Avosani et al., 2021; Polajnar et al., 2016; Parent et al., 2021). For example, the technique of vibrational mating disruption (VMD) has proven to be effective in preventing mating of the leafhopper *Scaphoideus titanus* Ball (Hemiptera Cicadellidae). VMD consists of the transmission of a species-specific disrupting vibrational signal, the 'disturbance noise' (DN), into plants, which covers the frequency span of the vibrations emitted by the insect (Mazzoni et al., 2019).

Scaphoideus titanus is the main vector of the phytoplasma causal agent of flavescence dorée, which is considered the most threatening among European grapevine yellow diseases (Chuche and Thiéry, 2014). Its reproductive behaviour relies on the establishment of a vibrational duet between a male and a female (Mazzoni et al., 2009a). Males search for sexually available females by emitting a calling song from a vine leaf. If they do not perceive a female response, they either repeat the call several times or jump/fly to another leaf to resume calling. This peculiar behaviour is named call-and-fly, and it is typical of many leafhoppers (Hunt and Nault, 1991). The reproductive strategy of *S. titanus* makes us hypothesize that, when males do not find a mate, they jump/fly significantly more than males that are engaged in mating (i.e., duets and copula). Our first hypothesis, therefore, is that by impairing communication, VMD could also affect the call-and-fly activity of males. Second, as previous studies on pheromones disruption reported, mating disruption techniques could also influence oviposition (Gibbs et al., 2010; Harari et al., 2015). Therefore, we expect that *S. titanus* females exposed to VMD could be disturbed by the DN and thus delay the oviposition and/or lay fewer eggs than undisturbed females.

2. Material and methods

2.1. Rearing

Adult virgin males and females of *S. titanus* were obtained by collecting two-year-old grapevine canes from organic infested vineyards in Trentino region (northern Italy) in January 2021. After collection, wood canes were kept in plastic boxes (30 × 20 × 10 cm) with net windows on the lid, in a controlled environment greenhouse (25 ± 1 °C; 16:8 L:D; 75 ± 1% RH) until eggs hatched. Boxes were sprayed daily with water to keep the humidity. After hatching, nymphs were reared in plastic cups following the protocol previously described by Eriksson et al. (2012). Plastic cups were checked daily. As the adults emerged, they were sexed and placed separately inside a cage (Bugdorm-6620, 60 × 60 × 120 cm) with potted grapevine plants (*Vitis vinifera* cv Solaris). All experiments were performed with sexually mature males and females that were at least 8 and 10 days old, respectively (Mazzoni et al., 2009a). The oviposition and the flight activity experiments took place from June to September of 2021. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

2.2. Experimental design

Test 1. *Flight activity*: Based on a previous 24h recording of *S. titanus* (Mazzoni et al., 2009a), we discovered that the species has a peak in calling activity and reproduction between 18:00 and 23:30, and thus performed the experiments during this time. A plant with two branches (approximately 25 cm long each) and 3 leaves each (Fig. 1A) was placed inside a Plexiglass cube (dimensions 60 × 40 × 40 cm). The cube was placed above a wooden plate (20 × 20 × 6 cm) that was vibrated by a Tremos exciter (CBC Europe Ltd). When the plate was turned on it transmitted to the plant the DN used for VMD (Eriksson et al., 2012). To check that the intensity of the DN reached the threshold of efficacy reported by Mazzoni et al. (2019), the vibrations on each leaf were measured by means of a laser Doppler vibrometer connected to a laptop through a LAN-XI data acquisition device (Brüel and Kjær Sound & Vibration A/S, Nærum, Denmark) and the recording was analysed using the BK Connect software (Brüel and Kjær Sound & Vibra-tion A/S, Nærum, Denmark). On all six leaves, the maximum intensity of DN at the dominant frequency (200 Hz) was above the safety threshold of VMD (safety threshold = 20 μ = m/s; measured range = 80−180 μm/s) (Fig. 1A). A total of 44 trials, in the form of three different treatments were performed: (i) two males in silence (M = 14); (ii) two males and two females in silence (MF/FM = 16); (iii) two males and two females exposed to DN vibrations (MFV/FMV = 14). Each trial began with each individual placed on a different leaf inside the cube and lasted until either a couple found each other and mated or for a maximum of 40 min. The behaviour of the leafhoppers was recorded by a digital camera (Panasonic HTC-TM700) and the number of flights for each individual over the trials was counted. To compare treatments, we estimated the flight activity of individuals as the number of flights or jumps per trial per individual. FM = flight of female when together with males in silence; FMV = flight of female when together with males exposed to DN; M = flight of male alone in silence; MF = flight of male when together with females in silence; MFV = flight of male when together with females exposed to DN.

Test 2. *Oviposition*: To test the effect of the DN on the oviposition behaviour of *S. titanus,* we performed oviposition trials in the same greenhouse as the rearing. We isolated grapevine shoots inside net sleeves (BugDorm, 40 × 20 cm) and placed each plant on a vibrational plate (20 × 20 cm, CBC Europe Ltd) emitting the DN. Inside each sleeve, we placed a single female (8−12 days old) that was either virgin or mated (mating occurred maximum 24 h before). Mated status was ensured by placing a virgin female inside a plastic cup together with a male and they were observed until mating occurred. We tested a total of 52 females, divided into three different groups: i) unmated females (uF = 19); ii) mated females, in silence (mF = 14); iii) mated females, exposed to DN vibrations (mFV = 19). The experiment started 36 h after the female was isolated into the sleeve with a piece of a 2 year old grapevine shoot (10 cm long) placed inside the sleeve, as an oviposition substrate (Bagnoli and Gargani, 2011). Each piece of shoot was replaced with a new one after 48 (2nd day of trial), 120 (5th day) and 192 h (8th day), respectively. In total, three pieces of wood were used for each female per trial. In this way, we were able to account not only for the total number of eggs laid, but also for the oviposition rate over time. Eggs were observed under a stereomicroscope by removing with a pin, the external layer of the bark under which *S. titanus* females lay eggs (Chuche and Thiéry, 2014).

2.3. Statistical analysis

All analyses were performed in R v.3.5.3 (R Core Team, 2020; RStudio, 2020). First, we tested the effect of treatments on the *S. titanus* males and females flight activity (number of flights per trial per individual). Given that data were not normally distributed, we performed the non-parametric test Kruskal−Wallis followed by Mann−Whitney pairwise test with Bonferroni correction for
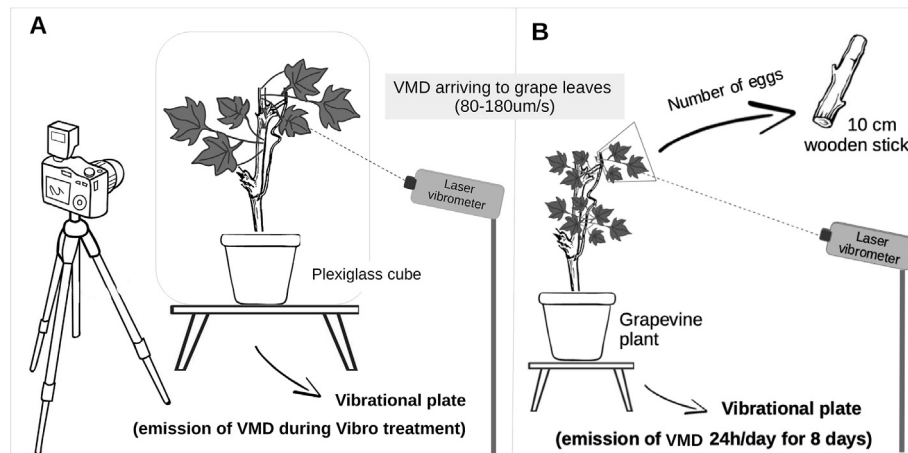
Fig. 1. Experimental design: tests performed to evaluate the effect of VMD on (A) flight activity and (B) oviposition in *Scaphoideus titanus.*

comparisons between each combination of treatments and sex. Second, we explored the effect of treatments on *S. titanus* oviposition with a generalized linear mixed-effects model (GLMM) (glmer; family = poisson). The response variable was *number of eggs*; *type of treatment* (uF, mF, mFV) and *day of check* (2nd, 5th, 8th) were included as a fixed factor and the *individual* as random factor. Data exploration followed the protocol described in Zuur et al. (2010) and model assumptions were verified following the protocol presented by Zuur and Ieno (2016). We ran the models using packages "lme4" (Bates et al., 2015). Visual inspection of Q−Q plots and residuals plotted against fitted values revealed no obvious deviation from the canonical assumptions of normally distributed and homogenous model residuals. Akaike information criterion (AIC, Sakamoto et al., 1986) was used to choose the best fitting model (Pinheiro and Bates, 2000). Plots and graphic designs were done using R packages: "dyplr", "tidyr", "ggplot2" (Wickham et al., 2018; Wickham and Henry, 2020; Wickham and Wickham, 2007), "ggsignif" (Ahlmann-Eltze and Patil, 2021).

3. Results

Test 1. Flight activity. Results showed that there was a significant difference between treatments in terms of flight activity (Kruskal−Wallis test: H = 37.367, df = 4; p = 1.513e-07) (Fig. 2). As for males, MFV flew significantly more than in the corresponding silence control conditions (MF), but at the same time they did not differ from M. Similarly, FMV flew significantly more than FM. For last, female's flight activity when subjected to vibrations (FMV) was similar to the flight activity of MF and lower compared to the flight activity of M and MFV.

Test 2. Oviposition. The simple model was the one fitting best in terms of AIC (185.2) including *type of treatment* and *day of check* as a fixed factor without interaction. It showed that mated females exposed to vibrations (mFV) and unmated females (uF) laid fewer eggs than control mated females (Fm) in the given time (Fig. 3; Tables 1 and 2). There was a significant difference in the time of oviposition, with females laying most of the eggs during the second and third period, so after the 2nd, and the 5th day of treatment (Tables 1 and 2). We have also tested the interaction between *treatment* and *day of check*, which was not significant and the AIC of this model was higher (195.4) than the simple one.

4. Discussion

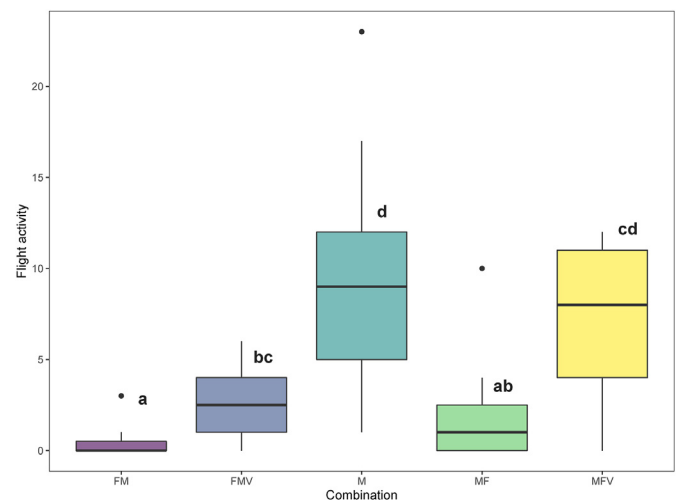This is the first insight that VMD, a method developed to disturb

Fig. 2. Effect of vibrations on the flight activity of *Scaphoideus titanus*. FM = flight of female when together with males in silence; FMV = flight of female when together with males exposed to DN; M = flight of male alone in silence; MF = flight of male when together with females in silence; MFV = flight of male when together with females exposed to DN; The box plot displays the median with a centreline, a variation of 1st and 3rd quartiles represented by the box, a full range of variation (from min to max) represented by "whiskers" above, and below and outliers are represented by the dots.

the mating behaviour of *S. titanus*, and in particular the establishment of the mating duet and the location of females by males (Mazzoni et al., 2019), also has the potential of indirecty affecting multiple biological aspects of this insect pest. Specifically, we found that the 'disturbance noise' (DN) used for VMD increases the flight activity of *S. titanus* males and females, while at the same time it reduces the oviposition rate, at least in the first eight days after the mating. Altogether, if confirmed at the field level, these new findings seem to reinforce the potential of this innovative technique for practical use in farms.

When a plant was vibrated with the DN, males tended to fly off regardless of the presence of a reproductively active female on the same plant. Instead of establishing a mating duet, males exposed to DN behaved in the same way as males in absence of a female. This outcome suggests that the DN interferes with the male-female reciprocal perception of vibrations (i.e., masking) and/or impede females reply (i.e., inhibition) by, for example, reducing their motivation to mate. The DN playback could act either way to impair
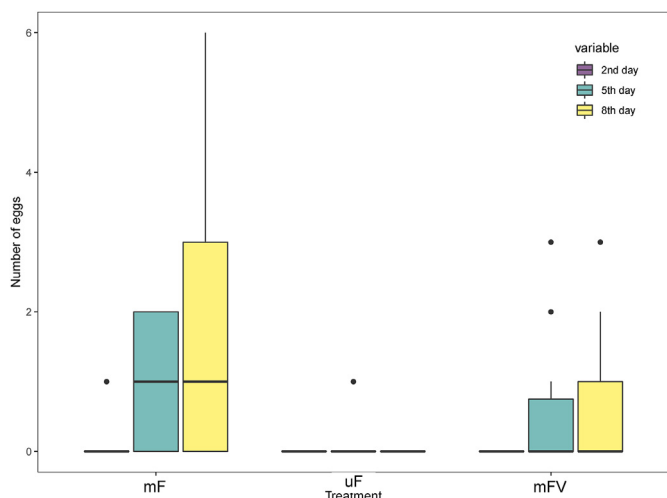
Fig. 3. Effect of the three different treatments on female *Scaphoideus titanus* oviposition. the number of eggs laid per treatment: uF = unmated females, mF = mated females, in silence, mFV = mated females, exposed to DN by the time of check (2nd, 5th, 8th days). The box plot displays the median with a centreline, a variation of 1st and 3rd quartiles represented by the box, a full range of variation (from min to max) represented by "whiskers" above and outliers are represented by the dots.

Table 1
Number of eggs (average ± SD) laid for each treatment in the 2nd, 5th, 8th day. uF = unmated females, mF = mated females, in silence, mFV = mated females, exposed to DN.

Treatment	2nd	5th	8th
uF	0	0.05 ± 0.2	0
mF	0.08 ± 0.3	1 ± 0.9	1.85 ± 2.1
mFV	0	0.4 ± 0.86	0.66 ± 1

Table 2
GLMM of oviposition by treatment and time of *Scaphoideus titanus* females. Reference level: Fm; Time 1. uF = unmated females, Fm = mated females, in silence, mFV = mated females, exposed to DN.

Combinations	Estimate	Std. Error	z-value	Pr(>|z|)
(Intercept)	−3.2280	1.0408	−3.102	0.001925 **
uF	−3.9482	1.0509	−3.757	0.000172 ***
mFV	−0.9611	0.3939	−2.440	0.014675 *
Time 2	3.1088	1.0296	3.019	0.002533 **
Time 3	3.5773	1.0196	3.509	0.000450 ***

mating communication; in both cases, the male would not perceive the female and act in the same way as a single male alone on the plant.

The DN is designed to mimic the rival signal of *S. titanus* (Mazzoni et al., 2009b). As for the mechanism of action, rivalry signals in hemipterans are emitted by rival males to disrupt ongoing mating duets and increase their chances of mating (Virant-Doberlet et al., 2014). In some species, the masking signals disable the male to perceive the female response (Kuhelj and Virant-Doberlet, 2017); whereas in others, the female stops replying to the male call in the presence of a masking signal (Legendre et al., 2012; Nieri and Mazzoni, 2019). In *S. titanus,* females often stop replying when a rival male interrupts the mating duet and they may leave the plant (Mazzoni et al., 2009b), so it is not surprising to us that also in our test, the flight activity of females was higher in the treatment than in the control. It is also possible that the DN acts as a stressor on *S. titanus* females and it induces them to leave the plant (Polajnar et al., 2015). The selection of the oviposition site is

crucial in many insects, because often the immature insects cannot move far away after hatching and thus the survival of the offspring strongly depends on the mother's choice of the reproductive site (Cury et al., 2019). In this way, from an evolutionary point of view, it is possible that females consider the vibrated plants an environment not suitable for oviposition. It is also possible that the vibrations physically prevent or make the insertion of the ovipositor in the plant tissue harder. Understanding whether the disruptive effect of VMD is due to masking or inhibition was beyond the scope of this study; in any case, not only mating was not achieved, but the flight activity increased significantly also in females, even if to a less extent than in males.

The increased flight activity of both males and females has several potential consequences on the pest management. First, the DN effect is known to be amplitude-dependent (Polajnar et al., 2016). This means that if the VMD is not applied uniformly to the plants, individuals could finally find sites subjected to low DN intensity where they mate and oviposit, thus increasing the already existing species aggregation in the vineyards (Lessio and Alma, 2006). In this regard, it would be crucial to provide a complete coverage and avoid any shelter in the vineyard under the safety threshold of amplitude (i.e., 20 μm/s Mazzoni et al., 2019). Second, the increased flight activity in vineyards treated with VMD should be considered when measuring the abundance of *S. titanus* adults, which is usually done by means of yellow sticky traps (Pavan et al., 2021). Sticky traps collect flying individuals, which is considered a good method to estimate leafhoppers' peak of flight. Although this method is not taken into account for absolute population density, the number of specimens captured is often used for relative comparisons between close vineyards to determine different levels of infestations (Pavan et al., 2021). However, in the case of vineyards treated with VMD, a high number of individuals caught by sticky traps could be due to the tendency of males and females to fly more and not to a higher population density. According to our results, where we found an increase of 75% male flying when exposed to VMD, we could expect a significant increase of individuals caught by sticky traps in vibrated fields compared to untreated fields. Third, the physiology of males and females could be negatively affected by spending considerably more time and energy flying and calling, which are associated with a high energetic cost for insects (Kuhelj et al., 2015; Reinhold, 1999), at detriment of other behaviours. Furthermore, flying insects spend less time on the plant, thus their feeding activity would be reduced as well as the consequent damage to the plant. It is known that unspecific vibrations can inhibit feeding in beetles (Takanashi et al., 2019) and leafhoppers (Avosani et al., 2021). Even if individuals flying more might spread the disease to more plants, in bacteria-insect vector systems, the inoculation time is relevant to ensure the transmission of the pathogen (Daugherty and Almeida, 2009); therefore the transmission rate of flavescence dorée phytoplasma to grapevine plants by *S. titanus* could be reduced. In this regard, it is important to underline that we tested the *S. titanus* flight activity, in the hours (dusk, early night) when males perform the call-and-fly behaviour (Mazzoni et al., 2009a). A more comprehensive study should address if the flying activity is affected by VMD throughout the day (24 h tests). If individuals are not induced to fly more at different times of the day, this aspect may not be significant in altering the disease transmission risks. Other biological aspects that can be negatively affected by an increased flying activity are longevity and reproduction (Harrison and Roberts, 2000). For instance, in honeybees and fruit flies, an increased flight activity has been associated with a shorter lifespan (Magwere et al., 2006; Neukirch, 1982).

In males, the energetic cost imposed by VMD could be even more relevant than in females, because they are the calling gender. Usually, insects that undergo disturbance noise tend to shift

frequencies or even extend the calling activity to an unusual time, thus increasing the predation risks (Čokl et al., 2015; Read et al., 2014). In our test, it was not possible to measure the calls of males because in the recording files, the calls were not distinguishable from the DN. On the other hand, it is possible that by increasing the number of flights they also increase their calling rate. However, if and how the calling activity is altered by VMD exposure needs to be addressed in future studies. In females, the extra use of resources by thoracic muscles during flight could result in a resource trade-off, with less energy available to be used in the maturation of eggs (i.e., the oogenesis − flight syndrome hypothesis; Jervis et al., 2005; Johnson, 1963). This hypothesis has been studied mainly in lepidopterans, in which a negative correlation is known to occur between the flight activity and the ovarian development due to the altered vitellogenin metabolism (Huang et al., 2019). In leafhoppers, a direct correlation between flight activity and egg maturation has not been unveiled yet. However, an abundant diet and high lipid content are correlated to an increased production of eggs in closely related sharpshooters (Sisterson et al., 2015).

In our study we found that females exposed to DN laid significantly fewer eggs than the control, thus our data seem to support the oogenesis-flight syndrome hypothesis also in leafhoppers. Forced flight can also negatively affect the reproduction of a species by shifting in the season, the peak fecundity and egg laying rate, as in the case of the speckled wood butterfly, P. aegeria (Gibbs et al., 2010). Our experiment lasted only eight days, and we cannot exclude that females exposed to VMD could compensate the reduced number of laid eggs during the experimental period. At any rate, this would mean at least a delay of the oviposition with respect to the untreated females that was not observed in the relatively short period of our test. Delay in mating and egg-laying are indirect ways known to reduce the reproduction success of insects (Harari et al., 2015; Mori and Evenden, 2013).

To conclude, an important outcome of this research is a new hypothesis to be tested in the field. According to our study, we can expect a substantial increase of adults captured by yellow sticky traps, especially of males, in treated areas compared to silent control. This would be particularly true in the case of abundant populations, whereas for low-density populations the gap would tend to be lower due to the reduced chance of mate. Additionally, with this study, we brought new insights into how vibrations disrupt the biology of S. titanus. Besides reducing mating success, VMD also negatively affects other crucial behaviours that could further reduce the occurrence of the pest in vineyards and its ability to transmit phytoplasmas. These results highlight the potential of mechanical stimuli in pest management strategies. In this way, the use of vibrational signals and more in general of applied biotremology, has the potential to open new and unexpected scenarios in the pest management strategies, both integrated and organic, by affecting different biology aspects of pest species by means of semiophysicals at low or null environmental impact (Nieri et al., 2021).

CRediT authorship contribution statement

Valentina Zaffaroni-Caorsi: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing − original draft, Writing − review & editing. **Rachele Nieri:** Conceptualization, Data curation, Investigation, Methodology, Validation, Visualization, Writing − original draft, Writing − review & editing. **Nicola M. Pugno:** Conceptualization, Funding acquisition, Investigation, Project administration, Supervision, Validation, Writing − review & editing. **Valerio Mazzoni:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Visualization, Writing − original draft, Writing − review & editing.

Declaration of competing interest

None.

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