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# Effectiveness of electric harps in reducing Vespa velutina predation pressure and consequences for honey bee colony development

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## **Abstract**

BACKGROUND: Vespa velutina has become a species of concern in invaded regions of Europe and Asia, due to its impacts on biodiversity, apiculture and society. This hornet, a ferocious hunter of pollinating insects, poses a serious threat to biodiversity and pollination services. Despite ongoing efforts, its extermination in continental Europe is hampered by a lack of effective control methods, thus effective mitigation measures are primary concerns. The aims of this work were: (i) to study the effects of V. velutina predating on honey bee colonies, and (ii) to assess the effectiveness of electric harps in reducing hunting pressure and predation. We assessed the predation pressure and compared honey bee colony performance, body weight of workers, and winter survivorship for protected versus unprotected colonies in 36 experimental hives across three apiaries.

RESULTS: Electric harps protected honey bees by reducing predation pressure and therefore mitigating foraging paralysis. Consequently, foraging activity, pollen income, brood production and worker body weight were higher in protected colonies which in turn showed greater winter survivorship than those that were unprotected, especially at sites with intermediate to high levels of predation.

CONCLUSION: The predation of *V. velutina* affects foraging activity, breeding, body weight and colony survivorship of *Apis mellifera*. Electric harps contribute significantly to mitigate the impact of this invasive hornet on apiaries; however, they should be deployed in tandem with additional measures to preserve honey bee colony stocks, such as facilitating access to food sources for colonies during the periods of highest predation pressure.

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**Keywords:** Apis mellifera; Asian hornet; control method; invasive species; pollinator; social vespid

## 1 INTRODUCTION

Human population growth necessitates the expansion of cultivated areas, and therefore a higher demand for pollination services. However, insect populations are declining worldwide, owing to multiple interacting stressors, including habitat loss, lack of floral resources, spread of parasites and diseases, and antagonistic interactions with invasive species. 3–5

Vespa velutina Lepeletier 1836, is an invasive species of concern in several European and Asian regions because of its impacts on biodiversity, economics, and human health.<sup>6,7</sup> This eusocial insect has a polyandrous mating system, and an annual cycle,<sup>8</sup> that increase their capacity to raise entire populations from the minimum propagule: one single mated foundress.<sup>9</sup>

Although native to East Asia, *V. velutina* was accidentally introduced to South Korea<sup>10</sup> and France.<sup>11</sup> It successfully expanded into neighboring areas affecting more than ten new countries in the last decade, <sup>12,13</sup> and continues to spread.

Vespa velutina has a generalist diet, feeding on floral nectar, sap, fruit, honeydew and honey as carbohydrate sources, while proteins are obtained from hunting arthropods and scavenging,<sup>8</sup> leading to impacts on biodiversity through predation and competition for resources.<sup>14–17</sup> Notably, V. velutina hunts pollinators in flower patches, leading to altered abundance and foraging habits, with detrimental effects on pollination for native plants.<sup>18</sup> It is also an effective and persistent hunter of honey bees at hive

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entrances, causing colony losses, and thus threatening the sustainability of beekeeping within invaded ranges.<sup>19</sup>

Western honey bees (*Apis mellifera* Linnaeus, 1758) perform defensive behaviors in response to hornet attacks.<sup>20</sup> Nevertheless, these are ineffective in reducing hunting pressure, allowing hornets to intensively predate honey bees at hive entrances.<sup>21</sup> This increases the expression of genes associated with oxidative stress, potentially harming bee health in colonies under attack.<sup>22</sup> Further, hornet hunting triggers a phenomenon known as foraging paralysis, i.e. the cessation of foraging activity in predated colonies, which in turn leads to a reduction in honey storage.<sup>23–25</sup> Population modeling points to this phenomenon as the cause of the increased winter mortality observed in apiaries within invaded areas,<sup>23</sup> however no empirical evidence confirming such a relationship has yet been reported.

In order to reduce the hornets' impact on honey bee colonies, a number of practices have been implemented in apiaries, but several of them have a low effectiveness and/or represent an additional pressure on biodiversity, and others need further development. Beehive muzzles are a biodiversity-friendly method that reduces foraging paralysis and likely enhances the survivorship of colonies, but the device does not capture or kill hornets, thus its impact is local. Electric harps are another method commonly used in apiaries, with a medium economic cost, and low side effects on native fauna. They consist of a frame with vertical parallel electrified wires that produce an electric shock when touched by a flying insect. Its actual performance in reducing hornet hunting activity at honey bee colonies requires further evaluation, but preliminary observations suggest that this could be an effective and selective method.

In an insular area, the eradication of *V. velutina* has been possible through a combination of effective tools, coordinated engagement of all sectors involved, and timely action.<sup>29</sup> The control of the species once it is established, however, is challenging and requires the development and evaluation of novel methods to reduce its spread and effects on biodiversity.<sup>30</sup> Here, we monitored colony parameters in 36 experimental hives, distributed across three apiaries within different environments. Our aims were to (i) study the effects of *V. velutina* predating on honey bee colonies in terms of foraging activity, pollen income, resource storage, population growth (area covered by brood and adults), bee weight, and winter survivorship, and (ii) assess the effectiveness of electric harps in reducing hunting pressure and predation.

## 2 MATERIALS AND METHODS

#### 2.1 Study sites

The experiment was performed from July to October 2020 in three apiaries in the southwest region of Pontevedra, Galicia, Spain (Supporting Information, Fig. S1). For this year a density of 1.92 nests/km² in the Pontevedra province, and 0.96 nests/km² for the whole Galician autonomous community, were reported to the authorities (Xunta de Galicia, unpublished data). However, it has been suggested that the actual density of nests in this region can be approximated to 14–17 nests/km². The three sites present different environmental conditions and each one represents a main ecosystem of this region (Fig. S1).

## 2.2 Experimental design

A total of 36 Langstroth hives were placed in three apiaries (12 hives per apiary). To ensure homogeneity in the state and genetics of the honey bees, the colonies of Iberian Western honey

bees (A. mellifera iberiensis Engel, 1999) were acquired from the same provider with queens reared early in the season and maintained in one apiary under same apicultural practices until shortly before the transport to the experimental apiaries.

Within each apiary two treatments were set: six hives protected from the predation of *V. velutina* with harps and six unprotected hives where *V. velutina* hunted honey bees *ad libitum*. The two groups of hives were placed in opposite corners of the apiary with a distance > 20 m between them. Each group of hives was placed in line, with the entrances oriented in the same direction, with a separation of 20 to 30 cm between them, and placed over bases at 30–40 cm height.

Electric harps were located perpendicularly to the hive entrances, between two contiguous hives (Fig. 1(a)). These devices were placed in the apiaries 1 month before first observations. During the first week the harps were turned-off to allow honey bees to habituate to their presence. The trap consists of a frame with parallel vertical wires alternatively connected to the positive and negative poles of an electric circuit. The model used here has a modification to minimize bycatches (Fig. S2). Flying-through hornets receive an electric shock whenever they touch two consecutive wires (Fig. 1(b)), paralyzing them for a few seconds and falling into a cage beneath with mesh walls that allow smaller insects to escape. Then hornets crawl within the cage until falling into a collector bottle.

## 2.3 Captures of *V. velutina* and non-target insects in harps

Monthly samples of captured insects were obtained. Trapped insects were identified and counted *in situ* to the level of order, family and, in the case of hymenopterans, species level. The captures of species or groups were expressed as the rate of captured insects per trap per day by dividing the number of captured insects by the number of capturing days at each trap. Selectivity was calculated as the fraction of trapped hornets over the total captured insects.

#### 2.4 Predation pressure of V. velutina on hives

Two methods were used to quantify the predation pressure of V. veluting on honey bees from July to October. The first one consisted of visually counting the number of hunting V. velutina in a period of 10 min, once a month, between 10:00 and 11:00 h, on the same day that the performance of experimental colonies was assessed. One to three observers were situated 3-5 m in front of each group of six experimental hives and counted the number of hornets that arrived at each group. No differences among countings were detected when multiple observers were present. To calculate the hunting rate per hive (HRH), the total number of observed hornets was divided by the number of hives and then expressed in terms of number of hornets/hive/10 min. In the same observation period, the number of successful hunting events was quantified. The predation rate was estimated as the number of captured honey bees/number of hunting hornets in 10 min. The second method to quantify the presence of V. velutina in front the hives made use of video recordings to calculate the Hive Entrance Predation Index (HEPIX). A camera (GoPro Hero7) was placed at 0.5 m in front of each hive for a recording duration of 10 min. Recordings were performed from 11:00 to 13:00 h. The videos were visually analyzed in the laboratory using Behavioral Observation Research Interactive Software (BORIS).31 The first 2 min were discarded to avoid operator interference in honey bee behavior and to allow habituation to the presence of the





**Figure 1.** Protection system: six hives placed in line, separated 20–30 cm each, protected with five electric harps (a). When hunting honey bees in front of the hives, hornets fly between electrified wires that paralyze them (b). Afterwards they fall into a cage from which smaller insects escape while hornets fall into a collection bottle.

camera. The optimal number of minutes to be analyzed, for a maximal efficiency with minimal variance, was set as five. Each minute was visualized three times by a single observer. One time to count the number of honey bees entering the hive, another to count the leaving ones and a last one to register the presence of *V. velutina* in front of the hive. HEPIX measures the time with at least one hunting *V. velutina* present in the video frame (Supporting Information, Table S1). During the observation periods, the observer could not visualize the presence or absence of the harps. HRH and HEPIX were positively correlated (Pearson correlation coefficient  $\rho = 0.57$ , df = 142, P < 0.001), however, in September and October at Gondomar, the hornets spent less time hunting near to the entrance of the hives, but were observed foraging at a greater distance (Fig. S3(a)). For this reason, HRH was used as an explanatory variable for the statistical analyses.

## 2.5 Performance of experimental honey bee colonies

## 2.5.1 Foraging activity

The videos were also used to quantify the number of honey bee foragers leaving and entering each hive during 5 min. To do this the videos were visualized at slow motion (speed 0.5) with the QuickTime Player software.

### 2.5.2 Pollen income

One pollen trap was installed at the entrance of each hive (see Fig. 1(a)). Once per month the door of the pollen trap was closed to collect the pollen brought by worker honey bees during 24 h. At the laboratory, the weight of the fresh pollen was measured with an OHAUS Pioneer® 0.01 mg precision balance.

## 2.5.3 Resources storage and assessment of individuals of different ages

Once a month, frames were extracted from the hives to assess the area covered by combs full with open honey, capped honey and pollen, and brood (eggs, larvae and pupae) by using a 5 cm  $\times$  5 cm grid. To calculate the number of adult honey bees a visual counting of individuals was carried out in a 10 cm  $\times$  10 cm grid for each side of the frames, then estimated for the entire frame and finally summed to calculate the total number of workers within the hive.  $^{32}$  The measurements were made from 10:00 to 16:00 h in sunny days.

#### 2.6 Bee weight

In October 2020, 30 worker bees were collected from the interior of each experimental hive by brushing them off from one or, at most, two brood combs. These were stored in 80% ethanol at 4 °C. In the laboratory they were dried up in an oven at 65 °C for 12 h and then individually weighed with an OHAUS Pioneer® 0.01 mg precision balance. The drying time was optimized and set after performing a drying curve by measuring consecutive weights of 30 individuals every 5 min.

## 2.7 Winter survivorship

In March 2021 the hives were inspected to assess the survivorship of each colony. Depopulated (with less than 50 individuals) or queenless colonies (with laying workers thus without female brood and with less than 50 workers) were considered as dead colonies. The minimum number of individuals was set below the critical level for colony survivorship according to the social hive model for a regular colony.<sup>33</sup> To compare winter survivorship of colonies under different predation pressure a number was assigned to each hive according to its survivorship (1 = alive, 0 = dead). The overall predation was assessed as a semi-quantitative variable: null (HRH = 0), low (HRH < 1), intermediate (1 < HRH 0.5 < 1.5) and high (HRH > 1.5). To assign each group of hives to one of these categories HRH had to be within these thresholds for more than 3 months (Fig. S3).

#### 2.8 Statistical analyses

A Pearson correlation was used to study the relationship between HRH and HEPIX. A Wilcoxon rank-sum test was used to compare differences between the capture rate of *V. velutina* in harps *versus* the capture of non-target taxa. To test the effect of the sampling period on the capture rate of *V. velutina* and selectiveness of harps, zero inflated generalized linear mixed models (GLMMs) with negative binomial distributions were fitted using the glmmTMB default non-linear optimizer function. These models included *month* as the fixed effect and *site* as the random effect. See Table S2 for a complete description of the models and scripts. To test differences in HRH across treatments (hives protected with harps *versus* unprotected) and sampling period a GLMM, with negative binomial distribution was fitted using the glmmTMB default non-linear optimizer function. The model included treatment and *month* as the fixed effects and *site* as the random effect.



To test the effect of HRH on the quantity of brood, adults, foragers, pollen brought by foragers (in milligrams), and honey and pollen stores of experimental hives across sampling period, GLMMs with negative binomial distributions were fitted using the glmmTMB default non-linear optimizer function. The models included HRH and month as the fixed effects and site as the random effect. The absence of overdispersion was tested via simulation-based dispersion tests (Table S2), with the 'DHARMa' package for R.34 A sequential Bonferroni correction was applied to correct for multiple comparison testing. The weight of workers of protected versus unprotected colonies was compared with a generalized linear model (GLM) using a Gaussian distribution. The model included treatment, site and their interaction as fixed effects. To analyze colony survivorship, a GLM with a binomial distribution was fitted. The overall predation and the mean weight of workers and their interaction were included as fixed effects. The analyses were performed using RStudio software version 1.2.5033. The packages 'glmmTMB' and 'car' were used for fitting GLMMs. 35,36

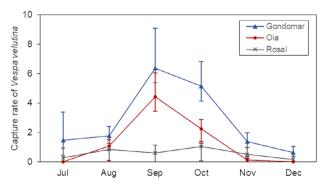
## 3 RESULTS

## 3.1 Captures of *V. velutina* and non-target insects in harps

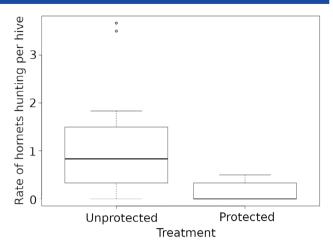
Vespa velutina represented > 90% of 4359 insects captured in electric harps (Table S3). The capture rate of V. velutina varied across time ( $\chi^2 = 78.88$ ; df = 5, P < 0.01; see Fig. 2). Overall, captures of V. velutina were significantly higher than the capture of non-target taxa [mean  $\pm$  standard deviation (SD) = 1.6  $\pm$  2.0 individuals/trap/day and mean  $\pm$  SD = 0.17  $\pm$  0.2 individuals/trap/day respectively; W = 1889, df = 90, P < 0.01], which consisted mostly of hymenopterans, such as A. mellifera, followed by dipterans of the families Sarcophagidae, Tachiniidae and Calliphoridae (Table S3). The selectivity of harps was high (mean  $\pm$  SD = 0.75  $\pm$  0.34) and remained high across time ( $\chi^2$  = 7.80; df = 5, P = 0.168).

### 3.2 Hunting pressure and predation rate

Overall, protected hives showed 88.8% less predation pressure than unprotected hives (Fig. 3). The rate of hornets hunting in front of the hives (HRH) varied significantly between treatments (protected with harps *versus* unprotected) and across sampling months ( $\chi^2 = 42.6$ , df = 1, P < 0.001 and  $\chi^2 = 24.76$ , df = 3, P < 0.001 respectively). The hunting activity of hornets exhibited a general tendency to increase over the study (Fig. S3(a)). HRH was highest in Gondomar (mean  $\pm$  SD = 1.4  $\pm$  1.41), medium in



**Figure 2.** Captures of *Vespa velutina* by electric harps in three apiaries. The colored lines represent the trend in the mean capture rate per site (n = 5 for each point). Vertical bars represent standard deviations.



**Figure 3.** Predation pressure of *Vespa velutina* on protected and unprotected hives. Whisker plots represent medians (bold horizontal lines), quartiles (boxes), 2.5–97.5 percentiles (vertical lines), and outliers (open dots).

Oia (mean  $\pm$  SD = 0.6  $\pm$  0.58) and lowest in O Rosal (mean  $\pm$  SD = 0.2  $\pm$  0.28). The success of hornets hunting bees (Fig. S3 (b)) had similar tendencies to HRH throughout the season (Fig. S3(a)), except for the site with high predation pressure where the highest HRH did not coincide the highest predation rate.

## 3.3 Performance of experimental honey bee colonies

#### 3.3.1 Foraging activity

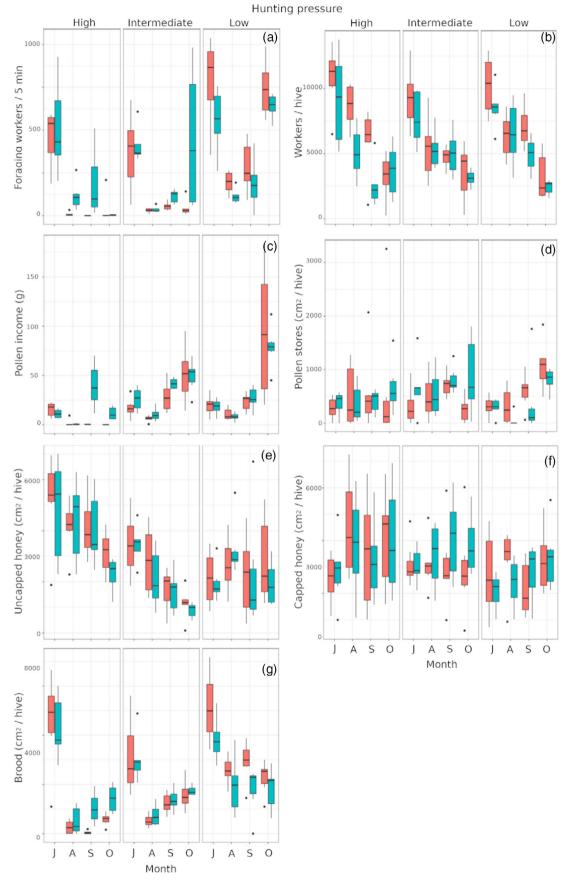
The number of foraging workers was affected by hunting pressure and month (Table 1). The foraging paralysis recorded in unprotected hives at the site with highest predation (Gondomar) started in August and persisted during the whole study despite the decrease in predation observed in September (Figs 4(a) and S3 (a)). Foraging paralysis occurred mostly in honey bee colonies that suffered hunting rates higher than 0.8 hornets/hive/10 min (from data in Figs 4(a) and S3(a)). In the site with highest HRH protected

**Table 1.** Effects of hunting pressure, site and time of the year on honey bee colony performance

Response variables	Predictors	$\chi^2$	Р
Pollen income (mg)	HRH	33.72	<0.001
	Month	84.25	< 0.001
Uncapped honey	HRH	0.03	0.854
	Month	27.59	< 0.001
Capped honey	HRH	0.31	0.580
	Month	4.16	0.245
Pollen stores	HRH	0.27	0.599
	Month	1.89	0.596
Brood	HRH	8.30	0.028
	Month	76.99	< 0.001
Adults	HRH	5.16	0.138
	Month	150.13	< 0.001
Foragers	HRH	8.85	0.024
	Month	67.27	<0.001

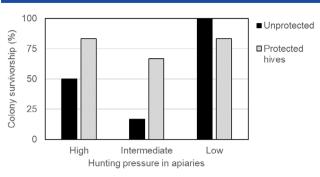
Brood includes eggs, larvae and capped brood. HRH, hunting rate per hive. Significant results (P < 0.05), applying the sequential Bonferroni correction, considering the 14 tests performed, are indicated in bold.





**Figure 4.** Honey bee colony performance and storage of resources for protected (blue bars) and unprotected (red bars) colonies in three apiaries throughout the monitoring season.





**Figure 5.** Winter survivorship of experimental honey bee colonies (unprotected and protected with electric harps in three apiaries. n = 6 for each bar).

colonies had larger population sizes within the hive than protected ones during August and September (Fig. 4(b)), precisely when these colonies showed paralysis (Fig. 4(a)). We observed workers of all ages remaining inside the hive in paralyzed colonies. Besides foraging, other common behaviors such as gathering of resins for propolis production or hygienic activities, such as cleaning flights, removal of sick individuals or corpses, also stopped.

#### 3.3.2 Resources

Unprotected hives had lower income of pollen with a significant effect of the month (Table 1 and Fig. 4(c)). The amount of pollen brought by foragers and the foragers' activity followed similar trends (Table 1 and Fig. 4(c)). Pollen and honey stores were not significantly affected by the predation of *V. velutina* (Table 1 and Fig. 4(d,f)).

## 3.3.3 Colony performance

The quantity of brood and the foraging activity were significantly affected by the predation pressure and the month (Table 1). The amount of brood had lower levels in unprotected hives than in protected hives in the apiary with the highest hunting pressure (Fig. 4(q)).

## 3.4 Weight of honey bees

Workers from unprotected hives were 6.7% lighter than those from protected hives. The GLM revealed that treatment, site and the interaction treatment X site influenced honey bees weight ( $\chi^2 = 14.20$ , df = 1, P < 0.001;  $\chi^2 = 95.77$ , df = 2, P < 0.001;  $\chi^2 = 23.19$ , df = 1, P < 0.001 respectively).

#### 3.5 Survivorship

Winter survivorship was 77.8% for protected and 55.6% for unprotected colonies. Survivorship of unprotected colonies was lower at the sites with intermediate and high hunting pressure (Fig. 5). The survivorship of honey bee colonies was linked to the overall hunting pressure and the interaction between hunting pressure and bees weight, but not to the weight of the bees alone ( $\chi^2 = 10.23$ , df = 3, P = 0.017;  $\chi^2 = 11.43$ , df = 3, P = 0.01; and  $\chi^2 = 0.02$ , df = 1, P = 0.90 respectively).

## 4 DISCUSSION

In this study, we examined the effectiveness of electric harps in protecting honey bee colonies from *V. velutina* predation and demonstrated that this method significantly reduces hunting pressure in front of hives. When comparing protected and

unprotected colonies, we also detected differences in foraging behavior, resources income, quantity of brood and adults, and worker body weight. As consequence of hunting pressure, honey bees enter the winter with lower food storage, a reduced population and malnourished individuals. Thus, the overwinter survivorship of colonies is jeopardized, leading to higher winter colony death rates for unprotected colonies.

## 4.1 Effectiveness and selectivity of harps

Electric harps, placed perpendicularly to a line of hives, are useful to reduce the predation pressure of *V. velutina* in honey bee hives. The trapping of hunting workers represents an advantage over other control methods, such as the beehive muzzles or baited traps, <sup>25,37–39</sup> as it effectively reduces foraging paralysis in a targeted manner, while minimizing bycatches. The protective effect of harps helps to reduce the foraging paralysis and allows bees to display natural behaviors, including foraging, hygiene or fanning, necessary for survivorship and health maintaining of colonies.

Hunting rates varied across time and space. A previous study revealed an increase in predation pressure over time which was explained as a consequence of the V. velutina population growth and the need for protein to rear new individuals.<sup>21</sup> According to the negative correlation between altitude and number of nests observed in a previous study, 40 we expected to find a gradient of hornet predation pressure reflecting altitudinal conditions. Consistently, the apiary placed at the highest elevation (Oia), showed intermediate levels of predation as compared with that of Gondomar, situated at mid altitude. However, contrary to expectations, the apiary located at the lowest altitude (O Rosal) exhibited the lowest predation rate. This goes in line with Monceau and Thiéry,<sup>37</sup> who reported that the distribution of this invasive species can be rather variable across time and space, and might be highly influenced by natural and/or human-mediated processes.

The GLMMs revealed that, besides predation, temporal factors also played important roles on the amount of resources available in the hive and the fitness of the colony. The reduction in pollen income coincided with the foraging paralysis on unprotected colonies and was probably related to the low amount of brood observed during the last months of the study (Fig. 4). These results support the idea of the foraging paralysis as the main reason for the weakening processes and subsequent collapse that affect colonies under hornet attack.<sup>24</sup> Our evidence suggests that in apiaries with low rates of predation (less than 1 hornet/hive/10 min), honey bees were better able to cope with the predator and the use of electric harps was useful to reduce predation at negligible levels. However, on sites where the blooming season is shorter and the winter is longer and with lower temperatures (as in Oia, the highest elevation site in our study), intermediate rates of hunting lead to lower colony survivorship in protected and particularly in unprotected hives (Fig. 5).

The lower body weight of workers in unprotected colonies provides new evidence of the physiological stress that honey bees suffer under this new threat. Pollen is a resource of capital relevance for honey bees since it is an important source of protein, lipids, vitamins and other nutrients, necessary to produce royal jelly, with which larvae are fed. Also, pollen quality and diversity influence honey bee health and live span and pollen quality is known to affect larvae weight in honey and bumble bees. Thus, a shortage in income of nutrients during the rearing of larvae is a plausible mechanism behind lighter workers. Additionally, the lower amount of brood observed in unprotected hives at the



end of the study suggests that the number of workers to overwinter is smaller than in protected colonies. Thus, our results revealed that besides the low storage of food resources, two factors are behind winter deaths of unprotected honey bee colonies: a deficiency in the nutritional levels of wintering adults and a reduced number of workers.

#### 4.2 Management of apiaries in invaded areas

The threshold in the levels of predation needed to produce significant changes in colony performance and survivorship is lower than previously reported.<sup>24</sup> This can be explained by several non-mutually exclusive factors that deserve attention for future studies and management of apiaries. One of them is related to environmental factors that determine how easy (or difficult) it is for bees to access resources during the predation season and the wintering conditions.

Additionally, we provide evidence that the physiological status of honey bee workers is affected by hornet predation. Therefore, we encourage beekeepers to facilitate the access of bees to diverse floral and freshwater resources, thus contributing to diminish their physiological stress and homing failure outside the hive. On that account, when colonies suffer foraging paralysis the supplement of a diverse diet rich in all necessary nutrients is recommendable. This must be provided not only during winter to avoid the starvation of weak colonies but also in autumn when the workers that are going to endure winter are in larval stage.

The installation of electric harps represents an important initial economic investment for beekeepers that depends on the number of harps and its commercial price. This, in turn, is related to the number and location of hives. It has been suggested a rational of one harp every two or three hives, which is probably unaffordable for large apiaries.<sup>26</sup> Also, in terms of the time necessary for maintaining a functional system. Besides, apiaries have to be often adapted, and it is suggested to form lines with a reduced distance between hives in order to reduce the distance from hive entrances to the harp, to achieve a higher protective effect.<sup>28</sup> Nevertheless, in this study, we observed that in apiaries placed in sites with a high abundance of V. velutina, with a compact line of hives (20-30 cm separation between them) and one harp between two consecutive hives, the reduction of hunting pressure was significant but still not enough to achieve a null predation. Therefore, in highly invaded areas, this control method should be deployed in tandem with additional measures, such as V. velutina's nest detection and destruction in the surroundings of the apiaries in order to reduce the number of hunters and their detrimental consequences on honey bee colony performance and survivorship.

## 5 CONCLUSIONS

The predation pressure by the invasive hornet *V. velutina* interferes with normal hive activity and affect biological traits of honey bees, such as foraging activity, breeding, body weight and colony survivorship. A reduced number of hornets hunting honey bees in front of the hives over a prolonged period is enough to trigger colony paralysis. The high mortality of honey bee colonies is a global phenomenon recorded since the end of last century. Here we demonstrate that beekeeping management techniques, such as the use of electric harps, help to improve the health of honey bee colonies and to extend their lifespan in invaded areas reducing the detrimental effects of *V. velutina* on pollinators. The predation pressure of *V. velutina* is added to the stressors that pollinators face in invaded areas. Therefore, it is indispensable to

avoid the establishment of efficient predators of bees, such as the hornet *V. velutina* or other invasive species of the *Vespa* genus, in regions at risk.<sup>46,47</sup> Thus, the development of prevention and long-term management plans are required, thus allowing beekeeping to remain viable, while preserving pollination of plants and biodiversity.

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## **CONFLICT OF INTEREST**

The authors declare they have no financial interests related to the work submitted for publication. SVRN was co-author of the Utility Model ES 1203011-U.

## **DATA AVAILABILITY STATEMENT**

The data that support the findings of this study are openly available in figshare at <a href="https://figshare.com/">https://figshare.com/</a>, reference number 10.6084/m9.figshare.19189784." cd value code="text"

## **SUPPORTING INFORMATION**

Supporting information may be found in the online version of this article.

### REFERENCES

- 1 Aizen MA and Harder LD, The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. Curr Biol 19:915–918 (2009)
- 2 Sánchez-Bayo F and Wyckhuys KA, Worldwide decline of the entomofauna: a review of its drivers. Biol Conserv 232:8–27 (2019).
- 3 Vanbergen AJ and Initiative IPI, Threats to an ecosystem service: pressures on pollinators. Front Ecol Environ 11:251–259 (2013).
- 4 Goulson D, Nicholls E, Botías C and Rotheray EL, Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 347:1255957 (2015).
- 5 Gabín-García LB, Bartolomé C, Guerra-Tort C, Rojas-Nossa SV, Llovo J and Maside X, Identification of pathogens in the invasive hornet Vespa velutina and in native Hymenoptera (Apidae, Vespidae) from SW-Europe. Sci Rep 11:1–12 (2021).
- 6 Choi MB, Martin SJ and Lee JW, Distribution, spread, and impact of the invasive hornet Vespa velutina in South Korea. J Asia Pac Entomol 15: 473–477 (2012).
- 7 Monceau K, Bonnard O and Thiéry D, Vespa velutina: a new invasive predator of honeybees in Europe. J Pest Sci 87:1–16 (2014).
- 8 Archer ME, Vespine Wasps of the World: Behaviour, Ecology and Taxonomy of the Vespinae. Siri Scientific Press, Manchester, UK (2012).
- 9 Arca M, Mougel F, Guillemaud T, Dupas S, Rome Q, Perrard A et al., Reconstructing the invasion and the demographic history of the yellow-legged hornet, Vespa velutina, in Europe. Biol Invasions 17: 2357–2371 (2015).
- 10 Kim JK, Choi M and Moon TY, Occurrence of *Vespa velutina* Lepeletier from Korea, and a revised key for Korean *Vespa* species (Hymenoptera: Vespidae). *Entomol Res* **36**:112–115 (2006).
- 11 Villemant C, Streito JC and Haxaire J, Premier bilan de l'invasion de Vespa velutina Lepeletier en France (Hymenoptera, Vespidae). Bull Soc Entomol France 111:535–538 (2006).



- 12 Minoshima YN, Yamane S and Ueno T. An invasive alien hornet, Vespa velutina nigrithorax du Buysson (Hymenoptera, Vespidae), found in Kitakyushu, Kyushu Island: a first record of the species from mainland Japan. Jpn J Syst Entomol 21:259-261 (2015).
- 13 Quaresma A, Henriques D, Godinho J, Maside X, Bortolotti L and Pinto MA, Invasion genetics of the Asian hornet Vespa velutina nigrithorax in Southern Europe. Biol Invasions 24:1479–1494 (2022). https://doi.org/10.1007/s10530-022-02730-9.
- 14 Cini A, Cappa F, Petrocelli I, Pepiciello I, Bortolotti L and Cervo R, Competition between the native and the introduced hornets Vespa crabro and Vespa velutina: a comparison of potentially relevant lifehistory traits. Ecol Entomol 43:351-362 (2018).
- 15 Ikegami M. Tsuiji K and Ishizuka A. Environments, spatial structures, and species competitions: determining the impact of yellow-legged hornets, Vespa velutina, on native wasps and bees on Tsushima Island, Japan. Biol Invasions 22:3131-3143 (2020).
- 16 Rojas-Nossa SV, Gil N, Mato S and Garrido J, Vespa velutina: Características e impactos de una exitosa especie exótica invasora. Ecosistemas 30:2159-2159, 10 (2021).
- 17 Rome Q, Perrard A, Muller F, Fontaine C, Quilès A, Zuccon D et al., Not just honeybees: predatory habits of Vespa velutina (Hymenoptera: Vespidae) in France. Annal Soc Entomol France **57**:1-11 (2021).
- 18 Rojas-Nossa SV and Calviño-Cancela M, The invasive hornet Vespa velutina affects pollination of a wild plant through changes in abundance and behaviour of floral visitors. Biol Invasions 22:2609-2618
- 19 Laurino D, Lioy S, Carisio L, Manino A and Porporato M, Vespa velutina: an alien driver of honey bee colony losses. Diversity 12:5 (2020).
- 20 Cappa F, Cini A, Bortolotti L, Poidatz J and Cervo R, Hornets and honey bees: a coevolutionary arms race between ancient adaptations and new invasive threats. Insects 12:1037 (2021).
- 21 Monceau K, Arca M and Leprêtre L, Native prey and invasive predator patterns of foraging activity: the case of the yellow-legged hornet predation at European honeybee hives. PLoS One 8:e66492 (2013).
- 22 Leza M, Herrera C, Margues A, Roca P, Sastre-Serra J and Pons DG, The impact of the invasive species Vespa velutina on honeybees: a new approach based on oxidative stress. Sci Total Environ 689:709-715
- 23 Monceau K, Arca M, Leprêtre L, Bonnard O, Arnold G and Thiéry D, How Apis mellifera behaves with its invasive hornet predator Vespa velutina? J Insect Behav 31:1-11 (2018).
- 24 Requier F, Rome Q and Chiron G, Predation of the invasive Asian hornet affects foraging activity and survival probability of honey bees in Western Europe. J Pest Sci 92:567-578 (2019).
- 25 Requier F, Rome Q, Villemant C and Henry M, A biodiversity-friendly method to mitigate the invasive Asian hornet's impact on European honey bees. J Pest Sci 93:1-9 (2020).
- 26 Turchi L and Derijard B, Options for the biological and physical control of Vespa velutina nigrithorax (Hym.: Vespidae) in Europe: a review. J Appl Entomol 142:553-562 (2018).
- 27 Bonnefond L, Paute S and Andalo C, Testing muzzle and ploy devices to reduce predation of bees by Asian hornets. J Appl Entomol 145: 145-157 (2021).
- 28 Rojas-Nossa SV and Calviño-Cancela M, Effectiveness of electric traps for the defence of honeybees against the invasive predator Vespa velutina. Proceedings of the COLOSS Velutina Task Force meeting -Bilbao, Spain 28-29/06/2018. Pp 22-23. https://www. vespavelutina.eu/Portals/0/Users/152/52/152/Proceedings\_ COLOSS\_Velutina\_Task\_Force\_Meeting\_Spain\_2018.pdf?ver= 2019-11-27-125039-853. [02 August 2021]

- 29 Leza M. Herrera C. Picó G. Morro T and Colomar V. Six years of controlling the invasive species Vespa velutina in a Mediterranean Island: the promising results of an eradication plan. Pest Manage Sci 77: 2375-2384 (2021).
- 30 Beggs JR, Brockerhoff EG, Corley JC, Kenis M, Masciocchi M, Muller F et al., Ecological effects and management of invasive alien Vespidae. BioControl 56:505-526 (2011).
- 31 Friard O and Gamba M, BORIS: a free, versatile open-source eventlogging software for video/audio coding and live observations. Methods Ecol Evol 7:1325-1330 (2016).
- 32 Delaplane KS, Van Der Steen J and Guzman-Novoa E, Standard methods for estimating strength parameters of Apis mellifera colonies. J Apic Res 52:1-12 (2013).
- 33 Dennis B and Kemp WP, How hives collapse: Allee effects, ecological resilience, and the honey bee. PLoS One 11:e0150055 (2016).
- 34 Hartig F, Package 'DHARMa.' http://florianhartig.github.io/DHARMa/. https://cran.r-project.org/web/packages/DHARMa/DHARMa.pdf (2018). [20 July 2022].
- 35 Fox J, Friendly GG, Graves S, Heiberger R, Monette G, Nilsson H et al., The car package. (2007). [20 July 2022]. Available: https://cran.rproject.org/web/packages/car/
- 36 Magnusson A, Skaug H, Nielsen A, Berg C, Kristensen K, Maechler M et al., Package 'glmmTMB'. R Package Version 0.2. 0. http://cran. uni-muenster.de/web/packages/glmmTMB/glmmTMB.pdf (2017). [20 July 2022].
- 37 Monceau K and Thiéry D, Vespa velutina nest distribution at a local scale: an 8-year survey of the invasive honeybee predator. Insect Sci 24:663-674 (2017).
- 38 Rojas-Nossa SV, Novoa N, Serrano A and Calviño-Cancela M, Performance of baited traps used as control tools for the invasive hornet Vespa velutina and their impact on non-target insects. Apidologie 49:872-885 (2018).
- 39 Lioy S, Laurino D, Capello M, Romano A, Manino A and Porporato M, Effectiveness and selectiveness of traps and baits for catching the invasive hornet Vespa velutina. Insects 11:706 (2020).
- 40 Rodríguez-Flores MS, Seijo-Rodríguez A, Escuredo O and Seijo-Coello M, Spreading of Vespa velutina in Northwestern Spain: influence of elevation and meteorological factors and effect of bait trapping on target and non-target living organisms. J Pest Sci 92:557-565 (2019).
- 41 Simpson J, The significance of the presence of pollen in the food of worker larvae of the honey-bee. J Cell Sci 3:117-120 (1955).
- 42 Manning R, Fatty acids in pollen: a review of their importance for honey bees. Bee World 82:60-75 (2001).
- 43 Di Pasquale G, Salignon M, Le Conte Y, Belzunces LP, Decourtye A, Kretzschmar A et al., Influence of pollen nutrition on honey bee health: do pollen quality and diversity matter? PLoS One 8:e72016 (2013).
- 44 Piou V, Tabart J, Hemptinne JL and Vétillard A, Effect of pollen extract supplementation on the varroatosis tolerance of honey bee (Apis mellifera) larvae reared in vitro. Exp Appl Acarol 74:25-41 (2018).
- 45 Tasei JN and Aupinel P, Nutritive value of 15 single pollens and pollen mixes tested on larvae produced by bumblebee workers (Bombus terrestris, hymenoptera: Apidae). Apidologie 39:397-409 (2008).
- 46 Castro L and del Pico C, Sobre el problema de Vespa orientalis Linnaeus 1771 (Hymenoptera: Vespidae) en el sur de España. Rev Gadit Entomol 12:183-206 (2021).
- 47 Nuñez-Penichet C, Osorio-Olvera L, Gonzalez VH, Cobos ME, Jiménez L, DeRaad DA et al., Geographic potential of the world's largest hornet, Vespa mandarinia Smith (Hymenoptera: Vespidae), worldwide and particularly in North America. PeerJ 9:e10690 (2021).