# How Apis mellifera Behaves with its Invasive Hornet Predator Vespa velutina?

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# How *Apis mellifera* Behaves with its Invasive Hornet Predator *Vespa velutina*?

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**Abstract** Invasive species are now recognized as a major cause of native biodiversity loss worldwide. In the current deleterious context for pollinators, the invasive yellow-legged hornet, *Vespa velutina*, represents an additional threat to the domestic honeybee, *Apis mellifera*, in Europe. Therefore, understanding the impact of this predator on honeybee colonies is of major importance. In the present study, we tried to assess the impact of *V. velutina* on the honeybee foraging and defence behaviour based on the video monitoring of two hives. Balling behaviour is reported here for the first time under natural conditions in *A. mellifera* against *V. velutina* in Europe. Although these results are preliminary and should be carefully considered, we found that the number of hornets impacted honeybee foraging and defence behaviours. More defensive behaviours were notified in the hive, which survives slightly longer. This may suggest that selecting for more defensive colonies may provide an interesting perspective.

**Keywords** Balling behaviour · Defence behaviour · Domestic honeybee · Foraging · Yellow-legged hornet

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**Electronic supplementary material** The online version of this article (https://doi.org/10.1007/s10905-017-9658-5) contains supplementary material, which is available to authorized users.

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## Introduction

Invasive species are recognized one of the major threat to the biodiversity (Vitousek et al. 1997) and related to the intensification of human trades worldwide (Pimentel et al. 2005; Hulme 2009; Essl et al. 2015). Recently, Europe engaged in a new legislation that is supposed to facilitate the coordination among state members to efficiently limit and fight against alien species (EU Regulation 1143/2014). Among the 37 alien species that were recognized harmful for biodiversity, *Vespa velutina* Lepeletier (Hymenoptera: Vespidae) is of major concern because of its impact on the European domestic honeybee, *Apis mellifera* Linnaeus (Hymenoptera: Apidae). Indeed, this hornet species is a predator of domestic honeybees and its predation has become critical in addition to several other factors such as pesticides, pests and pathogens in the actual pollinators decline in the north hemisphere (Goulson et al. 2015). Understanding the impact of the different factors that can alter alone or synergistically honeybee health is therefore crucial.

The yellow-legged hornet, *V. velutina,* was introduced from eastern Asia into France before 2004 (Arca et al. 2015) and then rapidly spread through Europe, now being present in France, Spain (López et al. 2011) including Mallorca, Portugal (Grosso-Silva and Maia 2012), Italy (Demichelis et al. 2013), Germany (Witt, 2015), and more recently in Belgium and in the United Kingdom (including Channel islands such as Jersey and Alderney, Budge et al. 2017). Colonisation of other European countries could thus be expected in a near future (Ibáñez-Justicia and Loomans 2011; Villemant et al. 2011; Barbet-Massin et al. 2013). *V. velutina* hunts domestic honeybee workers in a characteristic hovering position backwards to the hive called bee-hawking (Ken et al. 2005; Tan et al. 2007); hornet workers stay in front of the hive entrance in stationary flight to catch honeybees returning to their hive (Monceau et al. 2013a). In its native area, *V. velutina* preys on the Asian honeybee, *Apis cerana*, and the introduced European honeybee, *A. mellifera* that was imported first in the early twentieth century to China mainly because of its higher productivity (Ken et al. 2005; Yang 2005). To repel and defend its colony, *A. cerana* colonies display several behaviours such as the beecarpet, the heat balling or the abdomen shacking movement (i.e. shimmering, Ken et al. 2005; Tan et al. 2010, 2012, 2013). *A. mellifera* colonies only display the beecarpet and heat-balling behaviours and are less efficient than *A. cerana* colonies that coevolved with the *V. velutina* and thus evolved more effective defence strategies (Ken et al. 2005; Tan et al. 2007, 2012, 2013). Similarly in Europe, *A. mellifera*, the native prey species, is not efficient at defending the colony against *V. velutina*, the invasive predator. Up to now, heat balling had only been observed when the hornets were experimentally put on the flight board of the hive (Arca et al. 2014).

Although *V. velutina* is known as a threat for honeybees by direct predation, the quantification of the impact of the predation pressure on domestic honeybee colony foraging and defence activities was not really investigated to date in Europe. Especially, during summer when *V. velutina* colony grows, the needs for proteins to feed the brood increase that explains the increase of the predation pressure on beehives from mid-July to late October (Monceau et al. 2013b). As a response to the disturbance, one might expect that the recruitment of honeybees at the hive entrance should increase with increasing predation pressure (Arca et al. 2014; Nouvian et al. 2016 but see Rittschof and Robinson 2013). Moreover, honeybee foragers can also be recruited to contribute to colony defence if necessary (Kastberger et al. 2009) thus potentially resulting in a negative correlation between the number of honeybees on the flight board and the number of flying honeybees.

In the present study, we tested whether the predation pressure (i.e. the number of hornets in front of the hives) i) decreased the foraging activity of the honeybees and ii) provoked an increase of the number of honeybees on the flight board (i.e. forming the beecarpet, Papachristoforou et al. 2011; Arca et al. 2014). We also tested if honeybee foraging and defence behaviours were traded off. For this purpose, we took advantage of the experimental apparatus that was used to video monitor the predation behaviour of *V. velutina* at the hive entrance (see Monceau et al. 2013a). This allowed to survey the two honeybee hives through the whole period of predation of the hornet and thus allowed a fine tune analysis of the variation of the number of honeybees and hornets across the day and the season. Additionally, it also permitted to observe rare behaviours if existing such as balling that was only observed in experimental conditions.

## Materials and Methods

### Ethics Statements

This study complied with all relevant regulations relative to animal experimentations.

### Experimental Design

This study was realized at the same time with the experiment of Monceau et al. (2013a), thus following the same methodology of data acquisition and analyses. Two *A. mellifera mellifera* hives of equivalent visual appearance (H1 and H2 thereafter) located in an experimental apiary (INRA, Villenave d'Ornon, France, GPS: N 44°47′ 31.26" W 0°34′29.99″) were randomly chosen to be video monitored. The exact size of the honeybee colonies was unknown but they did not differ in the number of flying honeybees (Wilcoxon rank sum test: $W = 9040.5$, $P = 0.41$, $N = 138$ for H1 and 139 for H2) nor in the number of bees on the flight board ($W = 10{,}087$, $P = 0.45$) or in the number of hornets at the entrance ($W = 10{,}204.5$, $P = 0.35$). The hives were surveyed with a video camera in front of the hive throughout the entire season of predation by *V. velutina* from June to November 2009 without disturbing the honeybees (black and white Dragonfly Point Grey, 640 × 480 resolution, 100 FPS, see Fig. 1 in Monceau et al. 2013a). Cameras were programmed to start recording at sunrise and stop at sunset as both hornet and honeybees are diurnal from the 19/06/2009 to the 23/11/2009 (Numeriscope, Viewpoint, France).

### Video Analysis

*Sample Points*

The entire footage was >2000 h of observation per hive and was roughly viewed for potential anecdotic behaviours of hornets and honeybees. For the detailed analysis, we first determined the start and the end of the sampling session. The starting day (10/07/

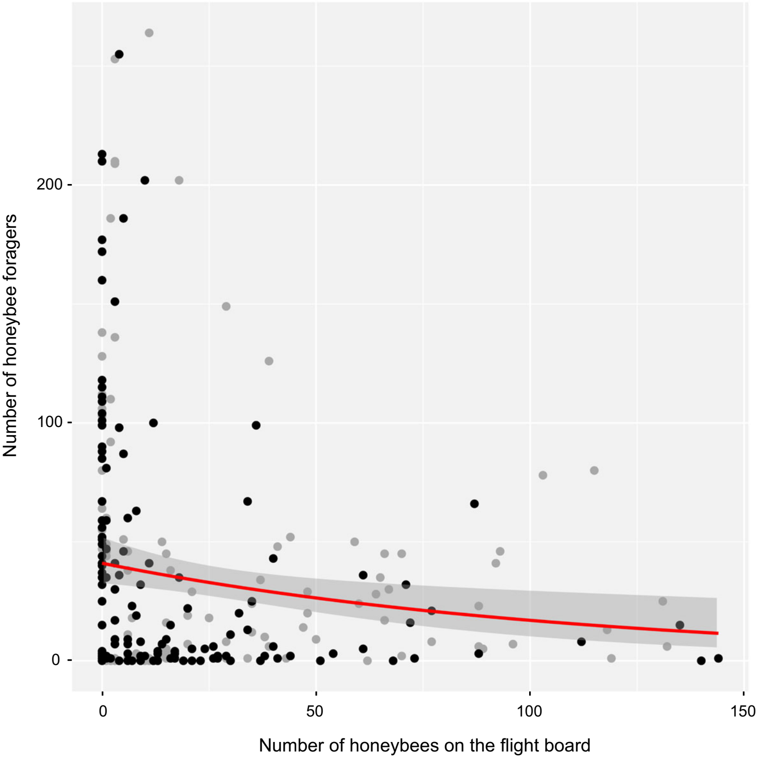

**Fig. 1** Relationship between the number of honeybee foragers and on the flight board. Data are pooled for H1 (grey dots) and H2 (black dots). The red line represents the predicted values fitted with the GLM assorted with their 95% confidence interval (grey)

2009) was defined when the first hornet of the season was spotted on the video on any of the both hives; the last day of the observation session was the 25/10/2009 when the colonies had no more honeybee activity. Between these time limits, diurnal sampling sessions were selected every 10 days only. Some of these sessions had to be postponed due to adverse climatic conditions or too poor video quality (see details in Monceau et al. 2013a). Finally, 11 sample days were taken to characterize the season of predation pressure by *V. velutina*. For each sample day, the behaviour of the hornets and the honeybees was analysed at the beginning of each hour (see details below), resulting in a total of 139 sample points per hive (range: 10–14 sample points per day per hive).

### *Hornet and Honeybee Behaviour*

The predation pressure by *V. velutina* was monitored during the first five minutes of each sample point in assessing the maximum number of hornets in the frame at the same time to avoid pseudo-replication that could artificially enhance the real number of hornets. The behaviour of the honeybees was monitored during the first two minutes of each sample point in assessing the number of honeybees i) on the hive flight board to account for colony defensiveness (i.e., the bee carpet, following Papachristoforou et al. 2011 and Arca et al. 2014) and ii) entering the hive (the number of honeybees flying in and out the hive was previously shown to be similar, see Monceau et al. 2013a) to account for the overall foraging activity.

Videos were visualized using VLC software (v. 1.1.11) and analysed by a single person (L.L.) to avoid experimenter bias.

### Statistical Analyses

Negative Binomial Generalized Linear Models (NBGLM) were used to analyse the relationship between: i) the number of foraging and defensive honeybees, ii) the number of foraging honeybees and the number of hornets, and iii) the number of defensive honeybees and the number of hornets. The date (linear and quadratic effects) was included in each model to account for seasonal variations in hornet and honeybees activity (Seeley 1985; Monceau et al. 2013a, b). For iii), the number of hornets was also included as a quadratic effect to account for potential maximum effect. One outlier was discarded from this analysis as it clearly biased the model (20 hornets, H2 on the 15th of September). Prior to NBGLM, collinearity between variables that may bias the estimators of the models was check using variance inflation factor (VIF, Dormann et al. 2013). Binomial tests were used for testing differences in anecdotic behaviours.

All statistics were done with R software (v. 3.3.1, R Core Team 2016) implemented with the *car* package for deviance analysis for unbalanced design and *usdm* for collinearity test.

## Results

### Relationship between Honeybee Foraging and Defence (through Beecarpet Behaviour)

The number of honeybees returning to the hive was negatively related to the number of individuals on the flight board forming the beecarpet (NBGLM: $\chi^2 = 9.22$, $df = 1$, $P < 0.01$, Fig. 1) and declined during the season (linear effect: $\chi^2 = 0.77$, $df = 1$, $P = 0.38$ and quadratic effect: $\chi^2 = 14.16$, $df = 1$, $P < 0.001$, Online Resource 1, see also Fig. 5b in Monceau et al. 2013a).

### Hornet Predation Pressure, Honeybee Foraging and Defence

The number of honeybee foragers declined during the season (NBGLM: linear effect: $\chi^2 = 0.10$, $df = 1$, $P = 0.75$ and quadratic effect: $\chi^2 = 8.85$, $df = 1$, $P < 0.01$, see above) but also due to the increasing hornet predation pressure ($\chi^2 = 4.46$, $df = 1$, $P = 0.03$, Fig. 2).

The number of honeybees on the flight board varied according to the date (NBGLM: linear effect: $\chi^2 = 37.38$, $df = 1$, $P < 0.0001$ and quadratic effect: $\chi^2 = 87.21$, $df = 1$, $P < 0.0001$ Fig. 3) and due to the number of hornet in front of the entrance of the hive (linear effect: $\chi^2 = 22.30$, $df = 1$, $P < 0.0001$ and quadratic effect: $\chi^2 = 12.10$, $df = 1$, $P < 0.001$, Fig. 4 The maximal number of honeybees on the flight board was reached in late August-early September and for a number of seven hornets (Figs. 3 and 4).

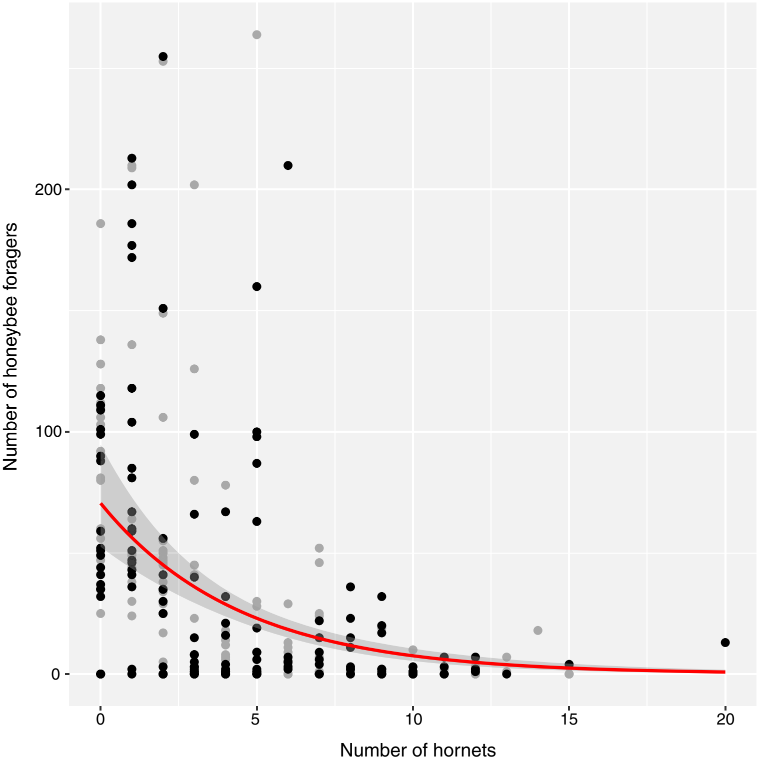

**Fig. 2** Relationship between the number of honeybee foragers and the number of hornets in front of the hive. Data are pooled for H1 (grey dots) and H2 (black dots). The red line represents the predicted values fitted with the GLM assorted with their 95% confidence interval (grey)

## Anecdotic and Unexpected Behaviours

Over the video monitored period, several punctual observations of honeybees tracking hornets were made (21 for H1 and 46 for H2, binomial test $P < 0.01$). Three occurrences of the so-called balling behaviour were also observed (2 for H1 and 1 for H2, $P > 0.05$). In each case, the hornet flying too closed from the beecarpet, was engulfed and killed (see Online Resource 2, once dead the hornet is in a typical death position, i.e. curled up on the side).

## Discussion

*Vespa velutina* has become a major threat to domestic honeybees in the last decade (see Monceau et al. 2014a for review). The population density of this pest varies greatly at a small scale (Monceau and Thiéry 2017) and at larger scale (Bessa et al. 2016; Robinet et al. 2017) depending on resource availability and climatic factors. As a consequence, the predation pressure on hives depends on local hornet density. Our experimental apiary is located in an area where six *V. velutina* nests were identified within a radius of 1 km from the hives, thus potentially contributing to the local predation. Southwestern

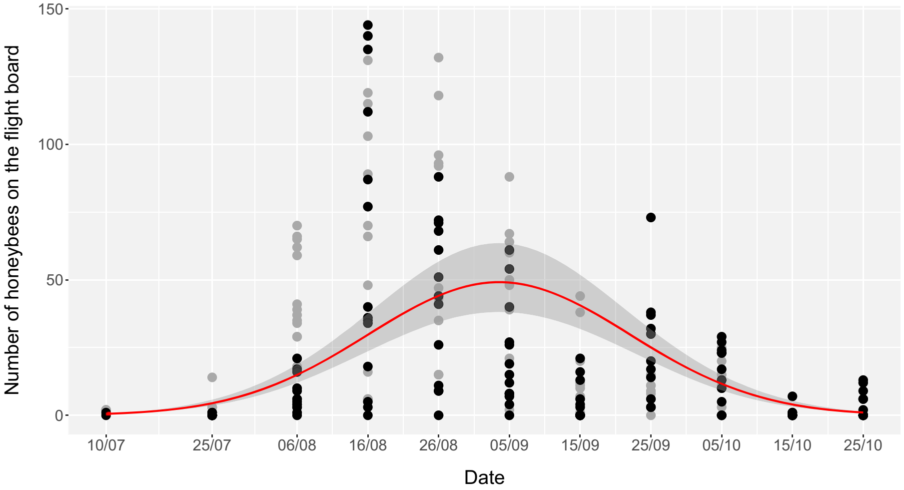

**Fig. 3** Seasonal variations in the number of honeybees on the flight board. Data are pooled for H1 (grey dots) and H2 (black dots). The red line represents the predicted values fitted with the GLM assorted with their 95% confidence interval (grey)

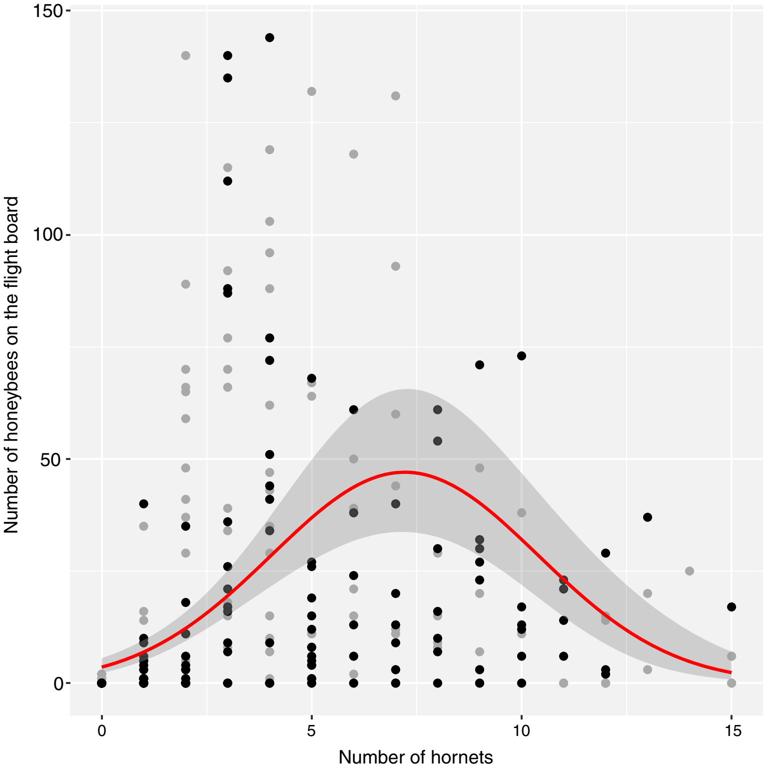

**Fig. 4** Relationship between the number of honeybee on the flight board and the number of hornets in front of the hive. Data are pooled for H1 (grey dots) and H2 (black dots). The red line represents the predicted values fitted with the GLM assorted with their 95% confidence interval (grey)

France is probably one of the most invaded areas within Europe, some areas displaying up to 12 nests/km$^2$ (Monceau and Thiéry 2017). Up to 20 hornets have been observed at the same time in this experiment. However, this does not represent the true number of the predator daily visits. A capture-mark-recapture study realised on the same site estimated to 360 hornets visiting daily the apiary (six hives) at the beginning of the summer predation (Monceau et al. 2014b). Also yet observed, the decrease in honeybee foraging behaviour has never been quantified to date neither the defence behaviour. Although our results should be carefully considered due to the low sample size, we show that hornet predation pressure affects the behaviour of the honeybee colony in reducing the foraging activity. Especially, we show that above ten hornets per hive, the number of honeybee foragers drops.

Temporal polyethism is one characteristic of honeybee colonies (Calderone 1998; Hölldobler and Wilson 2008; Johnson 2010). Basically, the oldest individuals of the colony assume foraging and defence tasks. This supposes a trade-off between the number of honeybees dedicated to foraging and to defence (Giray et al. 2000). However, there is no consensus in the literature; some studies found a negative correlation (Giray et al. 2000) while other found a positive correlation (Wray et al. 2011) or no relation at all (Page et al. 1995). In our study, we found a negative correlation between foraging and defence. Wray et al. (2011) have demonstrated that colonies may exhibit different behavioural profiles in regard to different traits including defence behaviour. Some colonies may adopt an offensive strategy against predators or intruders in increasing the number of individuals on the flight board or at the contrary, retreat inside the hive to block the entrance to the intruders (Kastberger et al. 2009; Papachristoforou et al. 2011). H2 adopted a more offensive strategy as suggested by the higher number of hornets tracked by honeybees although this behaviour is quite difficult to monitor since the protagonists regularly got out the frame of the camera. This quantitative study also allows confirming that balling naturally occurs in *A. mellifera mellifera* but in specific circumstances i.e. when the hornet felt down in the bee-carpet (see also Arca et al. 2014). To date, balling behaviour had only been observed when the hornets were experimentally introduced into the hive or placed near the entrance (Arca et al. 2014). It however remains unclear whether it is a heat balling similarly to Asian honeybees (Ken et al. 2005) or a balling leading to asphyxia like Cyprian honeybees (Papachristoforou et al. 2007) and/or associated with bee venom through stings (Baracchi et al. 2010). Anyway, the frequency of such behaviour is really low thus explaining why only intensive observation (video monitoring) allows its observation (Arca et al. 2014). Nevertheless, this means that *A. mellifera mellifera* is able to respond to *V. velutina* attack although the balling behaviour is rare and thus still not sufficient enough to limit the predation pressure.

Finally, H1 passed away first before winter; H2 survived longer but finally died later in the winter due to the reduction of the size of the colonies. All things being equal (similar size early in the season, same exposition to parasites and predators, same environment), this could suggest that H2 had slightly more store resources. The predation in apiaries is not homogeneous, some hives being more susceptible to *V. velutina* attacks than other within a small scale (Monceau et al. 2014b). The differences in colony behavioural type (i.e. personality, Wray et al. 2011) could explain such variability. In *A. mellifera mellifera*, defence behaviour is complex (see for a recent review Nouvian et al. 2016), could be genetically determined (Breed and Rogers

1991) and shows potential high level of heritability (Breed et al. 2004). This could therefore constitute an interesting perspective to consider. Indeed, selecting honeybee lineages for their defensiveness may represent a valuable method to limit the impact of *V. velutina* in a near future. Especially, one might consider that selection on specific behaviour such as the balling behaviour could help enhancing the defensiveness of the honeybee colonies.

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## References

Arca M, Papachristoforou A, Mougel F, Rortais A, Monceau K, Bonnard O, Tardy P, Thiéry D, Silvain J-F, Arnold G (2014) Defensive behaviour of *Apis mellifera* against *Vespa velutina* in France: testing whether European honeybees can develop an effective collective defence against a new predator. Behav Process 106:122–129

Arca M, Mougel F, Guillemaud T, Dupas S, Rome Q, Perrard A, Muller F, Fossoud A, Capdevielle-Dulac C, Torres-Leguizamon M, Chen XX, Tan JL, Villemant C, Arnold G, Silvain JF (2015) Reconstructing the invasion and the demographic history of the yellow-legged hornet, *Vespa velutina*, in Europe. Biol Invasions 17:2357–2371

Baracchi D, Cusseau G, Pradella D, Turillazzi S (2010) Defence reactions of *Apis mellifera ligustica* against attacks from the European hornet *Vespa crabro*. Ethol Ecol 22:281–294

Barbet-Massin M, Rome Q, Muller F, Perrard A, Villemant C, Jiguet F (2013) Climate change increases the risk of invasion by the yellow-legged hornet. Biol Conserv 157:4–10

Bessa AS, Carvalho J, Gomes A, Santarem F (2016) Climate and land-use drivers of invasion: predicting the expansion of *Vespa velutina nigrithorax* into the Iberian peninsula. Insect Conserv Divers 9:27–37

Breed MD, Rogers KB (1991) The behavioral genetics of colony defense in honeybees: genetic variability for guarding behaviour. Behav Genet 21:295–303

Breed MD, Guzmán-Novoa E, Hunt GJ (2004) Defensive behaviour of honey bees: organization, genetics, and comparisons with other bees. Annu Rev Entomol 49:271–298

Budge GE, Hodgetts J, Jones EP, Ostoja-tarzewski JC, Hall J, Tomkies V, Semmence N, Brown M, Wakefield M, Stainton K (2017) The invasion, provenance and diversity of *Vespa velutina* Lepeletier (hymenoptera: Vespidae) in great Britain. PLoS One 12:e0185172

Calderone NW (1998) Proximate mechanisms of age polyethism in the honey bee, *Apis mellifera* L. Apidologie 29:127–158

Demichelis S, Manimo A, Porporato M (2013) Trovato il primo nido di Vespa velutina a Vallecrosia (IM). http://wwwvespavelutinaeu/LinkClickaspx?fileticket=NhQAlzPdbcg%3d&tabid=111&portalid=0&mid=534&language=it-IT Accessed 5 April 2017

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46

Essl F, Bacher S, Blackburn TM, Booy O, Brundu G, Brunel S, Cardoso A-C, Eschen R, Gallardo B, Galil B, Garcia-Berthou E, Genovesi P, Groom Q, Harrower C, Hulme PE, Katsanevakis S, Kenis M, Kühn I, Kumschick S, Martinou AF, Nentwig W, O'Flynn C, Pagad S, Pergl J, Pysek P, Rabitsch W, Richardson DM, Roques A, Roy HE, Scalera R, Schindler S, Seebens H, Vanderhoeven S, Vila M, Wilson JRU, Zenetos A, Jeschke JM (2015) Crossing frontiers in tackling pathways of biological invasions. Bioscience DOI:https://doi.org/10.1093/biosci/biv082

Giray T, Guzmán-Novoa E, Aron CW, Zelinsky B, Fahrbach SE, Robinson GE (2000) Genetic variation in worker temporal polyethism and colony defensiveness in the honey bee, *Apis mellifera*. Behav Ecol 11: 44–55

Goulson D, Nicholls E, Botias C, Rotheray EL (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 347:1435–1444

Grosso-Silva JM, Maia M (2012) *Vespa velutina* Lepeletier, 1836 (Hymenoptera, Vespidae), new species for Portugal. Arquiv Entomol 6:53–54

Hölldobler B, Wilson EO (2008) The superorganism. Norton WW & Company, New York, In

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. J Appl Ecol 46:10–18

Ibáñez-Justicia A, Loomans AJM (2011) Mapping the potential occurrence of an invasive species by using CLIMEX: case of the Asian hornet (*Vespa velutina nigrithorax*) in The Netherlands. Proc Neth Entomol Soc Meet 22:39–46

Johnson BR (2010) Division of labor in honeybees: form, function, and proximate mechanisms. Behav Ecol Sociobiol 64:305–316

Kastberger G, Thenius G, Stabentheiner A, Hepburn R (2009) Aggressive and docile colony defence patterns in *Apis mellifera*. A retreater–releaser concept. J Insect Behav 22:65–85

Ken T, Hepburn HR, Radloff SE, Yusheng Y, Yiqiu L, Danyin Z, Neumann P (2005) Heat-balling wasps by honeybees. Naturwissenschaften 92:492–495

López S, Gonzáles M, Goldarazena A (2011) *Vespa velutina* Lepeletier, 1836 (hymenoptera: Vespidae): first records in Iberian peninsula. Bull. OEPP/EPPO Bull 41:439–441

Monceau K, Thiéry D (2017) *Vespa velutina* nest distribution at a local scale: an 8-year survey of the invasive honeybee predator. Insect Sci 24:663–674

Monceau K, Arca M, Leprêtre L, Mougel F, Bonnard O, Silvain J-F, Maher N, Arnold G, Thiéry D (2013a) 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

Monceau K, Maher N, Bonnard O, Thiéry D (2013b) Predation dynamics study of the recently introduced honeybee killer *Vespa velutina*: learning from the enemy. Apidologie 44:209–221

Monceau K, Bonnard O, Thiéry D (2014a) *Vespa velutina*: a new invasive predator of honeybees in Europe. J Pest Sci 87:1–16

Monceau K, Bonnard O, Moreau J, Thiéry D (2014b) Spatial distribution of *Vespa velutina* individuals hunting at domestic honeybee hives: heterogeneity at a local scale. Insect Sci 21:765–774

Nouvian M, Reinhard J, Giurfa M (2016) The defensive response of the honeybee *Apis mellifera*. J Exp Biol 219:3505–3517

Page RE, Robinson GE, Fondrk MK, Nasr ME (1995) Effects of worker genotypic diversity on honey bee colony development and behavior (*Apis mellifera* L.) Behav Ecol Sociobiol 36:387–396

Papachristoforou A, Rortais A, Zafeiridou G (2007) Smothered to death: hornets asphyxiated by honeybees. Curr Biol 1:795–796

Papachristoforou A, Rortais A, Sueur J, Arnold G (2011) Attack or retreat: contrasted defensive tactics used by Cyprian honeybee colonies under attack from hornets. Behav Process 86:236–241

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien invasive species in the United States. Ecol Econ 52:273–288

R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria URL https://wwwR-projectorg/Accessed 5 April 2017

Rittschof CC, Robinson GE (2013) Manipulation of colony environment modulates honey bee aggression and brain gene expression. Genes Brain Behav 12:802–811

Robinet C, Suppo C, Darrouzet E (2017) Rapid spread of the invasive yellow-legged hornet in France: the role of human-mediated dispersal and the effects of control measures. J Appl Ecol 54:205–215

Seeley TD (1985) Honeybee ecology a study of adaptation in social life. Princeton University Press, Princeton

Tan K, Radloff SE, Li JJ, Hepburn HR, Yang MX, Zhang LJ, Neumann P (2007) Bee-hawking by the wasp, *Vespa velutina*, on the honeybees *Apis cerana* and *A. mellifera*. Naturwissenschaften 94:469–472

Tan K, Li H, Yang MX, Hepburn HR, Radloff SE (2010) Wasp hawking induces endothermic heat production in guard bees. J Insect Sci 10:142 http://jinsectscience.oxfordjournals.org/content/10/1/142 Accessed 5 April 2017

Tan K, Wang Z, Li H, Yang S, Hu Z, Kastberger G, Oldroyd BP (2012) An 'I see you' prey–predator signal between the Asian honeybee, *Apis cerana*, and the hornet, *Vespa velutina*. Anim Behav 83:879–882

Tan K, Wang Z, Chen W, Hu Z, Oldroyd BP (2013) The 'I see you' prey–predator signal of *Apis cerana* is innate. Naturwissenschaften 100:245–248

Villemant C, Barbet-Massin M, Perrard A, Muller F, Gargominy O, Jiguet F, Rome Q (2011) Predicting the invasion risk by the alien bee-hawking yellow-legged hornet *Vespa velutina nigrithora*x across Europe and other continents with niche models. Biol Conserv 144:2150–2152

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. Science 277:494–499

Witt R (2015) Erstfund eines Nestes der Asiatischen Hornisse *Vespa velutina* Lepeletier, 1838 in Deutschland und Details zum Nestbau (Hymenoptera, Vespinae). Ampulex 7:42–53

Wray MK, Mattila HR, Seeley TD (2011) Collective personalities in honeybee colonies are linked to colony fitness. Anim Behav 81:559–568

Yang G-H (2005) Harm of introducing the western honeybee *Apis mellifera* L to the Chinese honeybee *Apis cerana* F and its ecological impact. Acta Entomol Sin 48:401–406 (in Chinese)