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Not just honeybees: predatory habits of *Vespa velutina* (Hymenoptera: Vespidae) in France

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Summary. Understanding the impact of a predatory invasive alien species requires data on its diet. *Vespa velutina* Lepeletier, 1836, is a notorious bee-hawking hornet accidentally introduced in France before 2004 which spread across the European continent. Despite numerous studies and the impact on beekeeping activities, there are very few data on the diet of this species in its invaded range in Europe. To fill this knowledge gap, we studied 16 nests in the south-west of France between 2008 and 2010. Using a combination of morphological and barcoding approaches, we identified 2151 prey pellets showing that *V. velutina* acts as a generalist predator, preying on honeybees (38.1%), flies (29.9%) and social wasps (19.7%), as well as a wide spectrum of animal organisms (no less than 159 species identified). The prey spectrum is influenced by the nest surroundings, urban colonies preying more on honeybees and forest colonies preying more on social wasps. The predation intensity reaches its peak in early October. By comparing the dry weight of prey pellets to that of *V. velutina* larvae and considering the colony dynamics, we estimated that a single hornet nest can consume on average 11.32 kg of insect biomass in one season. Overall, our results suggest that *V. velutina* is a generalist opportunistic predator targeting mostly locally abundant prey. While the species may have an impact on honeybees, its generalist, opportunistic behaviour on abundant insects suggests a minor impact on wild species. Instead, attempts to manage this species using non-selective traps have a much greater impact on wild and domesticated entomofauna than the hornet itself.

Résumé. Le spectre de proies du frelon asiatique (*Vespa velutina*) en France ne se limite pas aux abeilles. Pour comprendre l'impact d'une espèce prédatrice exotique et envahissante, il faut disposer de données sur son régime alimentaire. *Vespa velutina* Lepeletier, 1836 est un prédateur bien connu des abeilles domestiques, accidentellement introduit en France avant 2004 et qui colonise, depuis, le continent européen. Malgré de nombreuses études et son impact reconnu sur les activités apicoles, il existe très peu de données sur son régime alimentaire dans les régions envahies d'Europe. Pour combler cette lacune, nous avons suivi seize nids dans le sud-ouest de la France entre 2008 et 2010. En combinant des approches morphologiques et moléculaires (*barcode*), nous avons identifié 2151 boulettes de proies et démontré que *V. velutina* se comporte comme un prédateur généraliste, chassant des abeilles domestiques (38,1%), des mouches (29,9%) et des guêpes sociales (19,7%), ainsi qu'un large spectre d'autres animaux (pas moins de 159 espèces identifiées). Le spectre de proies varie selon l'environnement du nid ; les colonies urbaines chassant plus d'abeilles domestiques et les forestières plus de guêpes sociales. L'intensité de la prédation atteint son maximum début octobre. En comparant le poids sec des boulettes de proies avec celui des larves de *V. velutina* et en tenant compte de la dynamique de la colonie, nous avons estimé qu'une seule colonie de frelon pouvait consommer en moyenne 11,32 kg de biomasse d'insectes en une saison. Dans l'ensemble, nos résultats suggèrent que *V. velutina* est un prédateur opportuniste, ciblant surtout les proies localement abondantes. Bien que cette espèce puisse avoir un impact sur les abeilles domestiques, son comportement généraliste et opportuniste sur les insectes abondants suggère un impact limité sur les espèces sauvages. Alors que, par ailleurs, les tentatives de gestion de cette espèce à l'aide de pièges non sélectifs ont un impact beaucoup plus important sur l'entomofaune sauvage et domestiquée que le frelon lui-même.

Keywords: yellow-legged hornet; invasive alien species; predation; honeybees; diet

Predation underlies the most spectacular damages induced by invasive alien species in invaded ecosystems, sometimes cascading down to primary producers (Bruno et al. 2005; David et al. 2017; Graham et al. 2018). Intensification of human transport and commerce around the world has led to widespread movement of species

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*Corresponding author. Email: quentin.rome@mnhn.fr outside of their native range (Hulme 2009; Frost et al. 2019), including many arthropod generalist predators that feed not only upon herbivores but also upon other predators and detritivores. Due to their complex trophic role, these invaders can have particularly widespread impacts on the communities they invade (Snyder & Evans 2006). Documenting the dietary spectrum of invasive predators is not only necessary to assess their direct impact on prey but also to better define their niche width and understand how they might alter ecosystem services such as biological control or pollination.

The recent introduction of the Yellow-legged Asian hornet *Vespa velutina* Lepeletier, 1836 in France was the first successful invasion of an exotic Vespidae in Europe (Rasplus et al. 2010; Beggs et al. 2011). This species is of great concern among public authorities and beekeepers because of its rapid multiplication and high impact on beekeeping due to its strong predation on honeybees (Perrard et al. 2009) and its hawking behaviour that disrupts bee colony foraging (Rortais et al. 2010; Monceau et al. 2013; Arca et al. 2014; Requier et al. 2019). The species was observed for the first time in 2004 in south-west France and then it rapidly spread across most of French districts. Between 2010 and 2020, it successively established in nine neighbouring countries: Spain, Portugal, Italy, Germany, Belgium, UK, the Netherlands, Luxembourg and Switzerland (Rome & Villemant 2015; Burri-Schmassmann et al. 2017; Barbet-Massin et al. 2018). Climatic niche modelling suggests that *Vespa velutina* could spread throughout Europe (Villemant et al. 2011; Fournier et al. 2017). Taking into account recent climate change scenarios and the observed enlargement of its climatic niche, future range expansion may even be more rapid than expected (Barbet-Massin et al. 2013, 2018).

As for other *Vespa* species, *V. velutina* is a generalist predator that attacks a wide range of insects and spiders (Van der Vecht 1957). *Vespa velutina* generally catches its prey in flight and immediately hangs on a support to process it, most often by removing all parts except the thorax which contains the nutritious flight muscles. This flesh pellet is then brought back to the nest and chewed to feed larvae with proteins. Adults only consume sugar-rich liquids and an energetic protein-rich liquid regurgitated by the larvae (Matsuura & Yamane 1990). During its development, the hornet larva does not produce faeces. The gut content is only eliminated during the prepupal stage when the larva weaves a cocoon with an operculum, which closes its cell. The mass of released faeces is called meconium and will remain at the bottom of the cell after the adult emerges (Rome et al. 2015).

While *V. velutina* arrived in Europe more than a decade ago, our knowledge of its diet spectrum still relies on very limited data: anecdotal reports from its original range (Williams 1988; Abrol 1994) and only preliminary data in France (Perrard et al. 2009; Rome et al. 2011b; Villemant et al. 2014). These studies suggest that social hymenopterans and brachyceran flies are its main prey, although its scavenging behaviour on dead vertebrates and shrimps, in the field or in street markets have been reported (Williams 1988). Studies quantifying its diet in the invaded range are required to estimate the potential impact of this species on the local fauna. In addition to its prey spectrum, the pressure of a colony of *V. velutina* on European honeybees is also under-studied, considering its reputation as a bee-hawking predator in Asia and in Europe (Abrol 1994; Monceau et al. 2013). Beehive mortality data have helped to estimate such an impact (Requier et al. 2019), but no real quantification is available from the literature (Villemant et al. 2014).

In this paper, we assessed the diet of *V. velutina* in different environments in south-western France to estimate its predation pressure on the local entomofauna. We first estimated the diversity of prey predated by the hornet using a diversity index taking sampling biases into account. Second, we explored how the landscape around the nests may have influence the prey choices using a corresponding analysis. We then analysed the variation in predation activities across the season and during the day with field observation data. Finally, we used our data to estimate the consumption of an average-size nest in one season.

Material and methods

Collecting sites

The study was performed over three years (2008–2010) from August to October/November, in the Dordogne district, south-west of France. In these years, the colonized area was restricted to this region. This district is close to the point of introduction and had relatively high and stable nest densities. Sixteen colonies were studied for one day to up to four months, depending on the duration the landowners were willing to keep a living nest on their land (Figure 1, Table S1 in online supplementary material).

Prey collection

Once a nest was located, depending on the opportunity to access the nest and on its destruction date, we sampled workers to rob their prey almost every two weeks, either until the nest destruction or until the end of the season. Sampling sessions took place from 1 h after dawn to 1 h before dusk and lasted 90 min. Any two sessions were separated by at least a 30 min break to reduce the stress of the colony. Due to weather conditions or a too strong disturbance of the colony resulting in hornets stopping foraging, 14 sessions out of 138 did not last 90 min. In total, we performed 138 sessions corresponding to 199 h 23 min of sampling (Table S1).

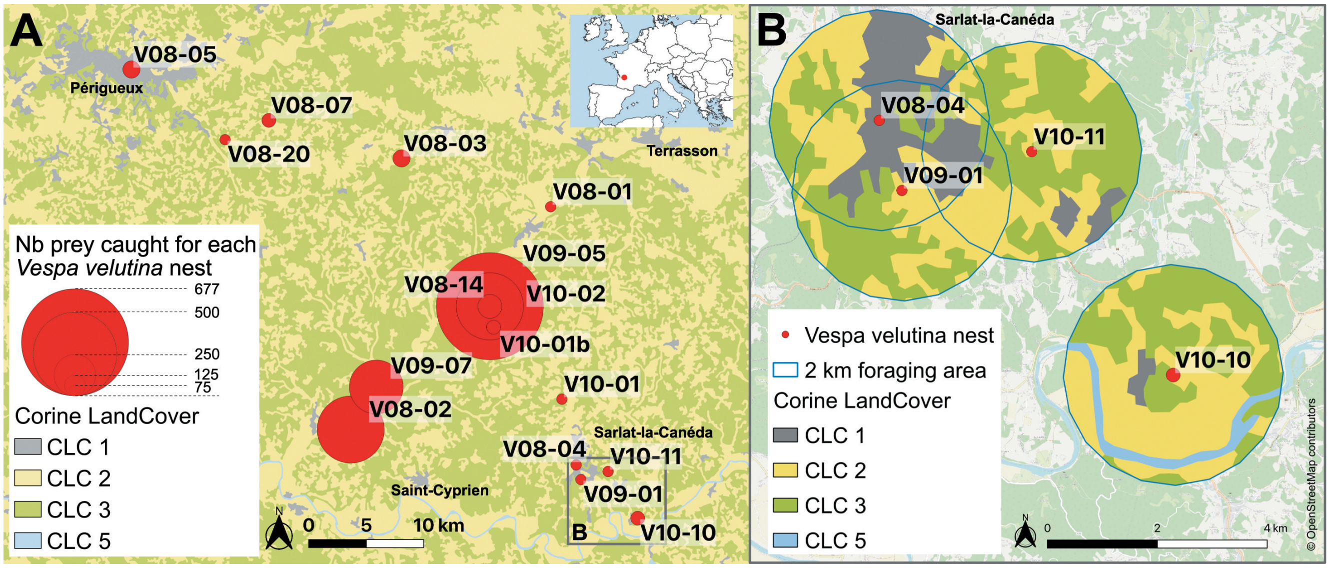

Figure 1. **A**, Total number of prey pellets caught (size of red spot) for each of the 16 studied colonies and CLC of the studied area. **B**, Detailed land use in foraging areas (blue circles) of four *Vespa velutina* colonies near the city of Sarlat-la-Canéda (Dordogne). Corine Land Cover codes: CLC 1, Artificial surfaces; CLC 2, Agricultural areas; CLC 3, Forests and semi-natural areas; CLC 5, Water bodies.

For each session, we tried to catch with a sweeping net a maximum of hornet workers returning to their nest. The rate of failure to catch a hornet was estimated to be low and relatively constant among sessions. When a worker carried a pellet in its mandibles, it was forced to abandon it in the net before being released. Prey pellets were preserved in individual tubes containing 95% ethanol. Returning workers also carried wood pellets as material to build the nest. Those pellets were preserved dry.

Prey identification

A first morphological identification of the prey pellets was made using a stereomicroscope (Nikon SMZ 1000, Minato, Tokyo, Japan) and with the help of the insect collections from the Museum national d'Histoire naturelle. Since many prey pellets were too strongly chewed by the hornets to be reliably identified by their morphology alone, a molecular identification was also performed when possible.

In the latter case, total genomic DNA was extracted from 50 mg of each pellet, using the Macherey-Nagel NucleoSpin 96 Tissue Kit (Düren, Germany) and following the manufacturer's protocol. The mitochondrial cytochrome oxidase I (COI) gene was selected for PCR amplification and barcode identification (Hebert et al. 2003).

The partial COI gene was amplified using the primers LepF1 and LepR1 (Hebert et al. 2004). Each PCR contained 2 µl of 10× PCR buffer, 13.94 µl of distilled water (DNAse free), 2.5 mM $MgCl_2$, 5% DMSO, 0.26 mM dNTPs, 0.3 µM of each primer, 1.5 units of Qiagen Taq polymerase and 1 µl of DNA template, with a final reaction volume of 20 µl. The PCR thermal regime consisted of: one cycle of 1 min initial denaturation at 94°C, 35 cycles of 30 s at 94°C, 30 s hybridization at 47° C, followed by an extension of 50 s at 72°C and a final cycle of 5 min at 72°C. PCR products were electrophoresed in 1% agarose gel stained with ethidium bromide and visualized under UV light. The positive PCRs were sequenced in both directions using the Sanger method and the sequences were assembled with CodonCode Aligner (CodonCode Corporation).

The molecular identification was performed comparing the COI sequences obtained from the prey pellets with those available in Genbank and BOLD, using the BLAST and the Identification Engine tools, respectively. In addition, we created our own barcode reference library of local flies, since a great number of flies were identified among the pellets based on morphology. We barcoded 104 flies identified at the species level by specialists: 78 hoverflies (Syrphidae, 41 species) and 26 carrion and flesh flies (Muscidae, Calliphoridae, Sarcophagidae, 26 species). The extraction was carried out with the same protocol used for the pellets. For the amplification we used either the primers described above or we amplified the COI gene in two fragments, using the primer combinations Lep-F1/COI-intR1 and COI-intF7/Lep-R1 (Hebert et al. 2004; Zuccon et al. 2012), with COI-intF7: 5′-GAAAGAGG AGTTGGAACAGGTTGAAC-3′. The new fly sequences have been submitted to GenBank under the accession numbers MW077745-MW077848 (Table S2).

Analyses

All analyses were performed using R (R Core Team 2018) except for the land-use estimation around the nests for which we used QGIS (QGIS Development Team 2016).

Prey spectrum. The total number of prey species collected by *Vespa velutina* in the study area was estimated with the ACE index using the 'vegan' R package (Oksanen et al. 2019).

Landscape influence. To investigate the influence of the landscape surrounding the nests on the diet of *V. velutina*, we performed a correspondence analysis (CoA) of prey per land-use types. We computed the proportion (%) of four main land-uses within buffers of 2 km radius centred on the nests (Figure 1). The choice of buffer size reflects the foraging range of workers reported from experimental and field studies (Budge et al. 2017; Sauvard et al. 2018; Kennedy et al. 2018). The land-use categories were extracted from the level one of the Corine Land Cover (CLC) categories: artificial surfaces (CLC1); agricultural areas (CLC2); forest and semi natural areas (CLC3) and water bodies (CLC 5) (Union Européenne – SOeS 2011).

Prey was grouped based on the abundance of the different taxa. Taxa with less than 10 individuals were grouped and analysed as a composite group, resulting in 17 prey groups (Table 1). Since prey from a nest could have been captured from areas of different CLC categories, prey groups were attributed to the four CLC categories using a fuzzy coding of individual prey. Each prey was not attributed to a single CLC category, but to each CLC category using a percentage relative to the CLC category proportions in the nest surrounding. Prey group attribution was computed using the sum of these CLC percentages across the different samples.

Seasonal dynamics of predation. In order to test for changes in the level of predation and in the content of the *Vespa velutina* diet throughout the season, we analysed the total number of prey, as well as the percentages of either honey bees, Vespidae or Diptera species, brought back to the nest per 90 min sessions using generalized linear mixed models. We only included in the analysis data from nests sampled for at least five sessions. Since the landscape diversity around the eight remaining nests was very limited, with only one nest in an urban area and no nests in wet areas, the land type was estimated using the proportion of forest and semi-natural areas in a radius of 2 km around the nest. Explanatory variables were date and hour as well as their quadratic terms, land type as fixed effects, and nest identity as random effect. Nine collecting sessions lasted less than 90 min, so the session duration was also taken into account to model the number of prey and their overall diversity. All variables were scaled beforehand. Poisson and binomial error distributions were used for the total number of prey and the percentages of prey groups, respectively. Model simplification was performed following the Akaike information criterion (AIC). Models were performed using the 'glmer' function of the package 'lme4' (Bates et al. 2015) and the effects tested using the 'Anova' function of the R package 'car' (Fox & Weisberg 2019).

Table 1. Diversity of *Vespa velutina* prey. Family and species number represent the minimum number of families or species for each order, whether they were identified by morphological or molecular criteria. Data for Diptera, Hymenoptera and Other Insecta are the sums of the different prey groups they encompass. The numbers in front of prey group names correspond to the different prey groups considered in the correspondence analysis. Numbers are in italics show the infra-order groups.

Prey group	Family no.	Species no.	Specimen no.
1. Araneae	3	7	40
2. Coleoptera	4	3	10
Diptera	13	102	643
3. Calliphoridae	*1*	*22*	*147*
4. Muscidae	*1*	*25*	*125*
5. Sarcophagidae	*1*	*9*	*61*
6. Syrphidae	*1*	*18*	*108*
7. Tachinidae	*1*	*10*	*22*
8. Other Diptera	*8*	*18*	*180*
9. Hemiptera	5	5	31
Hymenoptera	8	14	1293
10. *Apis mellifera*	*1*	*1*	*820*
11. Vespidae	*1*	*4*	*428*
12. Other Hymenoptera	*7*	*9*	*45*
13. Lepidoptera	6	13	17
14. Mecoptera	1	3	14
15. Orthoptera	1	2	12
16. Vertebrata	4	4	67
17. Other Insecta	5	6	19
Dermaptera	1	1	2
Dictyoptera	2	2	7
Nevroptera	1	1	2
Trichoptera	1	2	5
Unidentified Insecta	*NA*	*NA*	*3*
Unidentified	NA	NA	5
Total	**50**	**159**	**2151**

Prey consumption of a colony. To estimate the total consumption, C_{tot}, of prey necessary for the development of a medium size *V. velutina* colony, we use the following formula:

$$C_{tot} = \sum_{i=8}^{11} \frac{W_i}{W_p} \times N_i$$

In which i stands for month, W_i for the mean dry weight of pupa +meconium+cocoon in each month, W_p for the mean dry weight of a thorax prey and N_i for the mean number of hornets produced each month by a colony.

To estimate the mean monthly pupa weight W_i, we sampled pupae from three nests, not used for the observations, collected in July, September and October to account for increase in mean hornet, and thus pupa, size along the life cycle of a colony (Rome et al. 2015). The pupa weight of August was considered equivalent to that of September, and that of November equivalent to that of October. Then the mean weight of a meconium and a cocoon was added to the monthly pupa weight. Since there is no technique available today to properly breed a hornet larva, we could not consider the energetic cost due to larvo-pupal respiration and the protein-rich liquid regurgitated to adults. Note that, as previously said, meconium represents all the faeces produced during the larva's life. Cocoon weight was also included because it is secreted by larvae's silk-producing glands.

Having noted that all prey pellets brought back by *V. velutina* workers had approximatively the same size, we assumed that they also have approximatively the same weight. We estimated the mean dry weight W_p of a pellet by weighing together 30 thoraces of honeybees dried in an oven at 57°C for 72 h.

The number N_i of hornets produced per months follows Rome et al. (2015). On average, it reached 630.5, 508.6, 739.9, 3441.3 and 831.2 hornets respectively from July to November.

Finally, to link these results to a potential impact of a hornet colony on beekeeping activities, we compared the average number of bees potentially consumed to the average number of bees produced in a beehive during the same period. If we consider a 30-day life-span of an adult bee (Neukirch 1982), the number of bees produced by a hive during the foraging period of a *V. velutina* colony would be the sum of its adult population in June, July, August, September and October. This is knowing that adults emerging in July partly come from larvae fed in June while those emerging in

November come from larvae fed in October. Based on data in the literature (summarized in Becher et al. 2014), we can estimate a population of 10, 20, 30, 25 and 25 thousand adult bees in June, July, August, September and October respectively for an average hive in temperate region. This amounts to 110,000 bees produced during the entire period.

Results

Prey spectrum

As a whole, from the 12,200 hornets captured, 2151 prey pellets and 1925 wood pellets have been collected.

We identified 2151 prey pellets at least at the order level using morphological characters. Among these, 2063 were selected for the molecular analysis and 1397 (67.7%) COI sequences were recovered. By comparison to Genbank, BOLD and/or our barcode library, it has been possible to identify 1388 (99.2%) prey to the species level, while the nine other prey were identified to higher level.

Morphological identification was confirmed by barcoding at 95% for orders, 67.3% for families, 61.7% for genera and 43% for species, knowing that the number of specimens morphologically unidentified greatly increased from order to species level. Barcoding also showed that 89.7% of the prey pellets morphologically identified as *Apis mellifera* were correctly recognized.

In our sample, prey collected by *V. velutina* include at least 141 species identified through DNA barcoding as well as 18 putative species identified at family or order levels (Table 1; S2). This prey spectrum includes 11 orders and 43 families of insects, three families of spiders and four families of vertebrates. While our sample gathered 159 species, the ACE index suggested that about 411.25 (SE = 13.51) different species were predated by *Vespa velutina* in the study area.

By number, the prey pellets are mainly composed of Hymenoptera (60.1%), among which *Apis mellifera* (38.1%) and social wasps (19.7%) dominate, and Diptera (29.9%), with Calliphoridae, Muscidae and Syrphidae each representing at least 5% of total prey. Moreover, dipteran prey pellets (102 spp.) appear much more diverse than hymenopteran ones (14 spp.). Other prey is represented by 3.1% of vertebrates and 9.2% of a wide spectrum of other arthropods, each occurring at very low frequencies.

Landscape influence

The foraging area of the 16 studied colonies globally comprised 48.35% of forest and semi-natural areas (CLC 3), 41.24% of agricultural areas (CLC 2), 9.90% of artificial surfaces (CLC 1), and only 0.51% of water bodies (CLC 5).

Vespa velutina prey were collected mainly in field and forest areas (Table S3). The main axis of the CoA distinguished the prey spectrum of colonies found in fields and forests from those found in urban and wet areas (Figure 2). The latter, much less sampled, comprised relatively more *Apis mellifera*, Mecoptera, Tachinidae flies and other (non-Vespidae) Hymenoptera than the colonies from forest and field areas. The second axis of the CoA illustrates the less pronounced diet difference between colonies from forest and field areas.

Temporal dynamics

The variation in number of prey caught along the season was best modelled by taking quadratic effects of dates and hours into account, but not the land types (Table S4; Figure 3A). All remaining effects were significant. This model suggests a peak of predation activity around 4 October. Predation is also at its highest around midday. The diversity of captured species followed a similar trend (Figure S1).

Among the sampled prey, the proportion of *Apis mellifera* significantly decreased during the season (Table S5, Figure 3B). The best model included date and hour effects, both linear and quadratic, and excluded the land type. With a similar model, the proportion of vespid wasps increased in early season before reducing in late season (Table S6, Figure 3C). Diptera proportion in the diet of *Vespa velutina* was best modelled by using only the date as fixed effect. The model showed a significantly higher proportion of Diptera early (July) and especially late (November) in the flight season of the hornet than during its peak of activity (Table S7, Figure 3D). Diptera seemed to make for most of the hornet diet from November onward, at which point the prey diversity strongly decreases.

Prey consumption of a colony

The mean fresh prey pellet and mean dry prey pellet weights were 33.3 mg and 11.7 mg respectively (N = 30). Dry pupa weighed on average 159.5 mg (N = 79, SD = 25.1) in July, 174.6 mg (N = 55, SD = 20.5) in September and 192.4 mg (N = 66, SD = 41.1) in October. So, the lowest estimate of the mean consumption of one larva is 13.6 prey in July, 14.9 prey in September and 16.4 prey in October. Combining these data with the mean number of individuals produced by a colony over a season (Rome et al. 2015), we could estimate that a colony needs on average 97,246.45 honeybee-like prey along its life cycle, which corresponds to a mean of 3.24 kg of prey's thoraces. Assuming that each prey weighs as much as a honeybee, and that one honeybee weighs 116.37 mg (N = 165 SE = 0.61 mg); (Bowen-Walker & Gunn 2001), an average colony would consume on average 11.32 kg of insects.

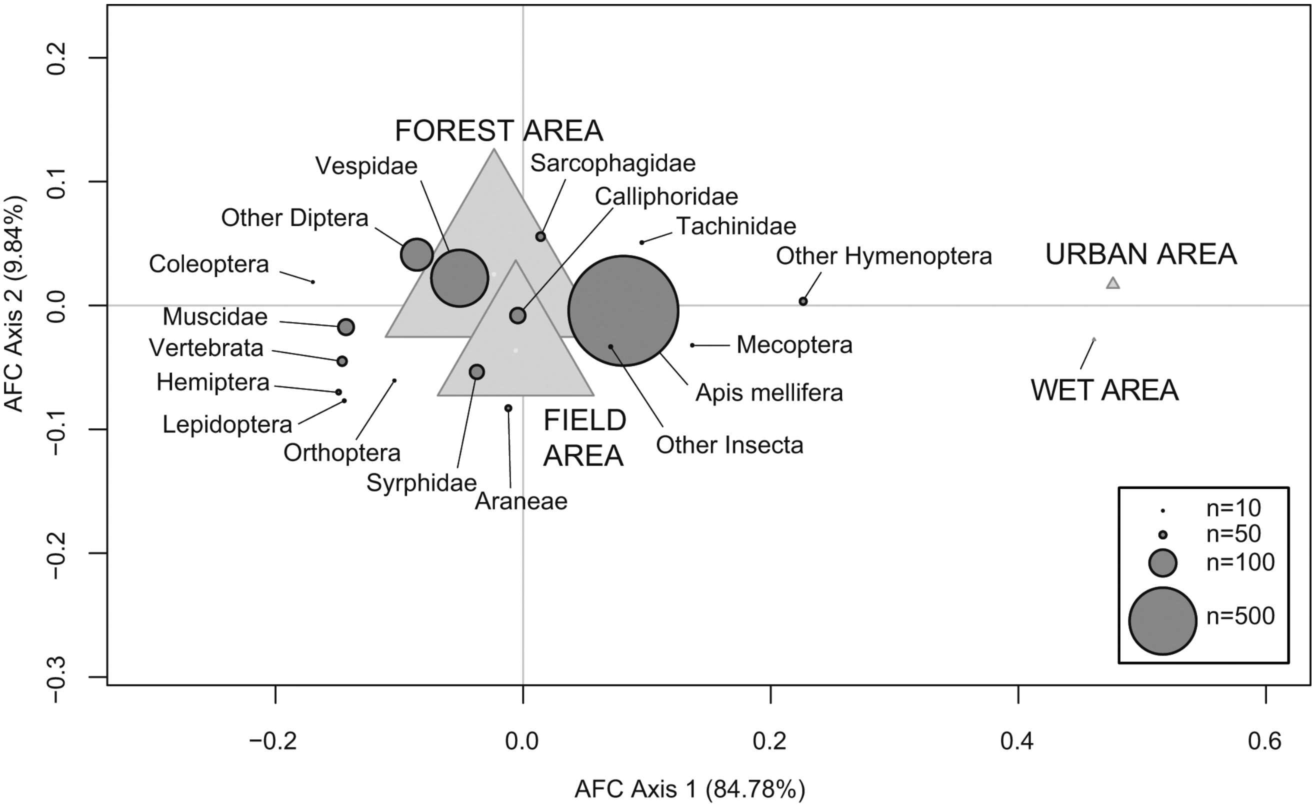

Figure 2. Results of the correspondence analysis on the prey groups relative to the land cover types in which the prey was captured. Only the two first axes are represented. Percentages indicate the amount of variation explained by each axis. Dot sizes illustrate the number of prey sampled in each group.

Discussion

Prey spectrum

Before its introduction in Europe, *Vespa velutina* was perceived as a predator focusing its attacks on honeybees and bumble bees (Williams 1988; Shah & Shah 1991; Abrol 1994). Its notorious hovering behaviour in front of beehives in France emphasized its reputation of bee killer (e.g. Monceau et al. 2014), although previous studies suggested that the species is preying on a wider diversity of insects (Van der Vecht 1957; Perrard et al. 2009). With 159 prey species found in our sample and with an estimated 411 species predated by the studied colonies, our results confirm that this species is a generalist predator.

Vespa velutina seems nonetheless to favour social Hymenoptera: more than half of the sampled prey are honeybees and social wasps other than hornets. There was also a non-negligible number of flies captured by the hornets. These abundances suggest that *Vespa velutina* would prey following an opportunistic pattern, attacking species of the right size that are abundant and with a high local density such as bees in front of a hive or flies around carrion or cattle (Perrard et al. 2011).

For the majority of the 22 known hornet species, the predation behaviour seems to match this description of opportunistic predators (Matsuura & Yamane 1990). Preference for brachyceran flies of *V. velutina* seems to be shared with a closely related species: *Vespa simillima* Smith, 1868. In the latter, flies make up to 60% of its diet. This preference may be related to the similar size of both *Vespa* species, which is on the lower side of size-range in hornets.

Nonetheless, the peculiar behaviour of *V. velutina* attacking honeybees in front of hives and the high proportion of honeybees in its diet suggest some kind of specialization. Other hornet species present some degree of diet specialization depending on the season or the locality: the European hornet *Vespa crabro* L., 1758 feeds mostly on cicadas in Japan (Matsuura 1984) and the great-banded hornet *Vespa ducalis* (Linnaeus, 1758) attacks mostly smaller social wasps (Sakagami & Fukushima 1957; Matsuura 1991). Specialization towards exploiting honeybees is well documented in another species: the giant hornet *Vespa mandarinia* Smith, 1852. This species has a unique way to exploit colonies of social Hymenoptera, including honeybees, using group predation. Workers attack the colonies as a group to annihilate the adults,

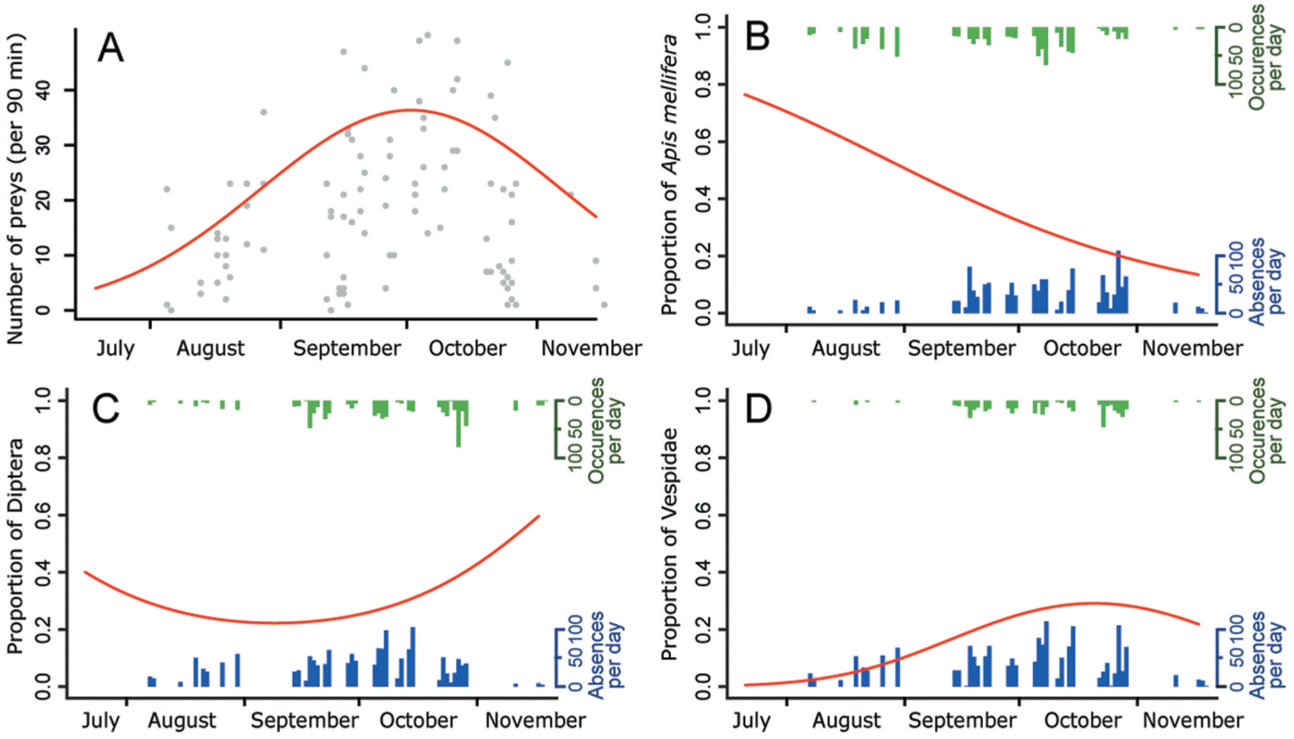

Figure 3. Evolution of the prey captured along the year. The x-axis represents the ordinal date, in days. **A**, Number of prey captured in a 90-minute session. The line models the evolution of these captures according to a linear model including date and hour as covariates, as well as nest type as random effect. The points illustrate the results of the 90-min collecting sessions; shorter session results were not represented. **B–D**, Proportion of prey types along the year. The line (red) illustrates the logistic regression of presence of a prey type among the prey, depending on the date (B, C & D) and hour (B & D), with nest identity as random effect. Top bars (green) indicate the number of prey of this type sampled per day. Bottom bars (blue) indicate the number of other prey sampled per day. Prey types: B, *Apis mellifera*; C, Diptera; D, Vespidae (social wasps).

then they collect the brood and resources (Matsuura & Sakagami 1973; Matsuura & Yamane 1990). This tendency of semi-specialization of hornets towards locally abundant prey could increase their foraging efficiency. It would be a strong evolutionary advantage for social wasps since their colonies require proteins in large quantities to feed the multitude of larvae in a growing nest. However, only *V. ducalis* has been recorded as an obligatory specialist towards social wasp prey (Matsuura 1984). Other hornet species, including *V. velutina*, retained enough plasticity in their behaviour to exploit a wide range of protein sources.

Landscape influence

The influence of the environment on the prey spectrum suggested by our data reinforce the idea of an opportunistic and generalist behaviour of *Vespa velutina*. While some prey such as *Apis mellifera* are part of every colony's diet, we found prey specific to colonies located in forest and in field areas. The diet was mainly characterized by its high proportion of social wasps and meat-flies, while colonies in open areas such as fields and cities captured more flower visitors such as bees and hoverflies, as well as spiders. These data further suggest that *V. velutina* preys mostly on species that it can find in abundance in the surroundings of the nest. Our results also show that there was no significant effect of the proportion of forest or semi-natural area in the nest surroundings on the number of prey, their diversity or the proportion of honeybees, hoverflies or social wasps captured. This result may in part be related to the limited number of nests that we could study long enough to include in the analyses. Further analyses to test the difference in predation between rural, urban and wet areas would be required, but getting authorizations to keep a nest alive long enough is often difficult, especially in urban areas.

Temporal dynamics

The predation dynamics suggest a peak of activity around late September and October (Figure 3A). Surprisingly, the proportion of honeybees in *V. velutina*'s diet seems to diminish later in the season, partly due to an increase in dipteran prey. Such a shift in diet may be related to the impact of *V. velutina*'s predation on beehives (Requier et al. 2019). This predation reduces the activity of honeybee foragers, which may in turn reduce their attractiveness as a prey source along the season. The number of available flies may also increase along the season relative to the number of available honeybees. An opposite trend was observed in a diet survey of *Vespula germanica* (Fabricius, 1793) from New Zealand (Harris 1996), in which dipteran prey was reduced in winter while lepidopteran prey increased. This trend was related to seasonal changes in prey abundance, which further emphasizes the impact of prey availability on the diet (Edwards 1980).

Prey consumption of a colony and its impact on the entomofauna

The opportunistic nature of *V. velutina*, which preys mostly on abundant species, suggests that this species has a milder impact on the entomofauna than its predation on honeybees could suggest. However, even a generalist invasive predator can have an impact on its environment, depending on the level of predation pressure it exerts on the local entomofauna (Snyder & Evans 2006).

Social wasps, like other social insects, have an especially strong impact on their direct surroundings (Beggs et al. 2011). Harris & Oliver (1993) estimated that a colony of *Vespula germanica* can predate around 1.8 kg of prey per season in New-Zealand, which corresponds to 236,842 prey. In some special cases, wasp nests can become enormous and their colony consumes more than 200 kg of prey (Pickett et al. 2001). While the predation of *Vespa velutina* does not reach such extreme values, it seems to have on average a higher impact than its smaller relatives of the genus *Vespula*. By focusing on larger prey, a colony of *V. velutina* may require less prey, but seems to consume a higher biomass of insects, with a mean of about 97,000 prey (11.31 kg) per season of equivalent honeybees (Bowen-Walker & Gunn 2001). It should be noted again that this impact is underestimated as metabolic losses due to larvo-pupal respiration and the protein-rich liquid regurgitated to adults were not considered. Moreover, the largest colonies are about twice as populous as the average and could therefore have twice the impact on the surrounding insects (Rome et al. 2015).

When comparing these results to the number of bees produced by a beehive in the same period, it appears that an average colony of *V. velutina* could consume about as many bees as those produced by a single hive. Of course, this comparison only aims at scaling the impact of a colony on the surrounding fauna: indeed one colony of *V. velutina* never consumes an entire hive since its predation pressure is not focused on a single hive of an apiary (Monceau et al. 2014), nor on the honeybees only as shown by our results. However, as honeybees represent in our results 39% of its diet, an average hornet colony could prey on about 40% of the individuals produced by one hive, which is non-negligible. While the greatest impact of the hornets is due to their presence hovering in front of beehives, which results in the disruption of the foraging activity (called "foraging paralysis") of the bee colonies, the predation *per se* appears to mainly threaten isolated or poorly populated and unhealthy beehives (Requier et al. 2019). Foraging paralysis increases the risk for a bee colony to die after wintering but the hornet impact can be significantly reduced by adding a simple protective wire mesh to the hive (Requier et al. 2019).

On the other hand, while the majority of preyed insects are pollinators with variable efficiency, wild bees (bumblebees and solitary bees, excluding wild honeybee colonies) represent only 0.02% of the *V. velutina*'s prey recorded in this study. The predation impact on these main pollinators appears therefore very low. However, a long-term monitoring of pollination success in presence or absence of *V. velutina* would be required before any conclusion on the actual impact of the hornet on pollination services.

As we currently lack data about the state of insect populations other than honeybees before the invasion, we cannot assess whether *V. velutina*'s predation may have had an impact on them. However, the mainly opportunistic nature of *V. velutina*'s predation behaviour suggests that the hornet has a limited impact on endangered entomofauna. If *V. velutina* catches non-abundant species by chance, it could be expected that few specimens of rare and endangered species are caught by the hornet, since they are locally scarce. Further studies are therefore required to compare *V. velutina*'s preying behaviour to local prey abundances, in order to clarify whether it preys randomly or could focus occasionally on some rare species and thus impact their populations. Particular attention should be paid to insects nesting in aggregation during the fall, like autumnal *Colletes* bees, which are sometimes actively predated by *V. velutina* (J. Raingeard, pers. comm.). A strong impact of the hornet could also be expected through competition with other predators of similar arthropods (Snyder & Evans 2006; Choi et al. 2012; Cini et al. 2018; Ikegami et al. 2020).

Since its introduction in Europe, the development of methods to control *V. velutina* without scientific evaluation is thriving; they range from poison baiting to rifle shooting on nests (Turchi & Derijard 2018). The most widely used method is sugar-beer trapping although less than 1% of the total catches are hornets and composed a wide diversity of other insects (Dauphin & Thomas 2009; Demichelis et al. 2014; Rojas-Nossa et al. 2018). A one litre trap would catch around 30,000 non targeted insects, and around 20,000 if they are placed after June and in the vicinity of beehives (Rome et al. 2011a). Although biomass was not estimated, and most of the caught insects were of small sizes (see the regularly updated list for French territories: https://inpn.mnhn.fr/espece/jeudonnees/22213), four to six small traps would catch as many insects as a *V. velutina* colony could prey. Control methods thus seem to be a greater threat to insect biodiversity than *V. velutina* predation. The effectiveness of most of these methods has not been demonstrated so far (Edwards 1980; Beggs et al. 2011; Monceau et al. 2012; Turchi & Derijard 2018), so that their impact on biodiversity probably adds up to that of *V. velutina*. The hornet is mostly present in degraded environments, while natural ones are mostly unsuitable (Fournier et al. 2017), suggesting that its impact on rare species is probably low. Instead of using trapping methods that negatively affect wild population of insects, it would be better to try to control the invasive hornet, whose eradication is illusory, by using only scientifically validated methods and developing protective or repulsing strategies to reduce its impact on beekeeping.

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Authors' contributions

QR and AP contribute equally to the paper. FM, QR, CV and AP conceived the idea, designed methodology and collected the prey pellets; CV and FM made the morphological identifications; FM, AQ, DZ and QR made the molecular identifications; AP, CF, QR and CV analysed the data, and AP, QR and CV wrote the first version of the manuscript; all authors contributed critically to the drafts and gave final approval for publication.

Supplementary material

Supplemental data for this article can be accessed here.

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