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

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

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

40 **Résumé. Le spectre de proies du frelon asiatique (*Vespa velutina*) en France ne se**
41 **limite pas aux abeilles.**

42 Pour comprendre l'impact d'une espèce prédatrice exotique et envahissante, il faut disposer
43 de données sur son régime alimentaire. *Vespa velutina* Lepeletier, 1836 est un prédateur
44 bien connu des abeilles domestiques, accidentellement introduit en France avant 2004 et qui
45 colonise, depuis, le continent européen. Malgré de nombreuses études et son impact
46 reconnu sur les activités apicoles, il existe très peu de données sur son régime alimentaire
47 dans les régions envahies d'Europe. Pour combler cette lacune, nous avons suivi seize nids
48 dans le sud-ouest de la France entre 2008 et 2010. En combinant des approches
49 morphologiques et moléculaires (barcode), nous avons identifié 2151 boulettes de proies et
50 démontré que *V. velutina* se comporte comme un prédateur généraliste, chassant des

51 abeilles domestiques (38.1 %), des mouches (29.9 %) et des guêpes sociales (19.7 %), ainsi
52 qu'un large spectre d'autres animaux (pas moins de 159 espèces identifiées). Le spectre de
53 proies varie selon l'environnement du nid ; les colonies urbaines chassant plus d'abeilles
54 domestiques et les forestières plus de guêpes sociales. L'intensité de la prédation atteint son
55 maximum début octobre. En comparant le poids sec des boulettes de proies avec celui des
56 larves de *V. velutina* et en tenant compte de la dynamique de la colonie, nous avons estimé
57 qu'une seule colonie de frelon pouvait consommer en moyenne 11,32 kg de biomasse
58 d'insectes en une saison. Dans l'ensemble, nos résultats suggèrent que *V. velutina* est un
59 prédateur opportuniste, ciblant surtout les proies localement abondantes. Bien que cette
60 espèce puisse avoir un impact sur les abeilles domestiques, son comportement généraliste et
61 opportuniste sur les insectes abondants suggère un impact limité sur les espèces sauvages.
62 Alors que, par ailleurs, les tentatives de gestion de cette espèce à l'aide de pièges non
63 sélectifs ont un impact beaucoup plus important sur l'entomofaune sauvage et domestiquée
64 que le frelon lui-même.

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

66 **Introduction**

67 Predation underlies the most spectacular damages induced by invasive alien species in invaded
68 ecosystems, sometimes cascading down to primary producers (Bruno et al. 2005; David et al.
69 2017; Graham et al. 2018). Intensification of human transport and commerce around the world
70 has led to widespread movement of species outside of their native range (Hulme 2009; Frost et al.
71 2019), including many arthropod generalist predators that feed not only upon herbivores but also
72 upon other predators and detritivores. Due to their complex trophic role, these invaders can have
73 particularly widespread impacts on the communities they invade (Snyder & Evans 2006).
74 Documenting dietary spectrum of invasive predators is not only necessary to assess their direct
75 impact on prey but also to better define their niche width and understand how they might alter
76 ecosystem services such as biological control or pollination.

77 The recent introduction of the Yellow-legged Asian hornet *Vespa velutina* Lepeletier,
78 1836, in France was the first successful invasion of an exotic Vespidae in Europe (Rasplus et al.
79 2010; Beggs et al. 2011). This species is of great concern among public authorities and
80 beekeepers because of its rapid multiplication and high impact on beekeeping due to its strong
81 predation on honeybees (Perrard et al. 2009) and its hawking behaviour that disrupts bee colony
82 foraging (Rortais et al. 2010; Monceau et al. 2013; Arca et al. 2014; Requier, Rome, Chiron, et
83 al. 2019). The species was observed for the first time in 2004 in Southwest France and then it
84 rapidly spread across most of French districts. Between 2010 and 2017, it successively
85 established in seven neighbouring countries: Spain, Portugal, Italy, Germany, Belgium, UK and
86 the Netherlands, and adults have also been observed in Switzerland (Rome & Villemant 2015;
87 Burri-Schmassmann et al. 2017; Barbet-Massin et al. 2018). Climatic niche modelling suggests
88 that *Vespa velutina* could spread throughout Europe (Villemant et al. 2011; Fournier et al. 2017).
89 Taking into account recent climate change scenarios and the observed enlargement of its climatic
90 niche, future range expansion may even be more rapid than expected (Barbet-Massin et al. 2013;
91 Barbet-Massin et al. 2018).

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

100 mass of released faeces is called meconium and will remain at the bottom of the cell after the
101 adult emerges (Rome et al. 2015).

102 While *V. velutina* arrived in Europe more than a decade ago, our knowledge of its diet
103 spectrum still relies on very limited data: anecdotal reports from its original range (Williams
104 1988; Abrol 1994) and only preliminary data in France (Perrard et al. 2009; Quentin Rome et al.
105 2011; Villemant et al. 2014). These studies suggest that social hymenopterans and brachyceran
106 flies are its main prey, although its scavenging behaviour on dead vertebrates and shrimps, in the
107 field or in street markets have been reported (Williams 1988). Studies quantifying its diet in the
108 invaded range are required to estimate the potential impact of this species on the local fauna. In
109 addition to its prey spectrum, the pressure of a colony of *V. velutina* on European honeybees is
110 also under-studied, considering its reputation as a bee-hawking predator in Asia and in Europe
111 (Abrol 1994; Monceau et al. 2013). Beehive mortality have helped to estimate such an impact
112 (Requier, Rome, Chiron, et al. 2019), but no real quantification is available from the literature
113 (Villemant et al. 2014).

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

121 **Material and methods**

122 *Collecting sites*

123 The study was performed over 3 years (2008-2010) from August to October/November, in the
124 Dordogne district, Southwest of France. These years, the colonized area was restricted to this
125 region. This district is close to the point of introduction and had relatively high and stable nest
126 densities. Sixteen colonies were studied for 1 day to up to 4 months depending on the duration
127 the landowners accepted to keep a living nest on their land (Fig. 1, Table S1).

128 *Prey collection*

129 Once a nest was located, depending on the opportunity to access the nest and on its destruction
130 date, we sampled workers to rob their prey almost every two weeks, either until the nest
131 destruction or until the end of the season. Sampling sessions took place from 1 h after dawn to
132 1 h before dusk and lasted 90 min. Any two sessions were separated by at least a 30 min break to
133 reduce the stress of the colony. Due to weather conditions or a too strong disturbance of the
134 colony resulting in hornets stopping to forage, 14 sessions out of 138 did not last 90 minutes. As
135 a whole, we performed 138 sessions corresponding to 199 h 23 min of sampling (Table S1).

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

142 ***Prey identification***

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

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

152 The partial COI gene was amplified using the primers LepF1 and LepR1 (Hebert et al.
153 2004). Each PCR contained 2 µl of 10 X PCR buffer, 13,94 µL of distilled water (DNase free),
154 2.5 mM MgCl₂, 5 % DMSO, 0.26 mM dNTPs, 0.3 µM of each primer, 1.5 units of Qiagen Taq
155 polymerase and 1 µl of DNA template, conducting to a final reaction volume of 20 µl. The PCR
156 thermal regime consisted of: one cycle of 1 min initial denaturation at 94 °C, 35 cycles of 30 s at
157 94 °C, 30 s hybridization at 47 °C, followed by an extension of 50 s at 72 °C and a final cycle of
158 5 min at 72 °C. PCR products were electrophoresed in 1 % agarose gel stained with ethidium
159 bromide and visualized under UV light. The positive PCRs were sequenced in both directions
160 using the Sanger method and the sequences were assembled with CodonCode Aligner
161 (CodonCode Corporation).

162 The molecular identification was performed comparing the COI sequences obtained from
163 the prey pellets with those available in Genbank and BOLD, using the BLAST and the
164 Identification Engine tools, respectively. In addition, we created our own barcode reference

165 library of local flies, since a great number of flies were identified among the pellets based on
166 morphology. We barcoded 104 flies identified at the species level by specialists: 78 hoverflies
167 (Syrphidae, 41 species) and 26 carrion and flesh flies (Muscidae, Calliphoridae, Sarcophagidae,
168 26 species). The extraction was carried out with the same protocol used for the pellets. For the
169 amplification we used either the primers described above or we amplified the COI gene in two
170 fragments, using the primer combinations Lep-F1/COI-intR1 and COI-intF7/Lep-R1 (Hebert et
171 al. 2004; Zuccon et al. 2012), with COI-intF7: 5'-GAAAGAGGAGTTGGAACAGGTTGAAC-
172 3'. The new fly sequences have been submitted to GenBank under the accession numbers
173 MW077745-MW077848(Table S2).

174 *Analyses*

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

177 *Prey spectrum*

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

180 *Landscape influence*

181 To investigate the influence of the landscape surrounding the nests on the diet of *V. velutina*, we
182 performed a correspondence analysis (CoA) of prey per land-use types. We computed the
183 proportion (%) of four main land-uses within buffers of 2 km radius centred on the nests (Fig. 1).
184 The choice of buffer size reflects the foraging range of workers reported from experimental and
185 field studies (Budge et al. 2017; Sauvard et al. 2018; Kennedy et al. 2018). The land-use

186 categories were extracted from the level one of the Corine Land Cover (CLC) categories:
187 artificial surfaces (CLC1); agricultural areas (CLC2); forest and semi natural areas (CLC3) and
188 water bodies (CLC 5) (Union Européenne - SOeS 2011).

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

196 *Seasonal dynamics of predation*

197 In order to test for changes in the level of predation and in the content of the *Vespa velutina* diet
198 throughout the season, we analysed the total number of prey, as well as the percentages of either
199 honey bees, Vespidae or Diptera species, brought back to the nest per 90 minutes sessions using
200 generalized linear mixed models. We only included in the analysis data from nests sampled for at
201 least 5 sessions. Since the landscape diversity around the 8 remaining nests was very limited,
202 with only one nest in urban area and no nest in wet area, the land type was estimated using the
203 proportion of forest and semi-natural areas in a radius of 2 km around the nest.. Explanatory
204 variables were date and hour as well as their quadratic terms, land type as fixed effects, and nest
205 identity as random effect. Nine collecting sessions lasted less than 90 minutes, so the session
206 duration was also taken into account to model the number of prey and their overall diversity. All
207 variables were scaled beforehand. Poisson and binomial error distributions were used for the total
208 number of prey and the percentages of prey groups, respectively. Model simplification was

209 performed following the Akaike Information Criterion (AIC). Models were performed using the
210 ‘glmer’ function of the package ‘lme4’ (Bates et al. 2015) and the effects tested using the
211 ‘Anova’ function of the R package ‘car’ (Fox & Weisberg 2019).

212 *Prey consumption of a colony*

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

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

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

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

228 Having noted that all prey pellets brought back by *V. velutina* workers had
229 approximatively the same size, we assumed that they also have approximatively the same weight.

230 We estimated the mean dry weight W_p of a pellet by weighting together 30 thoraces of honeybees
231 dried in an oven at 57°C for 72 hours.

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

234 Finally, to link these results to a potential impact of a hornet colony on beekeeping
235 activities, we compared the average number of bees potentially consumed to the average number
236 of bees produced in a beehive during the same period. If we consider a 30-days life-span of an
237 adult bee (Neukirch 1982), the number of bees produced by a hive during the foraging period of a
238 *V. velutina* colony would be the sum of its adult population in June, July, August, September and
239 October. Knowing that adults emerging in July partly come from larvae fed in June while those
240 emerging in November come from larvae fed in October. Based on data in the literature
241 (summarized in Becher et al. 2014), we can estimate a population of 10, 20, 30, 25 and 25
242 thousands of adult bees in June, July, August, September and October respectively for an average
243 hive in temperate region. Which amounts to 110,000 bees produced during the entire period.

244 **Results**

245 *Prey spectrum*

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

248 We identified 2151 prey pellets at least at the order level using morphological characters.
249 Among these, 2063 were selected for the molecular analysis and 1397 (67.7 %) COI sequences
250 were recovered. By comparison to Genbank, BOLD and/or our barcode library, it has been

251 possible to identify 1388 (99.2 %) prey to the species level, while the 9 other prey were identified
252 at higher level.

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

258 In our sample, prey collected by *V. velutina* include at least 141 species identified through
259 DNA barcode as well as 18 putative species identified at family or order levels (Table 1; S2).
260 This prey spectrum includes 11 orders and 43 families of insects, 3 families of spiders and 4
261 families of vertebrates. While our sample gathered 159 species, the ACE index suggested that
262 about 411.25 (se=13.51) different species were predated by *Vespa velutina* in the study area.

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

269 ***Landscape influence***

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

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

279 *Temporal dynamics*

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

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

294 ***Prey consumption of a colony***

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

305 **Discussion**

306 ***Prey spectrum***

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

314 *Vespa velutina* seems nonetheless to favour social Hymenoptera: more than half of the
315 sampled prey is honeybees and social wasps other than hornets. There was also a non-negligible

316 amount of flies captured by the hornets. These abundances suggest that *Vespa velutina* would
317 prey following an opportunistic pattern, attacking species of the right size that are abundant and
318 with a high local density such as bees in front of a hive or flies around carrions or cattles (Perrard
319 et al. 2011).

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

325 Nonetheless, the peculiar behaviour of *V. velutina* attacking honeybees in front of hives
326 and the high proportion of honeybees in its diet suggest some kind of specialization. Other hornet
327 species present some degree of diet specialization depending on the season or the locality: the
328 European hornet *Vespa crabro* L., 1758 feeds mostly on cicadas in Japan (Matsuura 1984) and
329 the great-banded hornet *Vespa ducalis* (L., 1758) attacks mostly smaller social wasps (Sakagami
330 & Fukushima 1957; Matsuura, Makoto 1991). Specialization towards exploiting honeybees is
331 well documented in another species: the giant hornet *Vespa mandarinia* Smith, 1852. This
332 species has a unique way to exploit colonies of social Hymenoptera, including honeybees, using
333 group predation. Workers attack the colonies as a group to annihilate the adults, then they collect
334 the brood and resources (Matsuura & Sakagami 1973; Matsuura & Yamane 1990). This tendency
335 of semi-specialization of hornets towards locally abundant prey could increase their foraging
336 efficiency. It would be a strong evolutionary advantage for social wasps since their colonies
337 require proteins in large quantities to feed the multitude of larvae in a growing nest. However,
338 only *V. ducalis* has been recorded as an obligatory specialist towards social wasp prey (Matsuura

339 1984). Other hornet species, including *V. velutina*, retained enough plasticity in their behaviour to
340 exploit a wide range of protein sources.

341 ***Landscape influence***

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

355 ***Temporal dynamics***

356 The predation dynamics suggest a peak of activity around late September and October (Fig. 3A).
357 Surprisingly, the proportion of honeybees in *V. velutina*'s diet seems to diminish along the late
358 season, partly due to an increase in dipteran prey. Such a shift in diet may be related to the impact
359 of *V. velutina*'s predation on beehives (Requier, Rome, Chiron, et al. 2019). This predation
360 reduces the activity of honeybee foragers, which may in turn reduce their attractiveness as a prey

361 source along the season. The number of available flies may also increase along the season
362 relative to the number of available honeybees. An opposite trend was observed in a diet survey of
363 *Vespula germanica* (Fabricius, 1793) from New Zealand (Harris 1996), in which dipteran prey
364 was reduced in winter while lepidopteran prey increased. This trend was related to seasonal
365 changes in prey abundance, which further emphasizes the impact of prey availability on the diet
366 (Edwards 1980).

367 ***Prey consumption of a colony and its impact on the entomofauna***

368 The opportunistic nature of *V. velutina*, which preys mostly on abundant species, suggests that
369 this species has a milder impact on the entomofauna than its predation on honeybees could
370 suggest. However, even a generalist invasive predator can have an impact on its environment,
371 depending on the level of predation pressure it exerts on the local entomofauna (Snyder & Evans
372 2006).

373 Social wasps, like other social insects, have an especially strong impact on their direct
374 surrounding (Beggs et al. 2011). Harris & Oliver (1993) estimated that a colony of *Vespula*
375 *germanica* can predate around 1.8 kg of prey per season in New-Zealand, which corresponds to
376 236,842 prey. In some special cases, wasp nests can become enormous and their colony consume
377 more than 200 kg of prey (Pickett et al. 2001). While the predation of *Vespa velutina* does not
378 reach such extreme values, it seems to have on average a higher impact than its smaller relatives
379 of the genus *Vespula*. By focusing on larger prey, a colony of *V. velutina* may require less prey,
380 but seems to consume a higher biomass of insects, with a mean of about 97,000 prey (11.31 kg)
381 per season of equivalent honeybees (Bowen-Walker & Gunn 2001). It should be noted again that
382 this impact is underestimated as metabolic losses due to larvo-pupal respiration and the protein-
383 rich liquid regurgitated to adults were not considered. Moreover, the largest colonies are about

384 twice as populous as the average and could therefore have twice the impact on the surrounding
385 insects (Rome et al. 2015).

386 When comparing these results to the number of bees produced by a beehive in the same
387 period, it appears that an average colony of *V. velutina* could consume about as many bees as the
388 ones produced by a single hive. Of course, this comparison only aims at scaling the impact of a
389 colony on the surrounding fauna: indeed one colony of *V. velutina* never consumes an entire hive
390 since its predation pressure is not focused on a single hive of an apiary (Monceau et al. 2014), nor
391 on the honeybees only as shown by our results. However, as honeybees represent in our results
392 39 % of its diet, an average hornet colony could prey on about 40 % of the individuals produced
393 by one hive, which is non-negligible. While the greatest impact of the hornets is due to their
394 presence hovering in front of beehives, which results in the disruption of the foraging activity
395 (called “foraging paralysis”) of the bee colonies, the predation *per se* appears to mainly threaten
396 isolated or poorly populated and unhealthy beehives (Requier, Rome, Chiron, et al. 2019).
397 Foraging paralysis increases the risk for a bee colony to die after wintering but the hornet impact
398 can be significantly reduced by adding a simple protective wire mesh to the hive (Requier, Rome,
399 Villemant, et al. 2019).

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

406 As we currently lack data about the state of insect populations other than honeybees
407 before the invasion, we cannot assess whether *V. velutina*’s predation may have had an impact on

408 them. However, the mainly opportunistic nature of *V. velutina*'s predation behaviour suggests
409 that the hornet has a limited impact on endangered entomofauna. If *V. velutina* catches non-
410 abundant species by chance, it could be expected that few specimens of rare and endangered
411 species are caught by the hornet, since they are locally scarce. Further studies are therefore
412 required to compare *V. velutina*'s preying behaviour to local prey abundances, in order to clarify
413 whether it preys randomly or could focus occasionally on some rare species and thus impact their
414 populations. Particular attention should be paid to insects nesting in aggregation during the fall,
415 like autumnal *Colletes* bees, which are sometimes actively predated by *V. velutina* (J. Raingeard,
416 com. pers.). A strong impact of the hornet could also be expected through competition with other
417 predators of similar arthropods (Snyder & Evans 2006; Choi et al. 2012; Cini et al. 2018; Ikegami
418 et al. 2020).

419 Since its introduction in Europe, the development of methods to control *V. velutina*
420 without scientific evaluation is thriving; they range from poison baiting to rifle shooting on nests
421 (Turchi & Derijard 2018). The most widely used method is sugar-beer trapping although less
422 than 1 % of the total catches are hornets and composed a wide diversity of other insects (Dauphin
423 & Thomas 2009; Demichelis et al. 2014; Rojas-Nossa et al. 2018). A 1 liter trap would catch
424 around 30,000 non targeted insects, and around 20,000 if they are placed after June and in the
425 vicinity of beehives (Q. Rome et al. 2011). Although biomass was not estimated, and most of the
426 caught insects were of small sizes (see the regularly updated list for French territories:
427 <https://inpn.mnhn.fr/espece/jeudonnees/22213>), four to six small traps would catch as many
428 insects as a *V. velutina* colony could prey. Control methods thus seem to be a greater threat to
429 insect biodiversity than *V. velutina* predation. The effectiveness of most of these methods has not
430 been demonstrated so far (Edwards 1980; Beggs et al. 2011; Monceau et al. 2012; Turchi &
431 Derijard 2018), so that their impact on biodiversity probably adds up to that of *V. velutina*. The

432 hornet is mostly present in degraded environments, while natural ones are mostly unsuitable
433 (Fournier et al. 2017), suggesting that its impact on rare species is probably low. Instead of using
434 trapping methods that negatively affect wild population of insects, it would be better to try to
435 control the invasive hornet, whose eradication is illusory, by using only scientifically validated
436 methods and developing protective or repulsing strategies to reduce its impact on beekeeping.

437 **Author contributions**

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

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633

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

Prey group	Family Nb	Species Nb	Specimen Nb
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. <i>Apis mellifera</i>	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

639

640

641 **Figure captions**

642 Figure 1. A. Total number of prey pellets caught (size of red spot) for each 16 studied colonies
643 and CLC of the studied area. B. Detailed land use in foraging areas (blue circles) of 4 *V. velutina*
644 colonies near the city of Sarlat-la-Canéda (Dordogne). Corine Land Cover codes: CLC 1
645 Artificial surfaces, CLC 2 Agricultural areas, CLC 3 Forests and semi-natural areas, CLC 5
646 Water bodies.

647
648 Figure 2. Results of the Correspondence analysis on the prey groups relative to the land cover
649 types in which the prey was captured. Only the two first axes are represented. Percentages
650 indicate the amount of variation explained by each axis. Dot sizes illustrate the number of prey
651 sampled in each group.

652
653 Figure 3. Evolution of the prey captured along the year. The x-axis represents the ordinal date, in
654 days. A. Number of prey captured in a 90-minute session. The line models the evolution of these
655 captures according to a linear model including date and hour as covariates, as well as nest type as
656 random effect. The points illustrate the results of the 90-minutes collecting sessions, shorter
657 session results were not represented. B, C and D. Proportion of prey types along the year. The
658 line (red) illustrates the logistic regression of presence of a prey type among the prey, depending
659 on the date (B, C & D) and hour (B & D), with nest identity as random effect. Top bars (green)
660 indicate the number of prey of this type sampled per day. Bottom bars (blue) indicate the number
661 of other prey sampled per day. Prey types: B. *Apis mellifera*; C. Diptera; D. Vespidae (social
662 wasps).

663

664 **Supplementary materials**

665 Table S1. Sampling summary by month. Lines in bold represent respectively the total number of
666 nests sampled, of sampling days, of sessions and the total duration of sampling of each month.
667 Regular lines represent the median, minimum and maximum number of days, sessions or the
668 duration nests were sampled each month.

669

670 Table S2. List of prey collection reference. MNHN_CollectionID is the catalog number of the
671 voucher in the MNHN-Paris Collection

672 https://science.mnhn.fr/institution/mnhn/collection/ey/item/search/form?lang=en_US The
673 complete informations on the specimens is also available in GenBank under the accession
674 numbers MW077745-MW077848.

675

676 Table S3. List of prey pellets identification. CLC correspond to the percentage of each Corine
677 Land Cover code around the monitored nest. Number_Vespa_caught, PreyPellet and
678 WoodPellets correspond to the number of the total corresponding session of capture.

679 MNHN_CollectionID is the catalog number of the voucher in the MNHN-Paris Collection

680 https://science.mnhn.fr/institution/mnhn/collection/ey/item/search/form?lang=en_US The
681 complete and updated list is also available in the INPN website

682 <https://inpn.mnhn.fr/espece/jeudonnees/40455>

683

684 Table S4. Fixed effects of number of prey collected per 90 minutes according to a generalized
685 linear mixed model following a Poisson distribution, with the site as a random effect.

686

687 Table S5. Fixed effects of the proportion of *Apis mellifera* collected among the prey of *V.*
688 *velutina*, per 90 minutes, according to a generalized linear mixed model following a binomial
689 distribution, with the site as a random effect.

690

691 Table S6. Fixed effects of the proportion of vespid wasps collected among the prey of *V.*
692 *velutina*, per 90 minutes, according to a generalized linear mixed model following a binomial
693 distribution, with the site as a random effect.

694

695 Table S7. Fixed effects of number of prey collected per session. Fixed effects of the proportion of
696 Diptera collected among the prey of *V. velutina*, per 90 minutes, according to a generalized linear
697 mixed model following a binomial distribution, with the site as a random effect.

698

699 Figure S1. Evolution of the number of species captured per 90 minutes along the year. The x-axis
700 represents the ordinal date. Each dot represents the number of prey captured in a session this day.
701 The line models the evolution of these captures according to a linear model including date, hour
702 and area type as covariates, as well as nest location as random effect.

703