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1 **Spatial distribution of *Vespa velutina*-mediated beekeeping risk in**
2 **France and Germany**

3
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28

29 **Abstract**

30 The Yellow-legged hornet (*Vespa velutina nigrithorax*) was accidentally brought to south-
31 western of France in 2004 and rapidly spread throughout France and neighbouring coun-
32 tries. This predator of insect hunts honey bees leading to a hornet-mediated beekeeping
33 risk (HBR) with potential mortality of honey bee colonies and important economic costs.
34 However, the spatial distribution of HBR is not yet assessed and is urgently required to
35 formulate suitable management plans in Western Europe. We carried out a two-year citi-
36 zen science survey in France and Germany in order to assess the spatial distribution of (1)
37 the hornet and (2) HBR, and to (3) determine the environmental factors involved. A total of
38 1697 beekeepers responded to the survey. The hornet was established throughout the
39 French territory as expected, and mostly detected near the French border in Germany. We
40 found that HBR was substantially lower in Germany than in France. Temperature had a
41 positive effect on both the hornet presence and HBR whereas the distance to the introduc-
42 tion point had a negative effect, both in France and Germany. These results suggest that
43 the impact of *V. velutina* on beekeeping is not homogenous throughout the invasion range
44 and could be reduced on the eastern front due to continental climate. Considering HBR
45 spatial variability could help formulating regionally adapted management plans to limit *V.*
46 *velutina* impacts on biodiversity, human health and economic sectors.

47

48 **Keywords:** *Apis mellifera*, expansion range, invasive species, risk assessment, *Vespa*
49 *velutina*, Yellow-legged hornet

50

51 **Key message**

- 52 • The Yellow-legged hornet impacts honey bee survival and beekeeping activity in
53 Western Europe
- 54 • Little is known on the spatial distribution of the hornet-mediated beekeeping risk
55 (HBR)
- 56 • We assessed HBR across France and Germany over two years
- 57 • HBR was substantially lower in Germany than in France and negatively affected by
58 temperature and distance to the introduction point
- 59 • Considering HBR spatial variability could help formulating regionally adapted man-
60 agement plans

61

62 **Author Contribution Statement**

63 F.R. and Q.R. conceived the ideas and deigned methodology; F.R., F.N. and Q.R. col-
64 lected the data; F.R. analysed the data; F.R. and S.R.N. wrote the paper and all authors
65 contributed significantly to the drafts and gave their final approval for publication.

66

67 **Introduction**

68 Wild and managed pollinators are suffering a combination of pressures including environ-
69 mental factors (e.g. pesticides and lack of flowers), biotic factors (e.g. parasites, patho-
70 gens and predators) and a lack of genetic diversity that affects populations, ecosystem
71 services and related food security (Potts et al. 2010, 2016). In addition, the interaction be-
72 tween these pressures can generate synergistic effects increasing their impacts (Goulson
73 et al. 2015, Henry et al. 2017). Among these pressures, the Yellow-legged hornet, *Vespa*
74 *velutina nigrithorax* represents a relatively new biotic pressure upon the Western honey
75 bee, *Apis mellifera* in Western Europe. *V. velutina* is native to China and was accidentally
76 introduced to southwestern France in 2004 (Arca et al. 2015). This species quickly spread
77 throughout France and beyond (Rome and Villemant 2023). As early as 2010, sightings of
78 the species were recorded successively in Spain (Lopez et al. 2011), Portugal (Grosso-
79 Silva and Maia 2012), Belgium (Rome et al. 2013), Italy (Bertolino et al. 2016), Germany
80 (Witt 2015), Great Britain (Budge et al. 2017), Switzerland (Sciences Switzerland 2017),
81 the Netherlands (Smit et al. 2017), and Luxembourg (Ries et al. 2021). Currently, *V. ve-*
82 *lutina nigrithorax* is a subspecies of Union Concern included in the EU list of invasive alien
83 species (Regulation EU No 1143/2014 of the European Parliament and of the Council).

84 Its expansion in Western and Central Europe is explained both by natural disper-
85 sal mechanisms of *V. velutina* but also by the effects of anthropogenic facilitation of long-
86 distance dispersal via the transport of goods (trucks, trains, etc.) creating new queen intro-
87 duction areas (Robinet et al. 2018; Husemann et al. 2020). Previous studies assessed the
88 dispersion range of this invasion and defined climate (e.g. temperature or precipitation;
89 Villemant et al. 2011, Barbet-Massin et al. 2013), habitat (e.g. artificial surfaces such as
90 urban areas; Fournier et al. 2017) and distance to the introduction place (located in the

91 south-west, in the Lot et Garonne department; Robinet et al. 2018) as robust predictors of
92 *V. velutina* invasion range. Moreover, scientific projections estimate that the expansion of
93 *V. velutina* could continue, or even accelerate under the impulse of climate change (Bar-
94 bet-Massin et al. 2013). In this sense, studies have reported other areas of introduction
95 around the world, such as South Korea (Kim et al. 2006) and Japan (Ueno et al. 2014).

96 *V. velutina* is an important predator of honey bees in Western Europe. The preda-
97 tion activity of *V. velutina* on honey bees increases during the summer and reaches its
98 peak between September and October (Requier et al. 2019). At this period, honey bees
99 can constitute 38% of the diet of *V. velutina* in average (Rome et al. 2021). This period
100 also corresponds to a critical time for honey bees as they prepare for overwintering (Re-
101 quier et al. 2019). Field observations show that honey bees are not yet able to defend itself
102 against *V. velutina* attacks and/or has not developed an effective defense mechanism
103 against *V. velutina* attacks (Monceau et al. 2018) comparatively to defense ability of *Apis*
104 *cerana* in *V. velutina*'s native range (Monceau et al. 2013; Arca et al. 2015). Thus, *V. ve-*
105 *lutina* predation poses an additional threat to honey bees that already face multiple pres-
106 sures and significant colony mortalities (Brodschneider et al. 2018).

107 *V. velutina* predation of worker honey bees at the entrance of the beehive, in par-
108 ticular on foragers returning to the beehive, can have a noticeable effect on the demogra-
109 phy of honey bee colonies (Monceau et al. 2013; Requier et al. 2019). More alarmingly,
110 the presence of hornets hovering in front of the beehive has the effect of paralyzing bee-
111 hive activity when the number of hornets is too high (Requier et al. 2019). When the num-
112 ber of hornets in front of a beehive exceeds a certain threshold, established at 12 individu-
113 als (Requier et al. 2019), honey bees no longer leave the hive and therefore no longer
114 bring back the resources necessary for the overwintering of the colony. This maladaptive

115 defensive behavior leads to the consumption of honey provisions planned for the winter
116 and significantly increases the risk of collapse of bee colonies during the winter (Requier et
117 al. 2019; Rojas-Nossa et al. 2022). Thus, the predation of honey bees leads to a hornet-
118 mediated beekeeping risk (HBR) that can provide mortality of honey bee colonies with im-
119 portant economic costs estimated reach as much as € 30.8 million per year due to colony
120 loss in France (Requier et al. 2023a).

121 Although the current and potential spatial distribution of *V. velutina* is well docu-
122 mented, the spatial distribution of the risk that this invasive species represents for bee-
123 keeping (i.e. HBR) is not yet assessed. Information of the spatial distribution, however, is
124 urgently required to formulate suitable management plans. In this study, we carried out a
125 large-scale citizen science program aimed at accurately mapping the distribution of *V. ve-*
126 *lutina* in apiaries across France and Germany, where uncertainty persists concerning the
127 eastern limit of the invasion front. Moreover, we mapped HBR in these two countries in
128 order to perform a spatial risk assessment that can help recommending management
129 measures for the species. Finally, we explored whether the spatial distributions of *V. ve-*
130 *lutina* and HBR can be determined by environmental variables (i.e. climate, habitat and
131 distance to the introduction place) in order to help formulating regionally adapted man-
132 agement plans.

133

134 **Materials and Methods**

135

136 **Franco-German citizen science program**

137 This study is based on two-year citizen-science program involving beekeepers in France
138 and Germany over the years 2018 and 2019. A standardized questionnaire was designed

139 to record the distribution and predation behavior of *V. velutina* at the country level. The
140 consideration of two countries resulted from the lack of information on the expansion of *V.*
141 *velutina* at the eastern distribution boundry (Germany) following the first records in 2014 in
142 southern Germany (“Rheinland-Pfalz” region) (Witt 2015). The beekeepers were invited to
143 record their observations in front of the beehives through a questionnaire (**Supporting**
144 **Information, Table S1**). The questionnaire was distributed across Germany via the solic-
145 ited publication in two major national beekeeping journals (Requier et al. 2018a, b). Addi-
146 tionally, the survey was advertised in a beekeeping newsletter published by the German
147 bee institutes. The survey was disseminated via beekeeping social networks in France, on
148 the website of the National Museum of Natural History of Paris, and promoted by a bee-
149 keeper on Youtube. The call to participate at the survey started in the fall (i.e. September
150 2018 for the first year and September 2019 for the second year) and the survey was open
151 until the end of the year studied, i.e. until December 2018 for the first year and December
152 2019 for the second year. This period of time represents the most likely time window to
153 observe *V. velutina* predating at the apiary (Requier et al. 2019).

154

155 **Record of *V. velutina* presence and hornet-mediated beekeeping risk (HBR)**

156 Volunteer beekeepers were asked to fill in their apiary location (city/region/country), if they
157 observed predation behavior of *V. velutina* in front of the beehives between September 1st
158 and October 31th (the most likely time window to observe *V. velutina* predating at the api-
159 ary and potentially leading to detrimental effect on colony survival; Requier et al. 2019),
160 and the maximum number of hornet individuals observed hunting simultaneously at each
161 beehive between September 1st and October 31st. Based on the answers to the survey,
162 the GPS data of all sightings was populated using the postal code recorded by the bee-

163 keeper and considering the center of the municipality. Whenever beekeepers observed
164 hornet predation on beehives, they were asked to report the maximum number of hornet
165 individuals observed simultaneously in front of a beehive. However, a few answers were
166 given in text form (less than 1% of answers), and these were quantitatively transformed as
167 follows. For closed intervals such as "1 to 6 hornets observed", we considered the high
168 interval as (maximum number requested in the question), namely "6" in this example. In
169 the case of open intervals, for example "more than 10 hornets observed", at least 10 hor-
170 nets have been observed, so this is the information that has been retained. Finally, in the
171 case of adjectives (e.g. "few", "too many") a binary reasoning was adopted, considering
172 that at least 1 hornet was observed. The answer was changed to "1". This recorded maxi-
173 mum number of hornet individuals observed at the same time predating in front of a bee-
174 hive was used to establish whether each apiary was over or below the hornet-mediated
175 beekeeping risk (HBR). According to the literature, more than 12 hornets observed at the
176 same time predating in front of a beehive induce bee foraging paralysis and can lead to
177 colony collapse (Requier et al. 2019). Therefore, we considered that reaching (or exceed-
178 ing) the critical threshold of 12 hornet individuals lead to HBR.

179

180 **Expert-based validation**

181 Given that *V. velutina* is a new invasive species in Western Europe, we carried out a vali-
182 dation by experts of the identifications (Q. Rome and F. Requier). To perform the confirma-
183 tion, beekeepers were invited to send pictures of the recorded insects. When validating the
184 detections, particular attention was paid to German regions for which little positive detec-
185 tion had been recorded to date. This validation was only carried out for the German data

186 because we followed the hypothesis that French beekeepers have knowledge of *V. ve-*
187 *lutina*.

188

189 **Environmental variables**

190 Based on the GPS data, the environmental parameters of each record were extracted from
191 Open Source databases to inform the climate of the site, habitat within a radius of 10 km²,
192 and distance to the introduction place. Habitat was extracted via the GlobCover2009 land
193 cover map database (http://due.esrin.esa.int/page_globcover.php) for the years 2018 and
194 2019. Given that the urbanization is the most likely landscape factor that affects the distri-
195 bution of *V. velutina* (Fournier et al. 2017), we calculated the proportion of urbanized areas
196 around the observation points in an area of 10 km² around the GPS coordinates (square of
197 about 3 km on each side, **Figure S1**). This distance was chosen because the average for-
198 aging distance of honey bees is about 1.5 km (Steffan-Dewenter and Kuhn 2003) and the
199 average foraging distance of *V. velutina* is about 2 km (Budge et al. 2017; Sauvard et al.
200 2018; Kennedy et al. 2018; Rome et al. 2021). Similarly, we selected the temperature
201 among the climatic factors, which is known to affect the distribution of the species (Barbet-
202 Massin et al. 2013). Temperature data were obtained from the WorldClim database ver-
203 sion 2.0 Beta (<https://www.worldclim.org/>). The 1970-2000 monthly mean temperatures at
204 each observation site were used to estimate the annual mean temperature (in °C, **Figure**
205 **S2**). Finally, we computed the distance to the introduction site as an euclidean distance in
206 kilometers considering the location of accidental introduction in 2004 in the south-western
207 France in the Lot et Garonne department (Robinet et al. 2018, **Figure S3**). We performed
208 Pearson's correlation tests to assess colinearity among environmental variables, showing
209 few colinearity (**Figure S4**).

210

211 **Statistical analyses**

212 The statistical analyses were performed with the R software, version 3.6.3 (R Develop-
213 ment Core Team, 2023).

214 *Spatial drivers of V. velutina presence.* A Generalized Linear Models with a bino-
215 mial distribution of errors (binomial GLM) was used to analyze whether the presence of the
216 *V. velutina* in apiaries (response variable) is affected by (1) the distance to the point of in-
217 troduction, (2) the temperature and (3) the percentage of urbanization (explanatory vari-
218 ables). The presence of *V. velutina* was considered in a binary way, with 0 for absence
219 and 1 for presence.

220 *Spatial drivers of HBR.* A Generalized Linear Model with a Poisson distribution of
221 errors (Poisson GLM) was used to analyze whether HBR (response variable) is affected by
222 (1) the distance to the point of introduction, (2) the temperature and (3) the percentage of
223 urbanization explanatory variables.

224 For all the statistics, model residuals were extracted and inspected against fitted
225 values (residuals versus fitted plot and normal Q–Q plot) to ensure residual normality and
226 homoscedasticity assumptions were fulfilled. The significance level for the statistical tests
227 was set at 5% for the probability of rejecting the true null hypothesis.

228

229 **Results**

230

231 **Spatial drivers of *V. velutina* presence**

232 We collected a total of 1697 responses from beekeepers on the presence or absence of *V.*
233 *velutina* predating in the apiaries across France (n=1368 responses) and Germany (n=329

234 responses). The responses were widely distributed throughout France and Germany (**Fig-**
235 **ure 1**). A large majority of French beekeepers observed the presence of *V. velutina* hunt-
236 ing in front of their beehives (72.9% of observations were positive). The frequency of ob-
237 servation of *V. velutina* presence in front of the beehives in Germany was lower than in
238 France (5.5% of positive records in Germany), with concentration of positive observation in
239 the Rhine valley, and in the south-west of Germany and in the north (Hamburg) with less
240 frequency (**Figure 1**).

241 We found that temperature, the distance to the point of introduction and the per-
242 centage of urbanization significantly explained the presence of *V. velutina* predating in the
243 apiaries across France and Germany (**Table 1**), with temperature and distance to the point
244 of introduction as the best explanatory variables (higher z values; **Table 1**). Therefore, the
245 distribution of *V. velutina* presence in France and Germany is strongly determined by the
246 temperature and the distance to the point of introduction, and in lesser extent on the ur-
247 banization rate. The temperature has a positive effect on the presence of *V. velutina* pre-
248 dating in the front of the beehives (**Figure 2A**), and the distance to the point of introduction
249 has a negative effect (**Figure 2B**). The presence of *V. velutina* increases slightly with the
250 percentage of urbanization (**Figure 2C**).

251

252 **Spatial drivers of HBR**

253 In total, 1015 validated positive observations of *V. velutina* in France and Germany were
254 collected over the years 2018 and 2019 (**Figure 3**). In France, the 3.5% of apiaries with
255 presence of *V. velutina* exceeded the HBR risk threshold of 12 hornet individuals observed
256 at the same time predating in front of a beehive, whereas in Germany this threshold was
257 never reached. The apiaries at risk of HBR (i.e. a minimum of 12 hornet individuals ob-

258 served simultaneously predated in front of a beehive) were located in south-western
259 France, in the region of the accidental introduction of the invasive species (**Figure 3**).

260 Temperature and the distance to the point of introduction significantly affect the
261 distribution of HBR (**Table 2**). The percentage of urbanization did not explain the spatial
262 variability in HBR (**Table 2**). The temperature had a positive effect on HBR (**Figure 4A**),
263 while the distance to the point of introduction had a negative effect on HBR (**Figure 4B**).
264 HBR increases slightly with the percentage of urbanization, but not significantly (**Figure**
265 **3C**).

266

267 **Discussion**

268 The first objective of this study was to assess the distribution boundary of *V. velutina* in
269 Germany, as the maximum front of the invasion of the species in Western Europe. The
270 results showed that the majority of sightings of *V. velutina* in Germany were in the already
271 known presence area, in the Rhine Valley (Witt 2015). These first results therefore confirm
272 the establishment of the species in the Rhine valley, in continuity of the French invasion
273 front. This valley has a microclimate in which the temperatures are slightly higher than the
274 surrounding region and therefore potentially more favorable to *V. velutina* (Villemant et al.
275 2011; Barbet-Massin et al. 2013). The results of this study support this hypothesis, show-
276 ing that the annual mean ambient temperature has a positive effect on the probability of
277 the presence of *V. velutina* in front of the beehives, in France and in Germany. However,
278 new observations have also been noted, such as in Hamburg (Husemann et al. 2020b),
279 and in other sites not connected to this first zone. These are indicators of secondary inva-
280 sions. The presence of the species in these areas suggests that the spread of *V. velutina*
281 is, as probably all other invasive species (e.g. Suarez et al. 2001), not only natural but is

282 also largely facilitated by the transport of goods (Rome et al. 2011; Robinet et al. 2018).
283 Indeed, the queens can be transported, in convoys of wood for example, thus favoring the
284 establishment of the species in areas not yet colonized (Robinet et al. 2018).

285 This study also shows the establishment of *V. velutina* in the whole metropolitan
286 French territory, and that the species is not yet present in Corsica (see also Rome and
287 Villemant 2023). However, the species density is not homogeneous across France. We
288 detected a lower density of *V. velutina* sightings in the Grand-Est region and in the Alps
289 and Massif Central mountains in France. The temperature effect explains this heterogene-
290 ity, as these two French regions have colder climates than the rest of France. The lower
291 annual mean ambient temperature can also explain the observation of fewer hornet indi-
292 viduals in the Alps. Indeed, we found that temperature is the predominant environmental
293 factor explaining the presence of the species in France and Germany. This result is in
294 agreement with previous studies that observed a positive effect of temperature on the dis-
295 tribution of the invasive species (Barbet-Massin et al. 2013; Rodríguez-Flores et al. 2019).
296 The distance to the point of introduction has a negative effect on the presence of *V.*
297 *velutina*, which is also in agreement with previous studies (Robinet et al. 2018). Finally, we
298 showed that urbanization had a positive effect on the presence of the species. A previous
299 study (Fournier et al. 2017) found that urbanization was one of the landscape elements
300 determining the rank of *V. velutina* invasion. Although *V. velutina* has established itself in
301 Germany through expansion by the French territory, climatic barriers seem to restrict its
302 natural expansion in the eastern front. Indeed, since its introduction in 2014 in Germany,
303 the species has made little progress, depending of more favourable years. However, cli-
304 mate change and rising temperatures could allow *V. velutina* to continue its expansion on
305 the eastern front of Europe in the years to come (Barbet-Massin et al. 2013).

306 Beyond the presence of the species, this study also aimed to study the spatial dis-
307 tribution of the hornet-mediated beekeeping risk (HBR) in France and Germany. The HBR
308 threshold was set at 12 individuals observed simultaneously in front of a beehive (Requier
309 et al. 2019). Once we reach or exceed this threshold, the bee colony is often paralyzed,
310 which leads to its collapse. This study confirms that this threshold is reached in France,
311 which can lead to a risk of losing colonies (Requier et al. 2019). In Germany, this risk does
312 not occur because the number of hornet individuals observed simultaneously in front of a
313 beehive never exceeds the risk threshold. However, there is evidence revealing that lower
314 predation pressure maintained over several weeks can also lead to the paralysis of the
315 colony (Rojas-Nossa et al. 2022). Therefore, further studies are needed to understand the
316 triggering factors for this antipredator behaviour, and it is important the awareness of be-
317 keepers about monitoring colonies' behaviour even in regions that have not a high
318 HBR. Temperature and distance to the point of introduction were identified as predictive
319 variables of HBR in France and Germany. Overall, temperature appears to be a critical
320 factor of both the presence of the species and HBR in France and Germany. Temperature
321 has a positive effect on HBR. The annual mean ambient temperature is lower in Germany
322 than in France, potentially explaining the fact that HBR is lower in Germany than in
323 France. The distance to the point of introduction is also a determining factor of *V. velutina*
324 presence and the pressure, unlike urbanization which is a predictive factor of the presence
325 of the species (in comparison with the temperature and the distance to the point of intro-
326 duction), and which does not explain the spatial variability of HBR. Thus, if a beekeeper is
327 located in an area where the temperature is conducive to the implementation of *V. ve-*
328 *lutina*, the risk of observing hornets and that they are a threat to bee colonies could in-
329 crease.

330 The risk of bee colony mortality linked to *V. velutina* predation is likely to occur in
331 France (i.e. number of hornet individuals observed simultaneously in front of a beehive
332 above the HBR threshold) but not in Germany (i.e. number of hornet individuals never ex-
333 ceeding the HBR threshold). Species control measures should be considered accordingly.
334 An important point to consider along with the limited risk to beekeeping is the conservation
335 status of the European hornet (*Vespa crabro*) in Germany. Indeed, the European hornet is
336 a species with a special protection category in Germany (the species is not protected in
337 France), and its capture is therefore illegal in Germany. All traps traditionally used to con-
338 trol the invasion of the hornet in France also have lethal effects on other parts of the ento-
339 mofauna including the European hornet (Rojas-Nossa et al. 2018; Requier et al. 2020a).
340 Therefore, baited traps are not suitable as a control method in Germany. Nevertheless, the
341 threat of *V. velutina* on beekeeping could increase in the future in Germany with climate
342 change and its impetus on the establishment of the species in Europe (Barbet-Massin et
343 al. 2013). We urge beekeepers and the public authorities to implement prevention and
344 management plans that involve biodiversity-friendly techniques (e.g. non-lethal tech-
345 niques) in order to control the potential impact of *V. velutina* on beekeeping.

346

347 **Conclusion**

348 Faced with the concern that represent *V. velutina* invasion and the risk it represents for
349 beekeeping (Laurino et al. 2019), a large diversity of methods of controlling hornet popula-
350 tions are put in place but are not always effective or even dangerous for other non-target
351 insect species (Rojas-Nossa et al 2018; Turchi and Derijard 2018; Requier et al. 2020b).
352 Beehive muzzles could be recommended to beekeepers since they reduce the risk of col-
353 ony mortality without causing adverse effects on biodiversity (Requier et al. 2020b). In ad-

354 dition, implementing effective measures to mitigate long-distance transport of hornets
355 should be considered (Robinet et al. 2018). The invasion of *V. velutina* places in a context
356 of increasing new species invasions leading to numerous ecological and socio-economic
357 impacts worldwide. These impacts include biodiversity loss and species extinction (Bellard
358 et al. 2016), health impacts (Mazza et al. 2014) and very significant economic costs (Brad-
359 shaw et al. 2016; Requier et al. 2023a). We suggest that considering the spatial variability
360 of the hornet-mediated beekeeping risk could help formulating regionally adapted man-
361 agement plans to limit *V. velutina* impacts on biodiversity, human health and economic
362 sectors.

363

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368

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372

373 **Competing Interests**

374 The authors declare that the research was conducted in the absence of any commercial or
375 financial relationships that could be construed as a potential conflict of interest.

376

377 **Data Availability**

378 Data available from the figshare repository <https://doi.org/10.6084/m9.figshare.24182721>
379 (Requier et al. 2023b).

380

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521

522 **Table 1.** Summary of the binomial Generalized Linear Model performed to evaluate the
523 effects of temperature (mean annual ambient temperature, in °C), distance to the point of
524 introduction (in km), and percentage of urbanization (proportion of urban habitat within
525 3km around the site in %) on the presence of *V. velutina* in apiaries (n=1697).

526

Parameters	Estimate	Std. Error	z value	P value
<i>Intercept</i>	-6.099	0.924	-6.601	<0.001
Temperature	0.828	0.077	10.684	<0.001
% Urbanization	0.033	0.007	4.606	<0.001
Distance	-0.005	0.001	-10.685	<0.001

527

528

529 **Table 2.** Summary of the Poisson Generalized Linear Model performed to evaluate the
530 effects of temperature (mean annual ambient temperature, in °C), distance to the point of
531 introduction (in km), and percentage of urbanization (proportion of urban habitat within
532 3km around the site in %) on the number of hornets observed simultaneously predating in
533 front of a beehive (n=1015).

534

Parameters	Estimate	Std. Error	z value	P value
<i>Intercept</i>	0.340	0.194	1.751	0.080
Temperature	0.118	0.015	8.123	<0.001
% Urbanization	0.002	0.001	1.780	0.075
Distance	-0.001	0.001	-11.164	<0.001

535

536 **Figure Captions**

537

538 **Figure 1.** Mapping the spatial distribution of presence of the Yellow-legged hornet (*Vespa*
539 *velutina nigrithorax*) in apiaries across France and Germany (n=1697).

540

541 **Figure 2.** Effects of (A) temperature (mean annual ambient temperature, in °C), (B) dis-
542 tance to the point of introduction (in km), and (C) percentage of urbanization (proportion of
543 urban habitat within 3km around the site in %) on the presence of *V. velutina* in apiaries
544 (n=1697). The dots represent the observations; the thick lines represent the binomial GLM
545 predictions with shaded areas indicating the 95% confidence interval.

546

547 **Figure 3.** Mapping the spatial distribution of the hornet-mediated beekeeping risk (HBR)
548 as the maximum number of individual hornets observed simultaneously in predation in
549 front of a beehive across France and Germany (n=1015).

550

551 **Figure 4.** Effects of (A) temperature (mean annual ambient temperature, in °C), (B) dis-
552 tance to the point of introduction (in km), and (C) percentage of urbanization (proportion of
553 urban habitat within 3km around the site in %) on the number of hornets observed simulta-
554 neously predating in front of a beehive (n=1015). The dots represent the observations; the
555 thick black lines represent the Poisson GLM predictions with shaded areas indicating the
556 95% confidence interval. These lines are dashed if they are non-significant. The dotted red
557 lines represent the HBR threshold (i.e. a minimum of 12 hornet individuals observed simul-
558 taneously predating in front of a beehive).

559