

ORIGINAL ARTICLE

Vespa velutina nest distribution at a local scale: An 8-year survey of the invasive honeybee predator

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Abstract *Vespa velutina* is an invasive species that was observed for the first time in France and Europe in 2004, which rapidly threatened domestic honeybees with active predation. For the first time in this study, we analyzed the distribution of *V. velutina* nests at a local scale to understand the pattern of nesting, and in 8 years of monitoring, a total of 528 nests were surveyed. With the exception of 2 years, the nests of *V. velutina* were randomly distributed within the monitored area, which suggested that intraspecific competition for nesting sites and/or food was unlikely. When the data for all years were combined, an aggregated distribution of nests at the seafront in the vicinity of the oyster farm and sportfishing activities was observed. This distribution suggested that seafood, attractive to vespids, might provide a valuable alternative food source that favored colony development. We also tested the effect of spring queen trapping of *V. velutina* on the distribution of nests in 2014, which was the year with the greatest number of colonies within the area; the position of the traps did not influence the distribution of the nests. For the first time, this study showed that (i) intraspecific competition was unlikely to be a mechanism for population regulation, (ii) some areas were more likely favored for hornet nests, and (iii) spring queen wasp trapping was inefficient as a method to limit the distribution of the *V. velutina* population.

Key words intraspecific competition; nesting habits; spring queen trapping; yellow-legged hornet

Introduction

For the last 2 centuries, human activities and exchanges of goods have fundamentally altered global biodiversity, particularly the human activities that contribute to the biological invasions worldwide and the emergence of new pests (Vitousek *et al.*, 1997; Chapin *et al.*, 2000). Understanding the factors that modulate the success and the spread of invasive species is therefore of major importance for envi-

ronmental management policies. One current problem is that reliable information on the ecology and the behavior of alien species is often lacking until these species become invasive. However, a detailed knowledge of the behavioral ecology of the invasive species in a novel environment is a requirement to determine the behavior that maximizes the fitness and therefore the expansion of the population of the alien species (Roitberg, 2007).

Because of the complex organization, social insects colonize a wide range of ecosystems worldwide (Moller, 1996; Chapman & Bourke, 2001; McGlynn, 2002; Beggs *et al.*, 2011). Social insects as invasive species are not only a threat to the native biodiversity but also are often responsible for huge economic losses. For example, in Texas, the overall cost associated with the damages and the control of the invasive red fire ant, *Solenopsis invicta*, was estimated to reach approximately \$500 million in 2000 (Pimentel

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et al., 2005). In the last decade, Europe faced the first invasion by a social Asian predator in the family Vespidae that was accidentally introduced from China (Rortais *et al.*, 2010; Monceau *et al.*, 2014; Arca *et al.*, 2015). The yellow-legged hornet, *Vespa velutina*, was first observed in France in 2004 and has since proliferated throughout the French territory, with spread also into Spain and Portugal and more recently, into Italy (Monceau *et al.*, 2014; Arca *et al.*, 2015). The invasion of this hornet species causes several ecological, economic and public health problems, with predation on domestic honeybees as the most obvious current problem (Monceau *et al.*, 2013a,b; Arca *et al.*, 2014). In addition to the effect on bees as pollinators, *V. velutina* is also a source of stress for beekeepers and has a clear, critical effect on the professional activities of small beekeepers (Monceau *et al.*, 2014). Additionally, *V. velutina*, which is an allergenic, large venomous insect, is now an increasing urban problem. However, within the invaded range in Europe, *V. velutina* is currently primarily dangerous only in the vicinity of the nests, and no significant increase in hymenopteran stings was reported during the first 5 years following the introduction (de Haro *et al.*, 2010).

Vespa velutina continues to spread through Europe, and efficient guidelines for a management programme are urgently required; the guidelines rely primarily on our ability to find and destroy the nests before the colony size reaches full maturity with the production of numerous gynes (Monceau *et al.*, 2014). *V. velutina* has several different nesting habits. The papier-mâché nests are founded by single overwintering queens and produce hundreds of fertile queens, the number of which is dependent on the size of the colony. The nests are found in various natural and artificial locations, including in treetops, bushes, and shrubs, on roofs, under eaves in urban areas, and more rarely, underground (Edwards, 1980; Starr & Jacobson, 1990; Starr, 1992; Nakamura & Sonthichai, 2004; Abrol, 2006; Kim *et al.*, 2006; Choi *et al.*, 2012). Because of the nest architecture, an important factor in nest site selection is protection from adverse weather (e.g., rainfall and wind) (Matsuura & Yamane, 1990). The site selection of a nest is also closely linked to foraging behavior. Indeed, *V. velutina* is a central place forager; this means that workers forage from their nest to food sources and come back to their home base. However, in *V. velutina* the radius distance of foraging from the nest is still unknown.

Intraspecific competition for nesting sites is often considered a mechanism for population regulation in vespids (Spradbery, 1973; Edwards, 1980; Matsuura & Yamane, 1990; Röseler, 1991). In the case of *V. velutina*, the intraspecific competition among foundresses in the spring during colony establishment is often cited to discredit

spring queen trapping for population control (Haxaire & Villemant, 2010). Indeed, the efficiency of intraspecific competition during colony establishment is supposedly more efficient than the queen trapping method for population regulation. This method of control is highly popular for wasp control but it is also highly controversial because of important side effects on the entomofauna (see Monceau *et al.*, 2012, 2014 and references therein). However, to date, the effect of intraspecific competition in *V. velutina* and the complete assessment of the efficiency of spring queen trapping on population regulation have not been determined.

Therefore, the analysis of the distribution of the nests in a defined geographical area might reveal potential interactions among colonies. In particular, a regular pattern may result from intraspecific competition for resources (Potts & Wilmer, 1998; Tanner & Keller, 2012). In this study, we used the results of an 8-year survey conducted at a local scale to our advantage to test this hypothesis. The analysis of the nest distribution at a small spatial scale limits the influence of climatic and environmental variations, which may affect the distribution of *V. velutina* (Ibáñez-Justicia & Loomans, 2011; Villemant *et al.*, 2011). Intraspecific competition in the hornets may occur because of limited resources, such as nest sites and/or food sources; therefore, with competition, one would predict a regular distribution of the nests, whereas, in the absence of competition, a random pattern would be predicted. In 2014, because many traps were placed within the area by local authorities and citizens, the relation between the spring queen trapping and the nesting behavior was also investigated as a first assessment of the effect of this method for regulating the populations of *V. velutina*. Thus, we tested whether the distribution of the traps influenced the distribution of the nests.

Materials and methods

Study location and data cleaning

The survey was conducted by the city services of Andernos, which is a city of 11 376 inhabitants (2012) that covers ca. 21 km² and is located on the northeast shore of Arcachon Bay near Bordeaux in southwest France (Gironde, France, GPS: N 44°44'47.36", W 1°6'9.40"). According to the CORINE land cover classification (<http://clc.developpement-durable.gouv.fr/>), Andernos has 4 types of environment: artificial territories (primarily urban zones, 11), industrial/commercial zones (12), forests (deciduous and coniferous, 31), and shrublands (32).

Table 1 Number of nests detected in the urban and suburban areas of Andernos each year since 2007 (total 545 nests). Only the nests found in the urban part of Andernos were considered in this study. The urban density (nests/km²) of nests within the urban area of 9.05 km² from 2007 to 2014 is also reported. The GPS coordinates for each nest are provided in Table S1.

Year	Number of nests		Urban density
	Urban	Suburban	
2007	4	0	0.44
2008	27	0	2.98
2009	78	4	8.62
2010	61	0	6.74
2011	72	5	7.96
2012	86	8	9.50
2013	89	0	9.83
2014	111	0	12.26
Total	528	17	–

In Andernos, the first nests were detected in 2007, which was 3 years after the onset of the European biological invasion located ca. 200 km away. From this date, each nest was detected, destroyed (when possible) and recorded in the current database. The data set was first checked, and redundant nest reports were discarded. In this study, we focused on the urban zone (urban and industrial/commercial areas 11 and 12) for 2 major reasons. First, the number of nests detected outside the urban zone is negligible (17 nests for a total of 545, see Table 1), probably due to lower human presence that may introduce an important bias in the analyses. Second, this small area forms a homogenous zone of ca. 9.05 km² thus limiting the confounding effects of environmental heterogeneity. A total of 528 nests were used in these analyses (Fig. 1, Tables 1 and S1). The distinction between embryonic and mature nests could not be determined in this study, considering that each embryo nest evolves in a mature nest in the same place (since relocation has never been clearly observed until now in Europe).

In 2014, the local authorities promoted spring queen trapping as a citizen action against *V. velutina* (see Blot, 2009 or Monceau *et al.*, 2012). A total of 152 traps with sweet bait (beer plus syrup) were placed throughout the area in the spring period (15 February to 22 June) (Fig. 2, Table S2). Of the total number of traps, a subset ($n = 60$) was analyzed to count the number of *V. velutina* caught. A total of 844 queens were captured in the 60 analyzed traps in this area (average = 14.8 per trap).



Fig. 1 Map of Andernos, including the sites of interest (1: Andernos oyster-farming port; 2a: Andernos marina; 2b: Lanton marina; 3: Andernos camping) and the distribution of the 528 nests within the urban area, displayed with different colors by year (2007: black; 2008: violet; 2009: blue; 2010: green; 2011: yellow; 2012: orange; 2013: pink; and 2014: red).

Statistical analyses

The variation in the number of *V. velutina* nests during the study period (2007–2014) within the area was tested using linear regression with *F*-ratio statistics. We did not use any classical model to estimate the growth rate of the population because in the present case, growth rate is confounded by the nest removal and of reinvasion from uncontrolled adjacent location. The Kruskal–Wallis tests were used to compare the mean inter-nest distance and the nearest-neighbor nest distance among years using the *spdep* package (Bivand, 2014). Then, pairwise Wilcoxon multiple comparison tests (implemented with the Benjamini–Hochberg correction, Benjamini & Hochberg, 1995) were used to identify the significant differences among the years. All distances were computed based on Great Circle distances (WGS-84 ellipsoid parameters). The complete spatial randomness (CSR) was tested using conditional Monte Carlo test of CSR using quadrat counts Pearson χ^2 statistic based on 10 000 simulations for each year separately (Table 2). For 1 year (2009), a deviation from CSR was observed. We therefore computed the Besag’s *L(r)* function (Besag, 1977) derived Ripley’s *K(r)* function (Ripley, 1977, 1979, 1981, 1988) for stationary Poisson point pattern to analyze the



Fig. 2 Distribution of traps used during spring 2014 in black triangles and nests in red dots.

Table 2 Conditional Monte Carlo test of complete spatial randomness (CSR) using quadrat counts Pearson χ^2 -statistic based 10 000 simulations. Twenty-three tiles were performed for each test thus corresponding to 22 df.

Year	χ^2	<i>P</i>
2007	62.78	0.05
2008	24.75	0.56
2009	48.13	0.01
2010	27.59	0.40
2011	31.36	0.19
2012	29.29	0.28
2013	33.53	0.13
2014	33.40	0.13

distribution of nests for each year separately and then for all years pooled. These functions are closely related because the $L(r)$ is a transformation of the $K(r)$ and both functions are based on the radial distance r between points. Briefly, the estimates for the $L(r)$ function were computed (with the correction for the edge effect from the *spatstat* package, Baddeley & Turner, 2005) and then were compared with the pattern expected under CSR. These estimates were associated with an envelope that was delimited by the critical points from a Monte Carlo test (10 000 simulations, see Ripley, 1981). If the estimates were included within the envelope, then the nests would be randomly distributed. If the estimates were above the up-

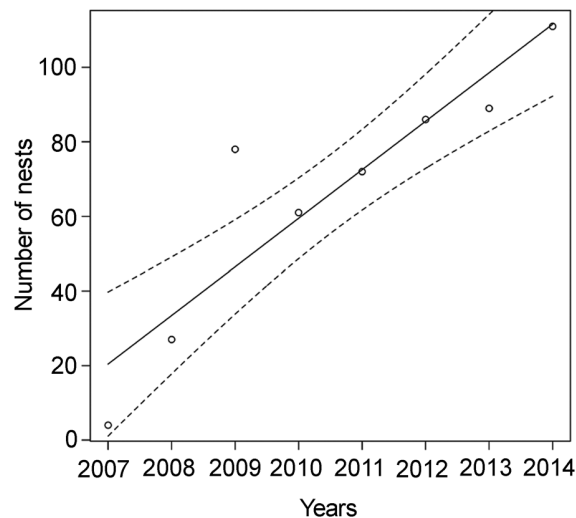


Fig. 3 Variation in the number of nests in Arcachon from 2007 to 2014. Predicted values fitted with the linear regression (plain line) with a 95% confidence interval (dash lines).

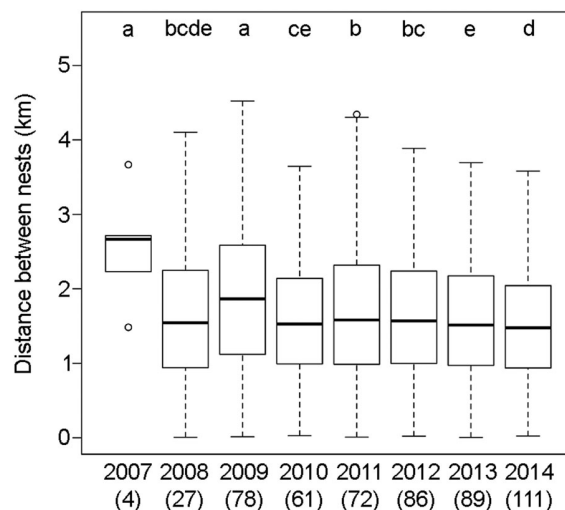


Fig. 4 Internest distances per year. Bold line: median; box: middle 2 quartiles; dashed lines: $1.5 \times$ interquartile range; and open circle: extreme value. The numbers inside parentheses indicate the number of nests. Columns with the same letter are not significantly different ($P > 0.05$), based on a nonparametric pairwise Wilcoxon multiple comparison test.

per critical envelope, then the nests would be aggregated. Finally, if the estimates were below the lower critical envelope, then the nests would be regularly distributed. The density estimates of the nests were also computed for the case of an aggregated pattern. To analyze the relation between the distribution of the nests and the distribution

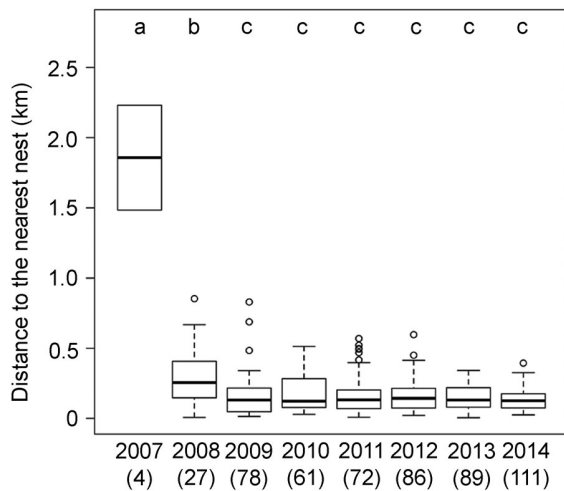


Fig. 5 Nearest neighbor nest distances per year. Bold line: median; box: middle 2 quartiles; dashed lines: $1.5\times$ interquartile range; and open circle: extreme value. The numbers inside parentheses indicate the number of nests. Columns with the same letter are not significantly different ($P > 0.05$), based on a nonparametric pairwise Wilcoxon multiple comparison test.

of the traps, the extensions of $L(r)$, respectively, the $L(r)$ cross-function was used. Briefly, these functions computed the radial distance r from the nests to the position of the traps and then compared this distance with the distance that was expected with the independent distributions of nests and traps, which was associated with an envelope that was delimited by the critical points from a Monte Carlo test (10 000 simulations). If the estimates were included in the envelope, then the distributions of traps and nests would be independent from one another. If the estimates were above the upper critical envelope, then the nests would be aggregated in relation to the traps. Finally, if the estimates were below the lower critical envelope, then the nests would be constructed distant from the traps (repulsion).

All statistical analyses were performed using the R statistical software package (v. 3.1.2, R Development Core Team, 2014), which was implemented with RgoogleMaps for the display of the maps (Loecher, 2014).

Results

Over the 8 years, the number of nests increased almost regularly from 2007 to 2014 ($R^2 = 0.81$, $F = 30.53$, 1 and 6 df, $P < 0.01$; Fig. 3) and in 2014, reached a density of 12.26 nests per km^2 (Table 1). The mean inter-nest distance varied among years (Kruskal–Wallis test:

$\chi^2 = 272.47$, $\text{df} = 7$, $P < 0.0001$), but no distinct pattern with distance emerged (Fig. 4). The distance to the nearest nest differed among years (Kruskal–Wallis test: $\chi^2 = 27.07$, $\text{df} = 7$, $P < 0.001$), and this distance decreased from 2007 to 2009 and then stabilized (Fig. 5): the average distance to the nearest neighbor was 153.36 m (95% confidence interval = [143.63; 163.09]). Based on the tests for CSR, the nests were randomly distributed within this area, with the exceptions of 2007 and 2009 (Fig. 6). In 2007, the nests were regularly distributed, whereas in 2009, the nests were aggregated with a clustered pattern of nests below 0.50 km. The diameter of the aggregates in 2009 was ca. 0.15 km, as indicated by the peak of the $L(r)-r$ (Fig. 6), and the aggregates were primarily at the periphery of the city (Fig. 7). Finally, when pooled for all years, a global pattern of aggregated nests was observed with an average diameter of the aggregates of ca. 0.70 km (Fig. 8), and the aggregates were located largely at the seafront (Fig. 9). Finally, the distribution of the *V. velutina* nests was independent of the distribution of the traps (Fig. 10).

Discussion

Invasive species are challenging biological models because in most cases, the biology, ecology and behavior often remain unknown until these species invade new territories. In the native range, the honeybee predator *V. velutina* is primarily confronted with the Asian honeybee, *Apis cerana*, which is very defensive (bee-carpet behavior, shimmering) and aggressive (balling behavior) but is also less abundant than the imported and less defensive European honeybee, *A. mellifera* (Ken *et al.*, 2005; Tan *et al.*, 2007, 2010, 2012a,b, 2013). In Europe, the introduction and the spread of *V. velutina* have most likely been favored during periods of intense colony growth by the weak defensive capabilities of the preferred prey, *A. mellifera* (Arca *et al.*, 2014). This alien species is now a major threat to European biodiversity because the predation on honeybees is likely to have profound effects on the pollination services of the honeybees. Although the complete effects of *V. velutina* have not been quantified to date, management guidelines are required to limit its expansion through Europe. One important key topic for research is the basic ecology and behavior of *V. velutina*, particularly with regard to the nesting habits. In Europe, and in South Korea in which *V. velutina* is also invasive (Choi *et al.*, 2012), the nests are often found in urbanized areas (Monceau *et al.*, 2014). However, whether these nest site locations most likely result from differences in

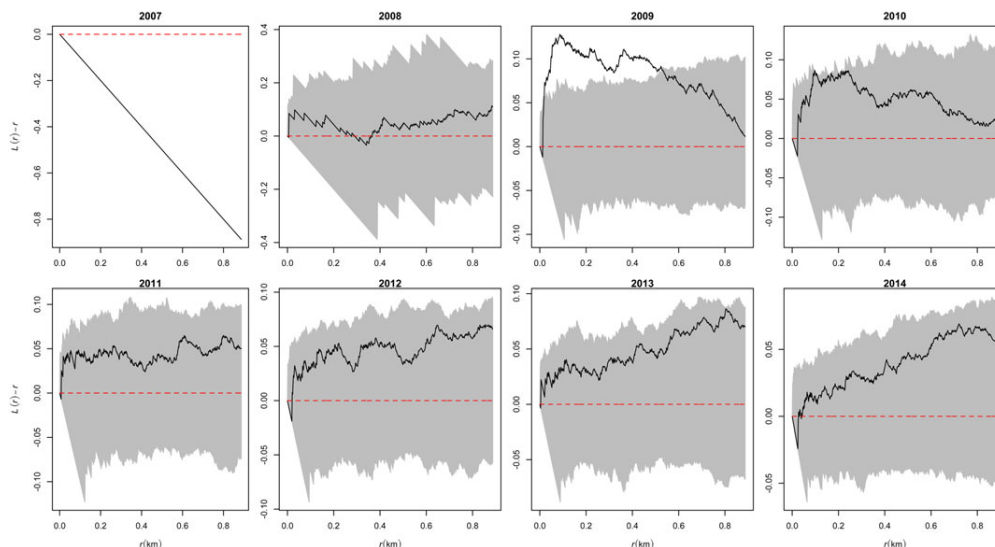


Fig. 6 Estimates of Besag’s $L(r)-r$ function in relation to the radial distance r between nests for each year from 2007 to 2014. The plain line represents the observed values for $L(r)-r$ based on values of the radial distance r (in km), the dotted line represents the expected values for $L(r)-r$ under complete spatial randomness (CSR), and the gray band around the expected values for $L(r)-r$ delimits the critical envelope from the Monte Carlo test: (i) random pattern: the observed values are inside the critical envelope, (ii) aggregative pattern: the observed values are above the critical envelope, and (iii) regular pattern: the observed values are below the critical envelope.

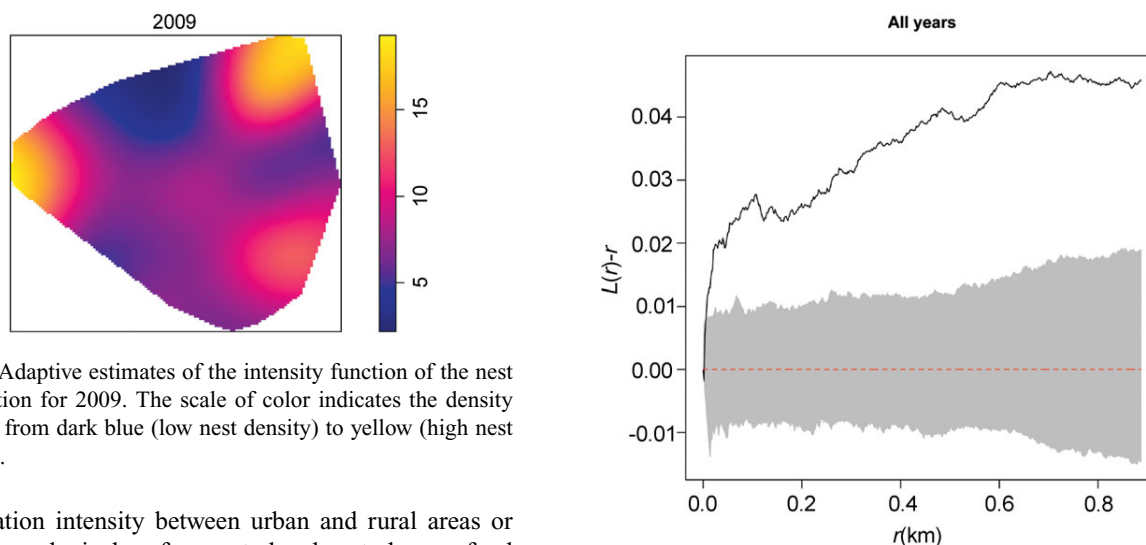


Fig. 7 Adaptive estimates of the intensity function of the nest distribution for 2009. The scale of color indicates the density of nests from dark blue (low nest density) to yellow (high nest density).

observation intensity between urban and rural areas or from an ecological preference to be close to human food resources, as alternatives to predation and other activities, remain to be determined.

Pattern of nest distribution

The analysis of the distribution of nests within this urban area was interpreted at 2 different scales as follows: (i) all years independently because *V. velutina* colonies are annual and nests are only used once and (ii) all years

Fig. 8 Estimates of Besag’s $L(r)-r$ function for all years pooled. The plain line represents the observed values for $L(r)-r$ based on values of the radial distance r between nests (in km), the dotted line represents the expected values for $L(r)-r$ under complete spatial randomness (CSR), and the gray band around the expected values for $L(r)-r$ delimits the critical envelope from the Monte Carlo test: (i) random pattern: the observed values are inside the critical envelope, (ii) aggregative pattern: the observed values are above the critical envelope, and (iii) regular pattern: the observed values are below the critical envelope.

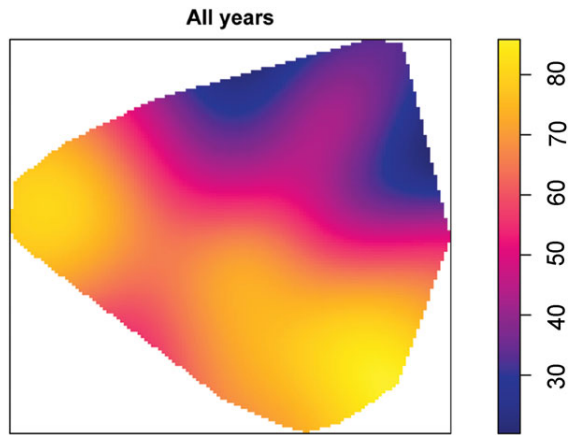


Fig. 9 Adaptive estimates of the intensity function of the nest distribution for all years pooled. The scale of color indicates the density of nests from dark blue (low nest density) to yellow (high nest density).

pooled to detect potential areas in which *V. velutina* nests were more frequently established. The analysis at the first level was to provide information on the relations among colonies; whereas the second-level analysis was to provide information on the overall preference for nesting sites within the area.

Annual nest distribution

We found that the nests were primarily randomly distributed within the area, which was congruent with the variable internest distances among years. The random distribution suggested that there were no restrictions for *V. velutina* queens to found a nest. Previously, intraspecific competition was thought to be a potential regulator of nest distribution (Haxaire & Villemant, 2010), but this assumption was questioned by Monceau *et al.* (2014, see Fig. 6 in this review). In the current study, the random spatial patterns of nesting suggested that intraspecific competition among queens was unlikely at the population level, which was a result that was in contrast to this commonly accepted hypothesis. Additionally, the distance to the nearest nest decreased through time and rapidly reached a range of few meters to a maximum of 700 m (see Fig. 4). Although the foraging range of *V. velutina* (queens and workers) is unknown, *Vespa* sp. forages at radial distances around the nest that range from a few meters to up to 8 km (Matsuura & Yamane, 1990). Therefore, the low distances to the nearest nest suggested that a large overlap occurred between adjacent colonies that is incompatible with high intraspecific territoriality. Re-

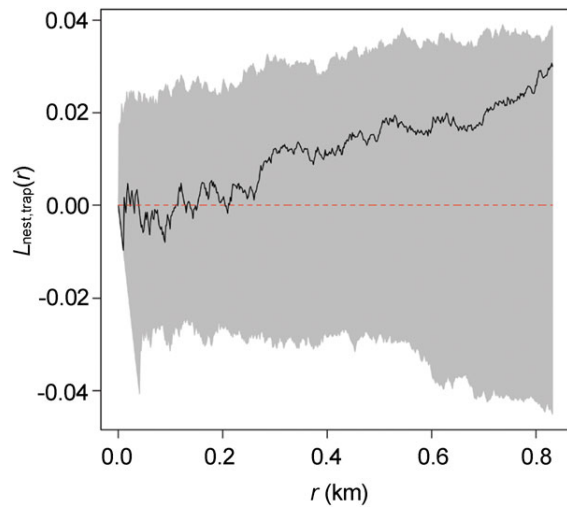


Fig. 10 Estimates of $L(r)$ - r cross-function for the nest distribution in regard to the trap distribution. The plain line represents the observed values for $L(r)$ - r cross-function based on values of the radial distance r between nests (in km), the dotted line represents the expected values for $L(r)$ - r under complete spatial randomness (CSR), and the gray band around the expected values for $L(r)$ - r delimits the critical envelope from the Monte Carlo test: (i) random pattern: the observed values are inside the critical envelope, (ii) aggregative pattern: the observed values are above the critical envelope, and (iii) regular pattern: the observed values are below the critical envelope.

laxed intraspecific competition is often acknowledged in invasive social insects; it is supposed to allow high population density and hence facilitate invasiveness (Moller, 1996; Holway *et al.*, 1998; Perdereau *et al.*, 2011). Our results are thus clearly in line with the impressive spread of *V. velutina* within France and Europe. Moreover, the number of nests continued to increase in our study area from year to year since the first appearance of *V. velutina* in 2007, which suggested that the carrying capacity of the area (i.e., the overall resource availability in support of nesting and/or food sources) was not reached yet. Indeed, *V. velutina* forms large colonies that produce thousands of individuals that require huge quantities of proteins, which explained the impressive predation pressure on honeybee colonies (Monceau *et al.*, 2013a,b; 2014). Therefore, the carrying capacity of the environment may yet affect the number of nests. Notably, however, this analysis was not based on the actual population size (i.e., number of individuals) but was based on the number of nests. Indeed, the regulation of the size of wasp and hornet populations might be modulated by the size of the colonies (Matsuura & Yamane, 1990). Although the argument that nest destruction artificially reduces potential competition

among colonies might be valid, the nest destruction occurs primarily after nest initiation when the intraspecific competition has supposedly already occurred.

In two of the 8 years, the distribution of the nests was not random. First, in 2007, the distribution of nests was regular, which was most likely caused by a statistical artefact of the small sample size (4 nests) and not because of biology. Second, in 2009, the nests were distributed as aggregates; and aggregated patterns are caused, for example, by philopatry (Polidori *et al.*, 2006), group protection against parasites and/or predators (Antonini *et al.*, 2003; Rosenheim, 1990), or intraspecific attraction and/or increased mating probability (Oldroyd *et al.*, 1995; Wattanachaiyingcharoen *et al.*, 2003; Paar *et al.*, 2004; Polidori *et al.*, 2008; Tanner & Keller, 2012; Asís *et al.*, 2014). For *V. velutina*, the pressure from parasitism and/or predation as a driver of nest aggregation was unlikely, because this invasive species has few natural enemies, many of which remain anecdotal (see Monceau *et al.*, 2014; Darrouzet *et al.*, 2015; Villemant *et al.*, 2015). Instead, conspecific attraction and/or philopatry might be involved (Edwards, 1980). Conspecific attraction occurs in different hymenopteran species such as honeybees (Oldroyd *et al.*, 1995), ants (Tanner & Keller, 2012) and solitary wasps (Asís *et al.*, 2014). Therefore, the *V. velutina* foundresses might use the occurrence of conspecifics as a cue to indicate, for example, nesting site quality. Additionally, little is known about the pre-/post-hibernation dispersal of the foundresses (Monceau *et al.*, 2014). These hornets most likely disperse over long distances but not all individuals display high dispersal abilities (see Monceau *et al.*, 2015b). Therefore, the foundresses that were less dispersive might initiate nests near the parent nest, which resulted in philopatry. To distinguish the philopatry from the conspecific attraction, a population genetic study must be conducted in testing isolation by distance with a Mantel test for instance (see Kozyra *et al.*, 2015 for a recent example).

Cumulative nest distribution over years

When the data were pooled for all years, some locations were preferred, primarily those along the seaside. This suggested that the surrounding environment offered suitable conditions for nesting and/or foraging. Moreover, the hornets might select human constructs (buildings) or natural tree (primarily *Pinus* sp.) supports for nest establishment within these locations. Additionally, because the seaside is a location for tourists, most human activities at the seafront occur during the summer when the *V. velutina* colonies are actively growing and the hor-

nets must find suitable food resources. Indeed, vespids are opportunistic foragers and are attracted to seafood products such as fishes, mussels or oysters, which can be used as bait in food traps (Spradbery, 1973; Edwards, 1980; Matsuura & Yamane, 1990; Monceau *et al.*, 2014, 2015a; Unelius *et al.*, 2014). *Vespa velutina* is also attracted by characteristic seafood odors such as *p*-xylene (Couto *et al.*, 2014), which is a component of oyster and fish odors (Piveteau *et al.*, 2000; Grigorakis *et al.*, 2003; Varlet *et al.*, 2006). Thus, a reasonable assumption was that fishery and oyster-farming wastes provided alternative fresh foods during the colony growth in the summer. Therefore, the oyster-farming port (Fig. 1, [1]), the 2 marinas (Fig. 1, Adernos [2a] and Lanton [2b]), and also the camping (Fig. 1, [3]) found on the seafront might provide valuable alternative food resources and might explain why the nests were found primarily in this part of the city and not farther inland in the environments that were mostly residential.

Relation between spring queen trapping and nest distribution

The trapping of spring queens is most likely one of the most popular methods to manage wasp populations. Moreover, this method was thought to be the most useful because foundresses are the most vulnerable during colony initiation (Spradbery, 1973). However, whether spring queen trapping achieves control is questionable. For example, spring queen trapping was promoted in the 1940s in New Zealand to eradicate *Vespula germanica*, and although more than 100 000 queens were trapped in 1948, no significant decrease in the population was observed the next year (Thomas, 1960). In France, because of the simplicity of the method (see Monceau *et al.*, 2012), beekeeper unions and local authorities have promoted spring queen trapping to fight against *V. velutina*. However, the capture yields are typically low, and several studies strongly indicate an effect on global entomofauna (Dauphin & Thomas, 2009; Haxaire & Villemant, 2010; Monceau *et al.*, 2012). To date, no experimental data have been produced to justify the use of this trapping method. In 2014 in Adernos, more than 800 *V. velutina* foundresses were trapped, but in that year, the highest number of nests was counted since the first appearance of the invader. As suggested by Archer and Halstead (2014) in a similar study, however, the *V. velutina* foundresses might have invaded this area from adjacent locations that were not managed with spring queen trapping. Nevertheless, if the trapping was efficient, one would expect that the traps would act against nest construction, and a clear

link between the trap locations and the spatial distribution of the nests would be observed. Instead, the distributions of the traps and the nests were clearly independent from one another. Collectively, these results showed that spring queen trapping was inefficient as a method to manage the populations of *V. velutina*.

Conclusions and perspectives for management

We believe this study is valuable for several different reasons. First, the analysis of the distribution of nests is commonly used in central place foragers such as *V. velutina* to examine population dynamics; several studies with ants (Kenne & Dejean, 1999; Schooley & Wiens, 2003; Tanner & Keller, 2012), wasps (Polidori *et al.*, 2008; Asís *et al.*, 2014) and bees (McNally & Schneider, 1996; Potts & Willmer, 1998; Rinderer *et al.*, 2002; Baum *et al.*, 2005) were released that provided important information about population regulation and dynamics. In this study, for the first time, we provided information on the nesting patterns of *V. velutina* and on the evolution of the nesting pattern in the years since the beginning of the invasion. We demonstrated that the number of nests increased from year to year from the beginning of the invasion and that intraspecific competition as a mechanism for the regulation of *V. velutina* populations is unlikely to be expected.

Second, this study provided information on local scale heterogeneity in nest distribution over 8 years. Although the patterns of distribution might be confirmed at similar scales or larger ones, the occurrence of alternative food sources (e.g., seafood, in the present case) might drive the establishment of *V. velutina* nests. Thus, at a local scale, it is possible to determine the areas (in this case, the seafront) in which to intensify surveys to increase the chances of early nest destruction. Indeed, this local scale approach is most likely one of the most promising techniques to limit the populations of *V. velutina* (review in Monceau *et al.*, 2014).

Third, our results should encourage efforts to abandon the trapping of queens in the early spring, because the balance between the benefits (i.e., managing *V. velutina* populations) and the costs (i.e., effects on entomofauna and logistical concerns) clearly weighed against the method (see also Monceau *et al.*, 2012 and Monceau *et al.*, 2014 for a discussion of this method).

Fourth, to date, the different simulations on the spatial expansion of *V. velutina* were based on the climatic suitability of the potential areas for invasion (Ibáñez-Justicia & Loomans, 2011; Villemant *et al.*, 2011; Barbet-Massin *et al.*, 2013). These studies were conducted at large spatial scales and no comparative study was performed at a local

scale. We believe that efforts should concentrate on the integration of the local scale framework to understand the finer scale mechanisms of colonization.

In our study, we did not have information on the size or the relatedness among colonies. A long-term survey to link the spatiotemporal nesting patterns with the genetic relatedness among colonies and the dispersing foundresses would provide valuable information on the colonization processes of this vespid alien predator, which would help in more accurate predictions of its expansion.

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Disclosure

The authors have no conflicts of interest, including specific financial interests and relationships and affiliations relevant to the subject of this manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site:

Table S1. GPS coordinates of nests in Andernos from 2007 to 2014.

Table S2. GPS coordinates of the 152 traps used for the spring queen trapping in 2014.