

# *Vespa velutina*: a new invasive predator of honeybees in Europe

Karine Monceau · Olivier Bonnard ·  
Denis Thiéry

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**Abstract** The yellow-legged hornet (*Vespa velutina*) is the first invasive Vespidae predator of honeybees to be accidentally introduced into Europe from Asia. In the current pollinator decline, *V. velutina* is an additional stressor for honeybees and other pollinators. Although *V. velutina* contributes to the loss of honeybee colonies, little is known about its biology and behaviour both in the native and in the invaded area. Here, we review the current knowledge of this species and describe its life cycle and life history traits (reproduction, overwintering, foraging and dispersal) in the light of the biology of other Vespidae. We also review the impact of this species on ecosystems, on the economics of beekeeping, and on human health (this species being potentially deadly for allergic people). Based on this information and on previous worldwide experiences with Vespidae invasions, we propose key research topics for the development of effective management plans. We identify methods to limit the impact and proliferation of *V. velutina* in Europe that are based on nest destruction, trapping, population genetics, and biological control. In our

opinion, research effort on the means to detect and destroy *V. velutina* nests at an early stage is required in order to short-circuit the colony cycle and thus limit both its impact on honeybees and its expansion through Europe. Finally, we discuss the impact of this biological invasion on the development of methods that should be used to manage alien species in the future.

**Keywords** *Apis mellifera* · Biodiversity · Invasive species · Pest management · Vespidae · Yellow-legged hornet

## Introduction

*Vespa velutina* (Lepeletier 1836), the yellow-legged hornet (Hymenoptera: Vespidae) is a recently introduced alien species in Europe. It was observed in southwest France for the first time in 2004 (Rortais et al. 2010). This is the first Vespidae predator accidentally introduced from Asia to Europe (Rortais et al. 2010; Roy et al. 2011) and the invasive population rapidly raised impressive size, especially in the west of the introduction area. This biological invasion has led to several serious problems because *V. velutina* preys on the domestic honeybee (*Apis mellifera*), disrupts the ecological role of the honeybee, potentially alters biodiversity, harms commercial beekeeping activities and is potentially deadly to allergic people. Beyond the ecological, economic and societal impacts common to all Vespidae invasions (Beggs et al. 2011), *V. velutina* invasion in Europe is a novel and dramatic example of the lack of emphasis on invasive species in Europe and demonstrates the urgency to establish efficient European policies to avoid future biological invasions.

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K. Monceau · O. Bonnard · D. Thiéry (✉)  
UMR 1065 Santé et Agroécologie du Vignoble, INRA, ISVV,  
33883 Villenave d'Ornon, France  
e-mail: thiery@bordeaux.inra.fr

K. Monceau · O. Bonnard · D. Thiéry  
UMR 1065 Santé et Agroécologie du Vignoble,  
Bordeaux Sciences Agro, ISVV, Université de Bordeaux,  
33883 Villenave d'Ornon, France

### Present Address:

K. Monceau  
Equipe Ecologie Evolutive, UMR 6282 Biogéosciences,  
Université de Bourgogne, 6 Bd Gabriel, 21000 Dijon, France

Despite this large impact on the whole ecosystem, several information about the biology and behaviour of *V. velutina* are still lacking. This limited knowledge represents a considerable disadvantage in the establishment of management plans. Given the current expanding distribution of *V. velutina*, it is increasingly important to identify research topics that will lead to the development of effective management strategies. In the present review, we first present the current situation of *V. velutina* invasion in Europe and then we propose a synthesis of the current literature on the biology and behaviour of *V. velutina* and its impact in the new invaded area. The knowledge of *V. velutina* is quite limited; hence we also examine the literature on closely related species in this review. Based on this information and on other reports of Vespidae invasions worldwide, we propose several key research areas and identify management methods that may limit the impact and dispersal of *V. velutina* in Europe. Our review is mostly based on data regarding the invasion of this species in France, the first European country to be invaded, but our identification of important research topics may also help other countries to develop effective methods for management of this species.

### Origin, invasion and current situation

Most *Vespa* species are native to Asia, except the European species, *Vespa crabro*, and the Oriental hornet, *Vespa orientalis*, which is mainly found in the sub-Mediterranean region (Spradbery 1973; Matsuura and Yamane 1990). *Vespa velutina* is common in central to eastern Asia (Yamane 1974; Starr 1992; Abrol 1994; Martin 1995; Carpenter and Kojima 1997; Nguyen and Carpenter 2002; Nakamura and Sonthichai 2004; Nguyen et al. 2006) and is currently spreading throughout Korea (Kim et al. 2006; Choi et al. 2012).

*Vespa velutina* was accidentally introduced into southwest France in a single event, probably via boat transport from the Zhejiang or Jiangsu provinces of eastern China (Arca 2012). The first European colony was recorded in 2004 close to Agen, beekeepers soon noted predation on honeybees in this area and the hornet rapidly colonized southwest France, followed by an increase in the number of nests (INPN 2013). Different simulations based on climatic similarities of locations in France and Asia predicted an expansion to most parts of France and neighbouring European countries (Ibáñez-Justicia and Loomans 2011; Villemant et al. 2011a). The comparison between native and invaded areas shows that they differ in their level of precipitation during the driest month of the year, the invaded areas receiving more precipitation than the native area (Villemant et al. 2011a). Increasing reports have



**Fig. 1** Queens of *Vespa crabro* (left) and *V. velutina* (right) (© K. Monceau)

mentioned *V. velutina* spread throughout Europe. Nests have been already destroyed in Spain (López et al. 2011) where beekeepers have already observed predation on their colonies in northwest Spain. Individuals have also been observed in Portugal (Grosso-Silva and Maia 2012) and in Belgium near the border with France where a flying male has been observed (Bruneau 2011; Thirion 2012). More recently, a nest has been destroyed for the first time in Italy at Vallecrosia near the French border (Demichelis et al. 2013).

### Biology and life history traits of *V. velutina*

#### Identification and description

*Vespa crabro* (the European hornet) and *V. velutina* can be easily distinguished from each other by their colours: brown and brownish yellow for *V. crabro* and black and yellow for *V. velutina* (Fig. 1) but also by their size, *V. crabro* being the largest (Fig. 1).

Within the species, sex differences in *V. velutina* are similar to those observed in other species: the presence/absence of sting (female/male) and the length of antennae (Edwards 1980). Indeed, the antennae of females are shorter and thinner than those of males (Fig. 2). Discrimination between queens and workers is less conspicuous because there is no apparent colour pattern which differentiates the individuals belonging in these castes. Body mass cannot be used with high confidence because it is highly variable across time (see Fig. 5 in Monceau et al. 2013a). Wing shape and size could, however, be used with more confidence although there is a slight overlap between queens and workers (Perrard et al. 2012).

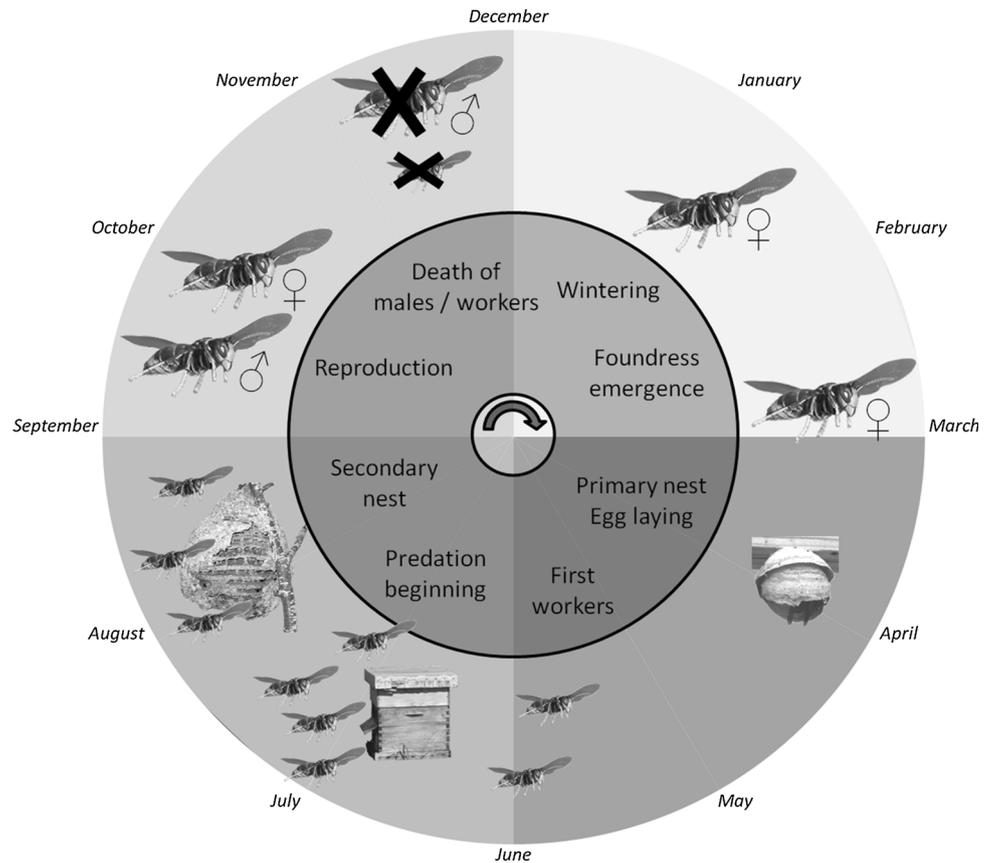
#### Life cycle (Fig. 3)

Like most *Vespa* species (Spradbery 1973; Matsuura and Yamane 1990; Takahashi et al. 2002, 2004a, b, 2007; but

**Fig. 2** Individuals belonging to the different castes in *Vespa velutina* (© K. Monceau)

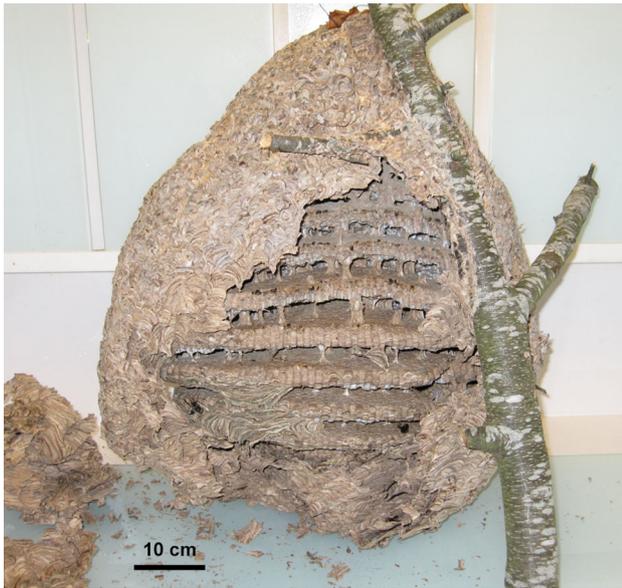


**Fig. 3** Life cycle of *Vespa velutina* in France. The crosses on males and workers in December stand for their death (only gynes survive winter) (© INRA, K. Monceau and D. Thiéry)



see, however, *V. affinis*, Ross and Carpenter 1991), nests in the French population of *V. velutina* are founded by a single queen (monogynous colonies; Arca 2012). The queen starts building its nest and rapidly lays eggs. During this phase (called “the queen colony phase”), the queen is alone and vulnerable until the first workers emerge. Then, colony and nest size increase throughout the summer. From spring to autumn, hundreds to thousands of individuals are produced (in average 6,000 individuals according to Villemant et al. 2011b). In autumn, the nest reaches its largest size (see Fig. 4 for an example). Autumnal colony

production is mainly focussed on gynes (potential queens) and males, and most activities are related to mating and dispersal. On average, three times more males seem to be produced from mid-September to end November (on average 350 gynes vs. 900 males; Villemant et al. 2011b). Although anecdotic observations reported the presence of living larvae in nests during the winter, only gynes (mated and unmated) are believed to over-winter (workers and males die before winter). The next spring, the fertilized foundresses initiate their new colony, but the fate of the unmated gynes and their proportion is unknown.



**Fig. 4** Example of the size of *Vespa velutina* nest in autumn (© K. Monceau)



**Fig. 5** Male *Vespa velutina* feeding on ivy (*Hedera helix*) (INRA Bordeaux-Aquitaine research centre, GPS: N44°47'18.20" W0°34'46.26", September 2011, © K. Monceau)

## Foraging behaviour

### Carbohydrates

Carbohydrates are the main source of energy for adult vespids (Raveret Richter 2000). These carbohydrates are provided by flower nectar, tree sap, or ripening fruits, depending on the environment and season. For example, in France, *V. velutina* foundresses often occur on camellia flowers (*Camellia* spp.) in spring and males often occur on ivy (*Hedera helix*; Fig. 5) during autumn. In southwest France, *V. velutina* frequently occurs in vineyards before and/or during grape harvest.

### Proteins

**Prey spectrum** The brood requires animal proteins which are transformed into flesh pellets and then offered to the larvae (Raveret Richter 2000). Proteins are collected by the queen during the queen colony phase and then by the workers. Vespids are opportunistic generalist foragers and scavengers, and feed on diverse arthropods, as well as on carrion, and stalls or waste from butchers and fishmongers (Spradbery 1973; Edwards 1980; Matsuura and Yamane 1990; Raveret Richter 2000). An analysis of *V. velutina* flesh pellets from few nests indicated that Apidae represented one-third to two-thirds of dietary protein, the proportion of which was suggested to depend on the nest location and environment (Villemant et al. 2011b). Indeed, the authors only qualified the nest environment but did not consider that the hornet hunting sites can differ, hornets potentially foraging in a large range around their nests (see “Foraging range” section below).

**Hunting behaviour with a special emphasis on honeybees** *Vespa velutina* predation on honeybee colonies increases throughout the summer and continues until the end of November in parallel with the population size of the hornet (Monceau et al. 2013a, b); the duration of the colony cycle might, however, vary according to the extension towards the north. Apiaries are large food sources that are concentrated in relatively small areas. *Vespa velutina* mainly preys upon flying honeybees that hover in front of the hive entrance (Abrol 1994; Monceau et al. 2013b). In Asia, they prey on the native Asian honeybee (*Apis cerana*) and on the introduced European honeybee (*A. mellifera*). Honeybee anti-predator behaviour against *V. velutina* has received a considerable interest because of the contrast between the native and the introduced species. Indeed, *A. cerana* which is likely to have coevolved with *V. velutina* exhibits efficient anti-predator behaviours against this hornet species, whereas *A. mellifera* suffers higher predation rate due to the inefficiency of its defence (Ken et al. 2005; Tan et al. 2007, 2010, 2012a, b, 2013). Anti-predator behaviours in *A. cerana* include a so-called defensive “bee-carpet” at the hive entrance, heat-balling and abdomen shacking movements (shimmering) (Ken et al. 2005; Tan et al. 2007, 2010, 2012a, b, 2013). With the exception of shimmering which has never been observed to date (Tan et al. 2013), *A. mellifera* is able to exhibit the same anti-predator behaviours as *A. cerana* but with lower efficiency. For example, *A. mellifera* workers may engulf hornets but the number of individuals recruited to produce the heat-ball and the temperature they are able to reach are lower than in *A. cerana* colonies (Ken et al. 2005). In Europe, *V. velutina* is the introduced species while *A. mellifera* is the native one, but the situation is equivalent. Although *A. mellifera*

can exhibit the bee-carpet behaviour and engulf hornets, the sustained and increasing predation of *V. velutina* from summer to autumn weakens honeybee colonies and may lead to increasing colony death rate during winter (Arca 2012; Monceau et al. 2013a, b).

#### Foraging range

Vespidae are central place foragers which can fly from 50 m to several kilometers from their nests (Edwards 1980; Matsuura and Yamane 1990). Currently, the foraging range of *V. velutina* is still unknown. Knowledge of *V. velutina* foraging range is crucial for pest management programme (Akre and Davis 1978) and could be studied, for example, by radio-tracking survey. Such data would be of major interest especially to understand the contribution of surrounding *V. velutina* colonies to predation on a given apiary (Monceau et al. 2013a).

#### Mating behaviour

Monandry is the most common mating system in eusocial Hymenoptera (Strassmann 2001), but previous research reported *Vespa* queens inseminated by multiple males in at least three species (*V. crabro*, *V. mandarinia*, and *V. simillima*, Foster et al. 1999; Takahashi et al. 2004a, b, 2007). Polyandry occurs from 10 % in *V. mandarinia* to 40 % in *V. simillima* (Takahashi et al. 2004a, 2007) and most colonies of these species are from a single queen (monogyny) who mated with a single male. Recent genetic analysis of nine colonies reveals that in eight of them, *V. velutina* gynes mated with several males (Arca 2012). In social insects, polyandry may be favoured because offspring from different patrines have increased genetic diversity (Keller and Reeve 1994; Boomsma and Ratnieks 1996; Jennions and Petrie 2000). Polyandry could thus be advantageous compared to monandry in increasing offspring genetic diversity and thus compensating the low genetic diversity due to the single introduction event (see Arca 2012).

Most gynes and males emerge during the autumn (Fig. 3). However, recent observations of nests maintained in laboratory conditions showed earlier production of males (Monceau et al. 2013c), and this has been confirmed by the presence of males captured in traps around hives during the early summer (Monceau et al. 2013a). Additionally, in captivity agonistic behaviours of workers against males were observed (Monceau et al. 2013c), which could be related to mating with kin avoidance (Tabadkani et al. 2012). This behaviour has, however, to be confirmed in the wild. Such agonistic behaviour has already been reported in *V. simillima* (Matsuura and Yamane 1990) and also occurs in the invasive paper wasp

(*Polistes dominulus*). In this species, females accept to mate more often with non-nestmate than with nestmate males which in consequence limit inbreeding (Liebert et al. 2010).

Depending on the *Vespa* species, mating may occur around the nests (and probably inside nests) and/or elsewhere (Matsuura and Yamane 1990; Ross and Carpenter 1991). For example, *V. mandarinia* males stay near the nest entrance and wait for emerging gynes, but males of other species may wait for females in other areas (Matsuura and Yamane 1990). So far, only few anecdotal observations of *V. velutina* copulations outside the nest have been reported (in captivity, N. Maher, pers. com.; on a sunny pavement, K. Monceau, pers. obs.). Additionally, male behaviour during autumn may argue for mating occurring outside the nest. Indeed, *V. velutina* males often occur on flowering plants, especially ivy (*H. helix*; Fig. 5), but the function of this attraction is unknown. Although they may forage for their own sustenance during their search for mates (ivy being a well-known autumnal source of nectar and pollen for many insects, Spradbery 1973), the plants visited by males during the autumn may represent a resource-based rendezvous site that improves their mating frequency (Ayasse et al. 2001; Boomsma et al. 2005; Spiewok et al. 2006). If so, then gynes should also occur on these plants. This hypothesis deserves further investigation because, like other social wasps, *V. velutina* may adopt resource defence polygamy (i.e. males patrolling in the female foraging range), with the gynes emerging asynchronously (Boomsma et al. 2005). Although resource defence polygamy may suggest the presence of competitive interactions between vespid males, this kind of interaction seems to be rare (Ross and Carpenter 1991) and no record of such behaviour has been reported so far for *V. velutina*.

Regardless of the mating location, sexual pheromones may play a role in mating. In social vespids, they can be produced by the males and the females (reviewed in Downing 1991; Ayasse et al. 2001). Although there is evidence for sex pheromone biological activity in several *Vespa* species (Ono and Sasaki 1987; Spiewok et al. 2006) and to a further extent in Vespidae, no specific sexual pheromone has yet been identified (Ayasse et al. 2001; Spiewok et al. 2006). Thus, focussing on sexual pheromones in *V. velutina* is an important task and would present interesting application to limit mating and thus to control populations. Several glands have been identified as potential source of sex pheromones such as venom gland in females (Post and Jeanne 1983; Keeping et al. 1986) and mandibular and/or sternal glands in males (Reed and Landolt 1990). Testing the secretion produced by these glands in *V. velutina* could therefore represent a first step to consider.

## Foundress dispersal, overwintering and emergence from overwintering

At the end of autumn, gynes search for hibernation sites outside the nest. They could be either mated or not; the proportion of mated ones is still unknown. Depending on the species, vespidae foundresses hibernate in the soil or tree crevices (Edwards 1980; Matsuura and Yamane 1990; Vetter and Visscher 1997) and *V. velutina* foundresses have been observed in woodpiles, shelters, or burrows during the winter. The dispersal range of *V. velutina* queens is not known, but the annual expansion range appears large and most probably favoured by passive dispersion through human-mediated transport (for example, in trucks transporting goods). However, it is not possible to separate natural from passive dispersion in the spatial expansion of this species. Evaluating and/or monitoring human-mediated dispersal would be difficult at least for two reasons: first such a dispersal occurs most of the time accidentally and second it represents a considerable amount of traffic through the French territory since France is a crossroads between eastern and western Europe.

Surprisingly, despite the fact that nest locations were recorded since 2004 in a French national database (INPN 2013), no predictive mathematical model of spatial expansion has been yet produced. Such an approach is, to our opinion, dramatically missing even though different studies attempted to evaluate the expansion risk as a function of climatic similarities with the native area of the hornet and climate change scenario (Ibáñez-Justicia and Loomans 2011; Villemant et al. 2011a; Barbet-Massin et al. 2013).

Like in other insects, abiotic conditions (temperature, day-length), genetic background, and endocrine levels affect the overwintering process in Vespidae (Spradbery 1973; Edwards 1980; Matsuura and Yamane 1990), but this has received too little attention. In *Polistes dominula*, the termination of diapause seems unrelated to the level of a juvenile hormone (JH) per se, but instead individual foundresses seem to have varying sensitivity to JH (Tibbetts et al. 2011). The overwintering of *V. velutina* ends in early spring, and foundresses fly from mid-March to late-June (Monceau et al. 2012, 2013a). Other research has documented long queen colony phase (see “Life cycle” section) in *V. crabro*, for example (Spradbery 1973). Variability in the duration of overwintering in other insects is documented as a “bet-hedging” strategy that may allow for adaptation to new or uncertain environments (Gourbière and Menu 2009) which is required for alien species colonizing new environments.

## Nesting behaviour

### Nest location

The characteristics of Vespidae nests vary among the different species (Edwards 1980; Matsuura and Yamane 1990). According to Kemper (1960), temperature, humidity, light intensity, shelter from rain, and shelter from wind are important for nest site selection because these factors determine the nest preservation which is essential for colony survival. Vespidae build papier-mâché nests by mixing plant fibres with water and saliva and add new layers over time (Edwards 1980), so easy access to suitable wood fibres is crucial. Vespidae may collect rotten or dead material from trees (Edwards 1980; Matsuura and Yamane 1990; Martin 1995), but no specific plant resource has been yet identified for *V. velutina* nest building, and it may depend upon the hornet species and the environment. In France, nests are often seen in poplars, which grow in riparian forest, i.e. in close vicinity to river. These trees may provide both a support and be located in close vicinity to a source of water for nest building. Indeed, queen trapping experiments in spring confirm that *V. velutina* foundresses occur mainly nearby water (Monceau et al. 2012). Initially, an analysis of the characteristics of the nest sites should help to identify the most important factors among those we have cited and thus defining the most suitable place for nest installation.

*Vespa velutina* nests are established either in or on tree tops, bushes, shrubs, roofs, and eaves in urban areas, and may also be underground (Edwards 1980; Starr and Jacobson 1990; Starr 1992; Martin 1995; Nakamura and Sonthichai 2004; Abrol 2006; Kim et al. 2006; Choi et al. 2012). Differences in the height of nests may be explained by the relocation of the colony (i.e. translocation of the entire colony from the embryo nest to a more suitable location for colony expansion; Matsuura and Yamane 1990). This behaviour occurring in Taiwan and South Korea (Matsuura 1991; Choi et al. 2012) is also expected to occur in Europe, but has not been yet documented to our knowledge. High nest locations mean that the workers must expend large amounts of energy for costly upward flight with a load (prey, nest material, or water). Thus, the increased cost should be balanced by other fitness gains like nest protection against enemies. Indeed, lower nests are more likely to be destroyed by humans because of their accessibility and thus, human destruction may lead to more nesting in treetops, with obvious consequences for *V. velutina* management.



**Fig. 6** Two nests of *Vespa velutina* (2, 3) in close vicinity each other and cohabiting with two other nests of *Polistes dominula* (1, 4). *Vespa velutina* nests are at 55 cm distance each other and the two nests of *P. dominula* are at about 15 cm distant to the hornet nests. (The picture was taken in May 2013 in a garden shed in Navailles-Angos, GPS: N43°23'43.53" W0°19'56.91", © K. Monceau with the courtesy of Mr Jacques Tardits)

#### Does competition between queens occur?

Intra- and inter-specific competition between foundresses (including competition for nesting sites and nest usurpation) could be considered a key factor that regulates population dynamics in *Vespa* species (Spradbery 1973; Edwards 1980; Matsuura and Yamane 1990; Röseler 1991). Such agonistic interactions are often evocated to discredit the reduction of queens by capture plans in spring (Haxaire and Villemant 2010), but to our knowledge no published data clearly shows such competition in France between *V. velutina* queens or between *V. velutina* and *V. crabro* queens. In spring 2013, two *V. velutina* nests have been observed in a garden shed, spaced half a meter from each other and surrounded by two *P. dominula* nests (Fig. 6). Although this observation is still anecdotic, it may question the hypothesis of intra-specific competition regulating alien hornet population. Inter-specific competition is also less likely to occur since it seems to be rare in areas where several *Vespa* species occur (Matsuura and Yamane 1990). Competition between *V. velutina* and *V. crabro* or wasp species (Fig. 6) has never been reported although this point should be clarified to estimate the potential threat of the alien on the native species.

#### Consequences of *V. velutina* invasion

Social Hymenopterans tend to be successful in invading new environments because their social organization allows a high degree of flexibility (Moller 1996; Wilson et al. 2009). In fact, many Vespidae have been reported as alien species worldwide (Cervo et al. 2000; Matthews et al. 2000; Beggs et al. 2011). The introduction of these species has had significant impact on the local ecology, economics, and human health (Beggs et al. 2011). Despite this, the impact of *V. velutina* in France has not been well-documented.

#### Impact on ecosystems

##### Predation

Although the causes and extent of the current pollinator decline is still debated (Ghazoul 2005a, b; Steffen-Dewenter et al. 2005; Biesmeijer et al. 2006), a decline of bee populations occurs in the northern Hemisphere (Brown 2011; Cameron et al. 2011; Bommarco et al. 2012). The introduction of alien parasite or predator species is one possible cause of this decline (Brown and Paxton 2009; Stout and Morales 2009; Schweiger et al. 2010). As previously evoked (see “Prey spectrum” section), bees have been observed to represent at least a third of the diet of *V. velutina*, but we do not yet have an accurate assessment of the consequence of the predation by *V. velutina* on pollination services. Considering the ecological and economic importance of pollinators, *V. velutina* is a particular concern. Surveys are therefore needed to locally assess the impact of *V. velutina* on pollination services either in different environmental conditions but also in interaction with other factors (i.e. parasites of bees, floral diversity, pesticides).

##### Intra-guild relations

Usually, the introduction of an alien predator can lead to displacement (i.e. niche exclusion) or replacement of the native predator from the same ecological guild (Snyder and Evans 2006). This may be caused by competition for the same resources, aggression between species, lower vulnerability of the alien species to native predators, or greater vulnerability of the native species to pathogens that were introduced with the alien (Snyder and Evans 2006; Kenis et al. 2009; Stout and Morales 2009; Crowder and Snyder 2010).

In the invaded areas of France, *V. velutina* may interfere with the European hornet (*V. crabro*), which is protected in some areas of its native range (e.g. in Germany since 1987, Federal Species Protection Ordinance—BArtSchV/Federal Nature Conservation Act—BNatSchG). *Vespa crabro* preys on diverse arthropods and is considered a beneficial organism in agriculture (Spradbery 1973; Matsuura and Yamane 1990). However, *V. crabro* can also prey upon honeybees (Baracchi et al. 2010), and be a direct competitor of *V. velutina* in apiaries where these species coexist. Moreover, since the introduction of *V. velutina*, some beekeepers have reported increased *V. crabro* predation on honeybees in southwest France. This feeds the hypothesis that *V. crabro* may benefit from the presence of *V. velutina* by facilitating prey access in weakening honeybee colony defences. We suggest that future studies investigate the

interaction between these two species and an eventual shift of habits in *V. crabro* as a consequence of *V. velutina* invasion.

#### *Alternative prey and/or host for native species*

Several organisms are known to feed upon and/or exploit Vespidae (Spradbery 1973; Edwards 1980; Matsuura and Yamane 1990). Some mammal and bird predators that inhabit the invaded areas prey upon Hymenopterans (including *V. crabro*), such as the Eurasian jay (*Garrulus glandarius*), the European bee-eater (*Merops apiaster*), and the European badger (*Meles meles*) (Spradbery 1973; Edwards 1980). A unique observation of the predation of *V. velutina* nest has been realized very recently in south west France near Bordeaux. The nest has been attacked and destroyed by a honey buzzard (*Pernis apivorus*), which is known to prey on hymenoptera nests (Vigneaud 2013). Additionally, domestic chickens (*Gallus gallus domesticus*) have been observed preying on *V. velutina* chasing in apiaries in south west France (Lescoutte-Garden 2013). A recent study identified *V. velutina* as potential additional host in China for the Israeli Acute Paralysis Virus (IAPV) which infects *A. mellifera* in China but also in France (Blanchard et al. 2008; Yañez et al. 2012). However, to date, there is currently no more evidence for predation or parasitism in France.

#### Effects on apiculture and economics

##### *Impact on honeybee colonies*

*Vespa velutina* predation on honeybees has clearly a direct economic impact on apiculture but, probably because the invasion is recent, sociological and economic studies quantifying this impact are lacking. In one report, a beekeeper claimed to have lost up to 80 % of his hives due to *V. velutina* predation (Cazenave 2013). Only a few recent estimates by beekeeper unions are available. In Gironde (southwest France), 30 % of hives were weakened and/or destroyed by *V. velutina* in 2010 (<http://www.unaf-apiculture.info>). One of the local beekeeper unions reported 7.5 % fewer hives during 2011 (7,110 in 2010, 6,576 in 2011) and almost 26 % fewer beekeepers insuring their hives (218 in 2010, 161 in 2011; Saunier 2011). In Dordogne, an epidemiological study (questionnaires sent to beekeepers) of 1,979 hives in 2009 and of 1,991 hives in 2010 indicated that ca. 5 % of the hives were destroyed by *V. velutina* each year, and that 16 and 27 % of the hives were weakened in 2009 and 2010, respectively (B. Darchen, pers. com.). These data should, however, be interpreted carefully, because not all beekeepers are professionals and not all of the hives were registered, making

the economic impact difficult to quantify. Clearly, the real impact appears much more over these data although no scientific publication is available. Moreover, it is difficult to distinguish damage from *V. velutina* from other factors that threaten *A. mellifera* colonies, such as parasites, viruses, habitat loss or fragmentation, insecticides and pesticides, and climate change (Cox-Foster et al. 2007; Brown and Paxton 2009; Johnson et al. 2010; Le Conte et al. 2010; Potts et al. 2010; vanEngelsdorp and Meixner 2010; Henry et al. 2012).

##### *Other societal impacts*

Another societal impact to consider is the cost associated with destruction of *V. velutina* nests. This task, mainly carried out by beekeepers, is risky, time-consuming, and expensive. In 2011, one French beekeeper union (GDSA) coordinated the destruction of more than 1,000 *V. velutina* nests in Aquitaine. Destruction of each nest took an average of one hour (displacement not included). In the geographical area of Toulouse (southwest France), a company specialized in pest eradication destroyed ca. 500 *V. velutina* nests in 2011. Such action cost €110 per nest and requires two visits: first to kill *V. velutina* by spraying insecticide powder directly into the nest, and second for removing the nest 1 week later to ensure that all individuals have returned to the nest and to avoid potential animal poisoning (E. Savary, pers. com.). There are reports that private companies have very high costs for nest destruction (over €500). Currently, these costs are mainly supported by the citizens, although some municipalities financially contribute.

##### Human health

*Vespa velutina* also has a direct impact on humans because colonies can occur in populated regions, and the occasionally spectacular size of the nests can generate frenzy. However, in contrast to its native range of Asia, where it is considered particularly aggressive with little provocation (Martin 1995), *V. velutina* in non-native regions is not considered to be aggressive when chasing or foraging. Since 2004, three deaths have been attributed to *V. velutina* stings. A recent study by the French Poison Control Centre reported only one confirmed human death due to *V. velutina* stings from 2007 to 2010, and no significant increase in Hymenoptera stings after its introduction (de Haro et al. 2010). However, the actual impact may be greater because many Hymenoptera stings are not reported. Moreover, the French media may contribute to the frenzy surrounding rare events. Finally, the number of deaths due to the anaphylactic shock from other Hymenoptera stings is not reported, so comparison with *V. velutina* is impossible.

## Pest management

Since the nineteenth century, several management plans have been tested worldwide against invasive vespids, but most attempts at eradication have failed (Beggs et al. 2011). In fact, eradication is generally considered impossible when an invasive vespid has widespread distribution. Assuming that total eradication is no longer possible and that geographical dispersal is still in progress, *V. velutina* management plans could target different stages of the life cycle (Fig. 3) and could involve: (1) nest destruction; (2) trapping of workers and queens; (3) control of reproduction; and (4) biological control.

In this section, we review the current pest management of *V. velutina* to identify promising techniques that should be undertaken or reinforced. We also identify several methods that should be investigated based on past experiences with vespid invasion worldwide.

### Nest destruction

Nest destruction (mechanically or chemically in using insecticides or biocide gas like sulphur dioxide injected in the nest) can be an effective method to control pest populations (Thomas 1960; Spradbery 1973), but would only be effective if all individuals, especially the queens, are destroyed so that the colony does not simply relocate. Ideally, all detected nests must be destroyed and removed as soon as possible to limit the impact on apiaries and the production of reproducers. However, in practice, complete destruction is almost impossible because most of the nests are cryptic until they reach a large size. Another problem is that newly emerged gynes may leave the nest while it is being destroyed. In such cases, the efficacy of nest destruction is very limited.

The number of nests actually reported to the French *V. velutina* nest database (INPN 2013) depends on the quality of the observation network. Scientists in charge of this database report that at least one-third of the public identifications are wrong (Rome et al. 2011). The inaccuracy of this database is suspected to increase as a function of the pest extension. Indeed, during the past 2 years, thousands of nests have been destroyed in southwest France, particularly those near human activities (schools, houses, etc.). However, nest destruction is neither locally nor nationally coordinated, making complete and relevant information about the number of destroyed nests unavailable.

### Trapping individuals

Hornets can be trapped using food baits (carbohydrates or proteins). Those traps can be used for monitoring (see for example, Monceau et al. 2012, 2013a) or for destruction

(mass trapping or traps baited with insecticides). Insecticides are currently assayed both for their direct and indirect effect (the adult hornet bring small doses of insecticide back to the nest) (Thomas 1960; Spradbery 1973; Edwards 1980; Beggs et al. 2011). To date, only traps baited with food are used to catch *V. velutina* (workers and queens), because this is a simple and inexpensive method that everybody can use. Insecticide-based baits have been used to control alien wasp species, and have effectively reduced invasive *Vespula* populations by up to 99.7 % (see Beggs et al. 2011 and references therein). Nevertheless, this method requires that the toxic bait only targets the alien species or is coupled with a specific attractant to avoid any side effect on other species. Presently, no such product is available for *V. velutina*.

### Trapping *V. velutina* workers to protect apiaries

The protection of beehives is currently the major concern. This can be achieved by placing lure traps in their vicinity. Obviously, apiary protection must allow trapping and/or killing of hornets but not honeybees. To date, beekeepers have used direct mechanical destruction (killing of hornets flying in front of their hives) and traps baited with carbohydrates (apple juice, for example Monceau et al. 2013a) or proteins. Nevertheless, such trapping should be considered as a local preventative rather than a real solution for limiting the dispersal of *V. velutina*. Depriving hornets and their brood from their major food source may also limit population size. However, *V. velutina* does not feed exclusively on honeybees and any possible risk of prey shift (e.g. to wild bees) should be considered. Nevertheless, we should note that food traps are not selective and should be used cautiously to limit the impact on non-target species (Monceau et al. 2013a).

### Trapping *V. velutina* queens

Queens are responsible for the establishment of new colonies, so they are optimal targets for *V. velutina* management. Queen trapping can be performed before and/or after hibernation (Fig. 3).

During autumn and the beginning of winter, the gyne population is at its largest, so this is a good time for trapping. This kind of trapping has been used in New Zealand, which was invaded by the European wasp (*Vespula germanica*) in the 1940s (Thomas 1960). In 1948, the New Zealand Department of Agriculture paid a bounty for each queen, and this led to the collection of 118,000 individuals. Unfortunately, this had no significant effect on the population density in the following year (Thomas 1960). Thomas (1960) postulated that this occurred simply because a single queen is sufficient for nest establishment.

For example, the survival rate of *Vespula vulgaris* queens has been estimated only 0.01 % (Archer 1980), making natural selection probably more efficient than human trapping.

According to Spradbery (1973), the most critical stage of the *V. velutina* life cycle is nest initiation by a single foundress during spring. Spring trapping of queens has been used in southwest France since 2007 and beekeepers unions currently promote this technique (Blot 2009). This method employs sweet bait that is mixed with beer (alcohol is supposed to repel honeybees) to lure foundresses. Nevertheless, spring queen trapping is controversial because of possible collateral damage to the entomofauna (Monceau et al. 2012). As far as agricultural activities are concerned, the use of pest trapping always has a potential effect on biodiversity, as the entomofauna (mostly dipterans) undoubtedly suffers from spring queen trapping (Dauphin and Thomas 2009; Haxaire and Villemant 2010; Monceau et al. 2012), and possibly from trapping at other times of year. This method is also questionable because its efficacy appears limited (Haxaire and Villemant 2010; Monceau et al. 2012). Currently, this controversy has not been resolved. Indeed, like for trapping before hibernation, reliable data about the efficacy of queen trapping are missing.

#### Limiting the reproduction: exploiting the Allee effect

Exploitation of the Allee effect (decrease in per capita population growth due to reduced population density; Courchamp et al. 1999) has been proposed as a management tool for alien species (Liebhold and Tobin 2008; Tobin et al. 2011; Suckling et al. 2012). The Allee effect may be mediated by reduced mate availability and/or inbreeding depression (Liebhold and Tobin 2008). This could be achieved in *V. velutina* by: (1) trapping queens (see above); (2) trapping males, and/or (3) mating disruption.

Trapping males using pheromones could reduce the number of potential mates and increase the proportion of unfertilized queens. In Hymenopterans, fertilized eggs develop into diploid females and unfertilized eggs develop into haploid males (haplodiploidy). Thus, unfertilized queens would still produce males, so the effectiveness of such method is doubtful (Fauvergue et al. 2007; but see Fauvergue and Hopper 2009). Nevertheless, this method could increase inbreeding and lead to the production of sterile diploid males. As previously stated, *V. velutina* invasion occurs as a single event, so the population has low genetic diversity due to the founder effect (Arca et al. 2011; Arca 2012). Although males are mostly haploid,

some of them can be diploid due to complementary sex determination, particularly in inbred populations (see Fig. 1 in Liebert et al. 2010 for an explanation). Diploid males are often sterile and impose a large fitness cost on the colony (Liebert et al. 2004), potentially leading to an extinction vortex (Zayed and Packer 2005). Diploid males have been already reported in French populations of *V. velutina* (Arca 2012). However, male trapping can be considered solely if the attraction of mate depends on the production of female pheromones.

Another possibility for exploitation of the Allee effect is mating disruption (i.e. altering the communication between males and females during reproduction to prevent them from finding mate; Cardé and Minks 1995; Witzgall et al. 2010) by use of sex pheromones. However, no sex pheromones have yet been identified in *V. velutina* and we do not know exactly where mating occurs. In general, mating behaviour and male behaviour are poorly characterized in this species, so research on these topics should be very useful.

#### Biological control

As previously stated (see “[Alternative prey and/or host for native species](#)”), several natural enemies are potential candidates for biological control of *V. velutina*. At present, there are few known potential predators of *V. velutina*, but parasites can also be used as biological control agents. An alien species can be free of parasites, parasitized by its native species, or may acquire parasites from its new environment. Parasites can have important roles in the success of an alien invasion and in population growth (Prenter et al. 2004; Dunn 2009). Indeed, since *V. velutina* and *A. mellifera* had not enough time to coevolve in France, *V. velutina* did not adapt to the endemic parasites. It is possible that *V. velutina* could be affected by the native parasites from *V. crabro*, native honeybees, and/or other pollinators. For example, honeybees are infected by several microparasites (microsporidia, viruses, fungi and bacteria) and macroparasites (parasitic mites; Schmid-Hempel 1995), so these species may also infect *V. velutina*. For example, *V. velutina* may be vulnerable to IAPV, which is present in France (Blanchard et al. 2008). In Asia, the Trigonalid parasitic wasp *Bareogonalos jezoensis* is a parasite of *V. velutina* (Matsuura and Yamane 1990). However, the presence of this parasitic wasp species has never been reported in France and its involvement in biological control for *V. velutina* cannot be considered since it also parasitizes *V. crabro*. Alternatively, the release of new parasites or viruses of *V. velutina* in France may have profound effects on other species. Thus, identification of

the organisms able to parasitize *V. velutina* may allow selecting potential biological control agents, but these biological control agents may be transmissible to native species.

Overall, the main limitation for developing a biological control programme for *V. velutina* is our poor knowledge of its basic ecology and biology. Consequently, biological control cannot be considered until such basic investigations are conducted.

#### Selection for resistant honeybee colonies

Surprisingly, the parallel between *V. velutina* and the parasitic mite *Varroa destructor* has never been realized. Indeed, varroa mites parasitize *A. cerana* in Asia and have been transmitted to *A. mellifera* colonies imported to Asia. This mite then spread worldwide with its new host, and invaded European countries in late 1960s (de Guzman et al. 1997; Oldroyd 1999; Sammataro et al. 2000; Rosenkranz et al. 2010; vanEngelsdorp and Meixner 2010). This mite feeds on the bee hemolymph and causes significant harm at the individual and colony level (Genersch 2010; Rosenkranz et al. 2010; vanEngelsdorp and Meixner 2010). Like *A. cerana* displays efficient anti-predator behaviour against *V. velutina*, this honeybee species displays hygienic and grooming behaviours that decrease the number of varroa mites (Boecking and Spivak 1999; Rath 1999; Rosenkranz et al. 2010). Although feral honeybees have been managed to obtain *Varroa*-resistant colonies (Büchler et al. 2010; Rosenkranz et al. 2010), unmanaged European honeybees have also developed resistance in recent years, based on reports in France (Le Conte et al. 2007) and Gotland Sweden (Fries et al. 2006). This suggests that natural selection has favoured the development of a honeybee defence or resistance mechanism (Fries and Bommarco 2007). Artificial selection may also play a role in mite resistance, but the heritability of traits such as grooming and other hygienic behaviours appears to be low, so this topic requires more investigation (Büchler et al. 2010; Rosenkranz et al. 2010).

Just as the invasion of *V. destructor* almost four decades ago had a significant impact on beekeeper activities, the invasion of *V. velutina* represents an additional source of stress for honeybee colonies in the current pollination decline. In France for instance, beekeeping has a long history of selection for colony docility, but selection for more defensive honeybees may be a strategy to limit *V. velutina* predation. Research on the behavioural characteristics of resistant colonies should be very fruitful. Indeed, honeybee colonies can differ significantly in their collective behaviour (Wray et al. 2011), and some colony behaviours may more effectively limit *V. velutina* predation. Thus, selection for colony defensiveness and other

behavioural traits should be considered as a strategy to reduce the impact of *V. velutina*.

#### Pest management policies

The invasion of *V. velutina* in Europe presents a practical challenge to current policies regarding management of invasive species. Indeed, our experience with *V. velutina* highlights the importance of early reaction following a pest introduction, a key parameter that affects the success of pest management (Myers et al. 1998). The success of the *V. velutina* invasion indicates that France, like several other European countries, does not have an effective preventive programme in place. This is in contrast to some other countries, which have strong pest preventive programmes (e.g. surveillance and quarantine programmes). In particular, island countries often have strong preventive programmes because they are aware that insular biota are more vulnerable to biological invasions (Reaser et al. 2007; Yoshida 2008). Australia is now the only country worldwide to be free of varroa mites and this is probably the result of their acute surveillance programmes (Clifford et al. 2011).

According to Myers et al. (2000), eradication can often be considered at the early stage of an alien invasion. In winter 2012, the French government legally classified *V. velutina* as a noxious pest species. As of December 26, 2012 (Journal Officiel de la République Française 2012), *V. velutina* is registered as “class 2 health hazard” (i.e. prevention, surveillance and/or management are not obligatory, but may be realized in the collective interest). To date, some neighbouring countries (Switzerland and the UK for example) have already proposed assessment risk plans or developed response programmes to manage the eventual invasion of this species (Péré and Kenis 2010; Marris et al. 2011) even though the pest did not yet enter these countries.

At the European level, invasive species policies are diverse, with little coordination within and between member states, and this may favour the proliferation of alien pests (Commission of the European Communities 2008; Shine et al. 2010; Keller et al. 2011). One of the most promising methods would be the enhancement of European border controls to limit invasions into new countries (Bacon et al. 2012). On April 20, 2012, the European Parliament adopted resolution EU 2020 Biodiversity Strategy [2011/2307(INI)], which included a directive concerning invasive species policy. A legislative proposal establishing European common policy has been released on September 9th, 2013 and should be soon examined by the European Council and Parliament before being adopted (European Commission 2013).

**Table 1** Summary of important key research topics for the management of *Vespa velutina* invasive populations

<b>Nest detection and destruction</b>	
Nest detection	Studies on colony behaviour/dynamics <sup>a</sup> Determination of nest site characteristics
Destruction methods	Find suitable and authorized biocides <sup>b</sup>
<b>Foraging range</b>	
Foraging range around the nest (central place foragers)	Mean foraging range Amount of prey (number of apiaries within the range) Resource-based rendezvous sites for reproduction
<b>Queen dispersal/pattern of expansion</b>	
Colonization history	Identify the colonization pathway(s) Identify the mean of dispersal (natural/human-mediated/both)
Monitoring the invasion (space and time)	Predictive spatial model of local/national expansion <sup>a</sup> Determine the risk of invasion in neighbouring countries <sup>a</sup>
Management network	Identify the most suitable actors to lead the management plan Coordination of the beekeepers Coordination between member states of the European Union International database for nest localization (open access for all actors)
<b>Chemical communication</b>	
Sexual pheromones	Knowledge of the sexual behaviour of <i>V. velutina</i> <sup>a</sup> Sexual pheromone characterization Male trapping Mating disruption
Pheromones	Trap selectivity/attractiveness/repellency <sup>a</sup>
Kairomones	Food preferences <sup>a</sup> Trap attractiveness <sup>a</sup>
<b>Honeybee behaviour</b>	
Strategies to defend/cope with predation pressure	Profile of resistant colonies <sup>a</sup> Heritability of the behaviours Selection based on defensiveness
<b>Pathogens and predators</b>	
Natural enemies	Find native predator/parasite candidates
Biological control	Susceptibility to honeybees and/or <i>V. crabro</i> pathogens
Disease transmission from hornet to native species	Sanitary status survey of <i>V. velutina</i> populations
<b>Ecological costs of the predation</b>	
Trophic chain	Impact on honeybee colonies (stress of the colony/the queen) <sup>a</sup> Impact on pollination services
Intra-guild relations	With <i>V. crabro</i> (competition, facilitation?) <sup>a</sup> Competition with other insect predators
Native predator/parasite	Impact on population dynamics of native predator and parasites

<sup>a</sup> Items on which researches have already started

<sup>b</sup> SO<sub>2</sub> is not considered a biocide by the European Union directive 98/8/CE and it is not legally used to kill hornets. In France, it has been authorized for a 120-day period in 2013 (Journal Officiel de la République Française 2013)

## Concluding remarks

Several lessons can be drawn from *V. velutina* invasion. First, European policies should be improved to avoid a novel dramatic invasion. The experience of Australia with *V. destructor* (Australia is still the only country free of varroa, thanks to the effectiveness of its policies) is probably the best example to illustrate that point. Second, the knowledge of the biology and behaviour of the alien

species is essential to establish management plans. In the current context, our lack of efficacy is mainly due to our lack of knowledge of the animal. Filling this gap of knowledge will considerably enhance our chance to manage the invasive population of *V. velutina* properly and thus to protect honeybees. Human, technical and obviously financial resources are especially needed and should be rapidly accessible. Third, whatever method is ultimately deemed effective, a well-organized and widespread control

plan must be implemented as soon as possible for the whole invaded area, because re-invasion will always occur from adjacent untreated regions, so widespread and well-coordinated plans are needed.

Obviously, funding dedicated to *V. velutina* research is not unlimited and priorities should be considered (see Table 1 for a summary). At the present time, to our knowledge, several research teams in France and Spain are already engaged on trap design and on the identification of attractants and/or pheromones. One promising lead which should also be promoted is the early and systematic detection and destruction of nests to short-circuit the colony cycle. However, even if the number of nests increases and the detection tools progress, finding them early in the season is like looking for a needle in a haystack and would require a large human and financial investment.

Finally, *V. velutina* is the first invasive species to have received significant media attention in Europe, probably because its preferred prey, the honeybee, is a symbol of biodiversity and because many people are afraid of wasps and hornets. However, we currently lack accurate and reliable data on the effects of this new alien species on ecosystems and human activities. Initial simulations suggest that this species will soon disperse throughout Europe and along the Mediterranean coast, so it will likely have a drastic impact in countries in which there is significant apiculture, if not managed before.

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## References

- Abrol DP (1994) Ecology, behaviour and management of social wasp, *Vespa velutina* Smith (Hymenoptera: Vespidae), attacking honeybee colonies. Korean J Apic 9:5–10
- Abrol DP (2006) Defensive behaviour of *Apis cerana* F. against predatory wasps. J Apic Sci 50:39–46
- Akre RD, Davis HG (1978) Biology and pest status of venomous wasps. Annu Rev Entomol 23:215–238
- Arca M (2012) Caractérisation génétique et étude comportementale d'une espèce envahissante en France: *Vespa velutina* Lepeletier (Hymenoptera, Vespidae). PhD dissertation. Université Pierre et Marie Curie, Paris
- Arca M, Capdevielle-Dulac C, Villemant C, Mougél F, Arnold G, Silvain J-F (2011) Development of microsatellite markers for the yellow-legged Asian hornet, *Vespa velutina*, a major threat for European bees. Conserv Genet Resour 4:283–286
- Archer ME (1980) Population dynamics. In: Edwards R (ed) Social wasps. Their behaviour and control. Rentokil Limited, Sussex, pp 172–207
- Ayasse M, Paxton RJ, Tengö J (2001) Mating behavior and chemical communication in Hymenoptera. Annu Rev Entomol 46:31–78
- Bacon SJ, Bacher S, Aebi A (2012) Gaps in border controls are related to quarantine alien insect invasions in Europe. PLoS One 7:e47689
- Baracchi D, Cusseau G, Pradella D, Turillazzi S (2010) Defence reactions of *Apis mellifera ligustica* against attacks from the European hornet *Vespa crabro*. Ethol Ecol Evol 22:1–14
- Barbet-Massin M, Rome Q, Muller F, Perrard A, Villemant C, Jiguet F (2013) Climate change increases the risk of invasion by the yellow-legged hornet. Biol Conserv 157:4–10
- Beggs JR, Brockerhoff EG, Corley JC, Kenis M, Masciocchi M, Muller F, Rome Q, Villemant C (2011) Ecological effects and management of invasive Vespidae. Biocontrol 56:505–526
- Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J, Kunin WE (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313:351–354
- Blanchard P, Schurr F, Celle O, Cougoule N, Drajnudel P, Thiéry R, Faucon J-P, Ribière M (2008) First detection of Israeli acute paralysis virus (IAPV) in France, a dicistrovirus affecting honeybees (*Apis mellifera*). J Invertebr Pathol 99:348–350
- Blot J (2009) Fiche technique apicole: Le frelon asiatique (*Vespa velutina*)—Le piégeage des fondatrices. Bull Tech Apic 36:55–58
- Boecking O, Spivak M (1999) Behavioral defenses of honey bees against *Varroa jacobsoni* Oud. Apidologie 30:141–158
- Bommarco R, Lundin O, Smith HG, Rundlöf M (2012) Drastic historic shifts in bumble-bee community composition in Sweden. Proc R Soc B Biol Sci 279:309–315
- Boomsma JJ, Ratnieks FLW (1996) Paternity in eusocial hymenoptera. Philos Trans R Soc B Biol Sci 351:947–975
- Boomsma JJ, Baer B, Heinze J (2005) The evolution of male traits in social insects. Annu Rev Entomol 50:395–420
- Brown MJF (2011) The trouble with bumblebees. Nature 469:169–170
- Brown MJF, Paxton RJ (2009) The conservation of bees: a global perspective. Apidologie 40:410–416
- Bruneau E (2011) Le frelon asiatique, déjà là! ActuApi 55:1–6
- Büchler R, Berg S, Le Conte Y (2010) Breeding for resistance to *Varroa destructor* in Europe. Apidologie 41:393–408
- Cameron SA, Lozier JD, Strange JP, Koch JB, Cordes N, Solter LF, Griswold TL (2011) Patterns of widespread decline in North American bumble bees. Proc Natl Acad Sci USA 108:662–667
- Cardé RT, Minks AK (1995) Control of moth pests by mating disruption: successes and constraints. Annu Rev Entomol 40:559–585
- Carpenter JM, Kojima J-I (1997) Checklist of the species in the subfamily Vespinae (Insecta: Hymenoptera: Vespidae). Nat Hist Bull Ibaraki Univ 1:51–92
- Cazenave C (2013) L'offensive éclair d'un tueur en série. Sciences et Avenir 175:58–61
- Cervo R, Zacchi F, Turillazzi S (2000) *Polistes dominulus* (Hymenoptera, Vespidae) invading North America: some hypotheses for its rapid spread. Insect Soc 47:155–157
- Choi MB, Martin SJ, Lee JW (2012) Distribution, spread, and impact of the invasive hornet *Vespa velutina* in South Korea. J Asia Pac Entomol 15:473–477
- Clifford D, Barry S, Cook D, Duthie R, Anderson D (2011) Using simulation to evaluate time to detect incursions in honeybee biosecurity in Australia. Risk Anal 31:1961–1968
- Commission of the European Communities (2008) Towards a strategy on invasive species. Communication from the Commission to the

- Council, the European Parliament, the European Economic and Social Committee and the Committee of Regions (COM (2008) 789 final). [http://ec.europa.eu/environment/nature/invasivealien/docs/1\\_EN\\_ACT\\_part1\\_v6.pdf](http://ec.europa.eu/environment/nature/invasivealien/docs/1_EN_ACT_part1_v6.pdf). Accessed 25 October 2013
- Courchamp F, Clutton-Brock T, Grenfell B (1999) Inverse density dependence and the Allee effect. *Trends Ecol Evol* 14:405–410
- Cox-Foster DL, Conlan S, Holmes EC, Palacios G, Evans JD, Moran NA, Quan P-L, Briese T, Hornig M, Geiser DM, Martinson V, vanEngelsdorp D, Kalkstein AL, Drysdale A, Hui J, Zhai J, Cui L, Hutchison SK, Simons JF, Egholm M, Pettis JS, Lipkin WI (2007) A metagenomic survey of microbes in honey bee colony collapse disorder. *Science* 318:283–287
- Crowder DW, Snyder WE (2010) Eating their way to the top? Mechanisms underlying the success of invasive insect generalist predators. *Biol Invasions* 12:2857–2876
- Dauphin P, Thomas H (2009) Quelques données sur le contenu des “pièges à frelons asiatiques” posés à Bordeaux (Gironde) en 2009. *Bull Soc Linn Bordeaux* 37:287–297
- de Guzman LI, Rinderer TE, Stelzer JA (1997) DNA evidence of the origin of *Varroa jacobsoni* Oudemans in the Americas. *Biochem Genet* 35:327–335
- de Haro L, Labadie M, Chanseau P, Cabot C, Blanc-Brisset I, Penouil F (2010) Medical consequences of the Asian black hornet (*Vespa velutina*) invasion in South Western France. *Toxicon* 55:650–652
- Demichelis S, Manimo A, Porporato M (2013) Trovato il primo nido di *Vespa velutina* a Vallecrosia (IM). In: Comunicato Stampa. Università Degli Studi di Torino, Turin. <http://www.apilandia.it/capt/doc/Vespa%20velutina%202013.pdf>. Accessed 25 October 2013
- Downing HA (1991) The function and evolution of exocrine glands. In: Ross KG, Matthews RW (eds) *The social biology of wasps*. Cornell University Press, New York, pp 540–569
- Dunn AM (2009) Parasites and biological invasions. *Adv Parasitol* 68:161–184
- Edwards R (1980) *Social wasps. Their behaviour and control*. Rentokil Limited, Sussex
- European Commission (2013) Proposal for a regulation of the European Parliament and the Council on the prevention and management of the introduction and spread of invasive alien species, 2013/0307 (COD). <http://ec.europa.eu/environment/nature/invasivealien/docs/proposal/en.pdf>. Accessed 25 October 2013
- Fauvergue X, Hopper KR (2009) French wasps in the New World: experimental biological control introductions reveal a demographic Allee effect. *Popul Ecol* 51:385–397
- Fauvergue X, Malausa J-C, Giuge L, Courchamp F (2007) Invading parasitoids suffer no Allee effect: a manipulative field experiment. *Ecology* 88:2392–2403
- Foster KR, Seppä P, Ratnieks FLW, Thören PA (1999) Low paternity in the hornet *Vespa crabro* indicates that multiple mating by queens is derived in vespine wasps. *Behav Ecol Sociobiol* 46:252–257
- Fries I, Bommarco R (2007) Possible host-parasite adaptations in honey bees infested by *Varroa destructor* mites. *Apidologie* 38:525–533
- Fries I, Imdorf A, Rosenkrank P (2006) Survival of mite infested (*Varroa destructor*) honey bee (*Apis mellifera*) colonies in a Nordic climate. *Apidologie* 37:1–7
- Genersch E (2010) Honey bee pathology: current threats to honey bees and beekeeping. *Appl Microbiol Biotechnol* 87:87–97
- Ghazoul J (2005a) Buzziness as usual? Questioning the global pollination crisis. *Trends Ecol Evol* 20:367–373
- Ghazoul J (2005b) Response to Steffan-Dewenter et al.: questioning the global pollination crisis. *Trends Ecol Evol* 20:52–653
- Gourbière S, Menu F (2009) Adaptive dynamics of dormancy duration variability: evolutionary trade-off and priority effect lead to suboptimal adaptation. *Evolution* 63:1879–1892
- Grosso-Silva JM, Maia M (2012) *Vespa velutina* Lepeletier, 1836 (Hymenoptera, Vespidae), new species for Portugal. *Arquivos Entomoloxicos* 6:53–54
- Haxaire J, Villemant C (2010) Impact sur l'entomofaune des “pièges à frelon asiatique”. *Insectes* 159:1–6
- Henry M, Béguin M, Requier F, Rollin O, Odoux J-F, Aupinel P, Aptel J, Tchamitchian S, Decourtye A (2012) A common pesticide decreases foraging success and survival in honey bees. *Science* 336:348–350
- Ibáñez-Justicia A, Loomans AJM (2011) Mapping the potential occurrence of an invasive species by using CLIMEX: case of the Asian hornet (*Vespa velutina nigrithorax*) in The Netherlands. *Proc Neth Entomol Soc Meet* 22:39–46
- INPN (2013) Inventaire National du Patrimoine Naturel. <http://inpn.mnhn.fr>. Accessed 25 October 2013
- Jennions MD, Petrie M (2000) Why do females mate multiply? A review of the genetic benefits. *Biol Rev* 75:21–64
- Johnson RM, Ellis MD, Mullin CA, Frazier M (2010) Pesticides and honey bee toxicity—USA. *Apidologie* 41:312–331
- Journal Officiel de la République Française (2012) Vendredi 28 décembre 2012/No 302. Arrêté du 26 décembre 2012 relatif au classement dans la liste des dangers sanitaires du frelon asiatique. NOR: AGRG1240147A. <http://www.journal-officiel.gouv.fr/frameset.html>. Accessed 25 October 2013
- Journal Officiel de la République Française (2013) Samedi 7 Septembre 2013/No 208. Arrêté du 21 août 2013 autorisant provisoirement la mise sur le marché et l'utilisation du dioxyde de soufre. NOR: DEVP1321388A. <http://www.journal-officiel.gouv.fr/frameset.html>. Accessed 25 October 2013
- Keeping MG, Lipschitz D, Crewe RM (1986) Chemical mate recognition and release of male sexual behavior in polybiine wasp, *Belonogaster petiolata* (DeGeer) (Hymenoptera: Vespidae). *J Chem Ecol* 12:773–779
- Keller L, Reeve HK (1994) Genetic variability, queen number, and polyandry in social Hymenoptera. *Evolution* 48:694–704
- Keller RP, Geist J, Jeschke JM, Kühn I (2011) Invasive species in Europe: ecology, status, and policy. *Environ Sci Europe* 23:23
- Kemper H (1960) Über die nistplatz auswahl bei den sozialen faltenwespen Deutschlands. *Z Angew Zool* 47:457–483
- Ken T, Hepburn HR, Radloff SE, Yusheng Y, Yiqiu L, Danyin Z, Neumann P (2005) Heat-balling wasps by honeybees. *Naturwissenschaften* 92:492–495
- Kenis M, Auger-Rozenberg M-A, Roques A, Timms L, Péré C, Cock MJW, Settele J, Augustin S, Lopez-Vaamonde C (2009) Ecological effects of invasive alien insects. *Biol Invasions* 11:21–45
- Kim J-K, Choi MB, Moon T-Y (2006) Occurrence of *Vespa velutina* Lepeletier from Korea, and a revised key for Korean *Vespa* species (Hymenoptera: Vespidae). *Entomol Res* 36:112–115
- Le Conte Y, de Vaublanc G, Crauser D, Jeanne F, Rousselle J-C, Bécard J-M (2007) Honey bee colonies that have survived *Varroa destructor*. *Apidologie* 38:566–572
- Le Conte Y, Ellis M, Ritter W (2010) *Varroa* mites and honey bee health: can *Varroa* explain part of the colony losses? *Apidologie* 41:353–363
- Lescoutte-Garden C (2013) Landes : le poulet, l'arme fatale contre le frelon asiatique ? Sud Ouest 01/10/2013. <http://www.sudouest.fr/2013/10/01/poulet-contre-frelon-1185067-3452.php>. Accessed 25 October 2013
- Liebert AE, Johnson RN, Switz GT, Starks PT (2004) Triploid females and diploid males: underreported phenomena in *Polistes* wasps? *Insect Soc* 51:205–211
- Liebert AE, Wilson-Rich N, Johnson CE, Starks PT (2010) Sexual interactions and nestmate recognition in invasive populations of *Polistes dominulus* wasps. *Insect Soc* 57:457–463

- Liebhold AM, Tobin PC (2008) Population ecology of insect invasions and their management. *Annu Rev Entomol* 53:387–408
- López S, González M, Goldarazena A (2011) *Vespa velutina* Lepeletier, 1836 (Hymenoptera: Vespidae): first records in Iberian Peninsula. *Bull OEPP/EPPO Bull* 41:439–441
- Marris G, Brown M, Cuthbertson AG (2011) GB non-native organism risk assessment for *Vespa velutina nigrithorax*. <http://www.nonnativespecies.org>. Accessed 25 October 2013
- Martin SJ (1995) Hornets (Hymenoptera: Vespinae) of Malaysia. *Malay Nat J* 49:71–82
- Matsuura M (1991) *Vespa* and *Provespa*. In: Ross KG, Matthews RW (eds) *The social biology of wasps*. Cornell University Press, New York, pp 232–262
- Matsuura M, Yamane S (1990) *Biology of vespine wasps*. Springer-Verlag, Berlin
- Matthews RW, Goodisman MAD, Austin AD, Bashford R (2000) The introduced English wasp *Vespula vulgaris* (L.) (Hymenoptera: Vespidae) newly recorded invading native forests in Tasmania. *Aust J Entomol* 39:177–179
- Moller H (1996) Lessons for invasion theory from social insects. *Biol Conserv* 78:125–142
- Monceau K, Bonnard O, Thiéry D (2012) Chasing the queens of the alien predator of honeybee: a water drop in the invasiveness ocean. *Open J Ecol* 2:183–191
- Monceau K, Maher N, Bonnard O, Thiéry D (2013a) Predation dynamics study of the recently introduced honeybee killer *Vespa velutina*: learning from the enemy. *Apidologie* 44:209–221
- Monceau K, Arca M, Leprêtre L, Mougél F, Bonnard O, Silvain J-F, Maher N, Arnold G, Thiéry D (2013b) Native prey and invasive predator patterns of foraging activity: the case of the yellow-legged hornet predation at European honeybee hives. *PLoS One* 8:e66492
- Monceau K, Bonnard O, Thiéry D (2013c) Relationship between the age of *Vespa velutina* workers and their defensive behaviour established from colonies maintained in the laboratory. *Insect Soc* 60:437–444
- Myers JH, Savoie A, van Randen E (1998) Eradication and pest management. *Annu Rev Entomol* 43:471–491
- Myers JH, Simberloff D, Kuris AM, Carey JR (2000) Eradication revisited: dealing with exotic species. *Trends Ecol Evol* 15:316–320
- Nakamura M, Sonthichai S (2004) Nesting habits of some hornet species (Hymenoptera, Vespidae) in Northern Thailand. *Kasetsart J (Nat Sci)* 38:196–206
- Nguyen LTP, Carpenter JM (2002) Vespidae of Viet Nam (Insecta: Hymenoptera) 1. Vespinae. *J N Y Entomol Soc* 110:199–211
- Nguyen LTP, Saito F, Kojima J-I, Carpenter JM (2006) Vespidae of Viet Nam (Insecta: Hymenoptera) 2. Taxonomic notes on Vespinae. *Zool Sci* 23:95–104
- Oldroyd BP (1999) Coevolution while you wait: *Varroa jacobsoni*, a new parasite of western honeybees. *Trends Ecol Evol* 14:312–315
- Ono M, Sasaki M (1987) Sex pheromones and their cross-activities in six Japanese sympatric species of the genus *Vespa*. *Insect Soc* 34:252–260
- Péré C, Kenis M (2010) Le frelon asiatique (*Vespa velutina*): état des connaissances et évaluation du risque pour la Suisse. Rapport pour l'Office Fédéral de l'Environnement, CABI, pp 16
- Perrard A, Villemant C, Carpenter JM, Baylac M (2012) Differences in caste dimorphism among three hornet species (Hymenoptera: Vespidae): forewing size, shape and allometry. *J Evol Biol* 25:1389–1398
- Post DC, Jeanne RL (1983) Venom: source of a sex pheromone in the social wasp *Polistes fuscatus* (Hymenoptera: Vespidae). *J Chem Ecol* 9:259–266
- Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. *Trends Ecol Evol* 25:345–353
- Prenter J, MacNeil C, Dick JTA, Dunn AM (2004) Roles of parasites in animal invasions. *Trends Ecol Evol* 19:385–390
- Rath W (1999) Co-adaptation of *Apis cerana* Fabr. and *Varroa jacobsoni* Oud. *Apidologie* 30:97–110
- Raveret Richter M (2000) Social wasp (Hymenoptera: Vespidae) foraging behaviour. *Annu Rev Entomol* 45:121–150
- Reaser JK, Meyerson LA, Cronk Q, de Poorter M, Eldrege LG, Green E, Kairo M, Latasi P, Mack RN, Mauremootoo J, O'Dowd D, Orapa W, Sastroutomo S, Saunders A, Shine C, Thrainsson S, Vaiutu L (2007) Ecological and socioeconomic impacts of invasive alien species in island ecosystems. *Environ Conserv* 34:98–111
- Reed HC, Landolt PJ (1990) Sex attraction in paper wasp, *Polistes exclamans* Viereck (Hymenoptera: Vespidae), in a wind tunnel. *J Chem Ecol* 16:1277–1287
- Rome Q, Perrard A, Muller F, Villemant C (2011) Monitoring and control modalities of a honeybee predator, the yellow-legged hornet *Vespa velutina nigrithorax* (Hymenoptera: Vespidae). *Aliens* 31:7–15
- Rortais A, Villemant C, Gargominy O, Rome Q, Haxaire J, Papachristoforou A, Arnold G (2010) A new enemy of honeybees in Europe: the Asian hornet *Vespa velutina*. In: Settele J (ed) *Atlas of biodiversity risks—from Europe to the globe, from stories to maps*. Pensoft, Sofia, p 11
- Röseler P-F (1991) Reproductive competition during colony establishment. In: Ross KG, Matthews RW (eds) *The social biology of wasps*. Cornell University Press, New York, pp 309–335
- Rosenkranz P, Aumeier P, Ziegelmann B (2010) Biology and control of *Varroa destructor*. *J Invertebr Pathol* 103:S96–S119
- Ross KG, Carpenter JM (1991) Population genetic structure, relatedness, and breeding systems. In: Ross KG, Matthews RW (eds) *The social biology of wasps*. Cornell University Press, New York, pp 451–479
- Roy HE, Roy DB, Roques A (2011) Inventory of terrestrial alien arthropod predators and parasites established in Europe. *Bio-control* 56:477–504
- Sammataro D, Gerson U, Needham G (2000) Parasitic mites of honey bees: life history, implications, and impact. *Annu Rev Entomol* 45:519–548
- Saunier R (2011) Actualité syndicale. *Abeilles Fleurs* 732:6
- Schmid-Hempel P (1995) Parasites and social insects. *Apidologie* 26:255–271
- Schweiger O, Biesmeijer JC, Bommarco R, Hickler T, Hulme PE, Klotz S, Kühn I, Moora M, Nielsen A, Ohlemüller R, Petanidou T, Potts SG, Pyšek P, Stout JC, Sykes MT, Tscheulin T, Vilà M, Walthe G-R, Westphal C, Winter M, Zobel M, Settele J (2010) Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. *Bio Rev* 85:777–795
- Shine C, Kettunen M, Genovesi P, Essl F, Gollasch S, Rabitsch W, Scalera R, Starfinger U, ten Brink P (2010) Assessment to support continued development of the EU Strategy to combat invasive alien species. In: *Final report for the European Commission. Institute for European Environmental Policy (IEEP), Brussels*
- Snyder WE, Evans EW (2006) Ecological effects of invasive arthropod generalist predators. *Annu Rev Ecol Syst* 37:95–122
- Spiewok S, Schmolz E, Ruther J (2006) Mating system of the European hornet *Vespa crabro*: male seeking strategies and evidence for the involvement of a sex pheromone. *J Chem Ecol* 32:2777–2788
- Spradbery JP (1973) *Wasps: an account of the biology and natural history of social and solitary wasps*. University of Washington Press, Seattle
- Starr CK (1992) *The social wasps (Hymenoptera: Vespidae) of Taiwan*. *Bull Natl Mus Nat Sci* 3:93–138
- Starr CK, Jacobson RS (1990) Nest structure in Philippine hornets (Hymenoptera, Vespidae, *Vespa* spp.). *Jpn J Entomol* 58:125–143

- Steffen-Dewenter I, Potts SG, Packer L (2005) Pollinator diversity and crop pollination services are at risk. *Trends Ecol Evol* 20:651–652
- Stout JC, Morales CL (2009) Ecological impacts of invasive alien species on bees. *Apidologie* 40:388–409
- Strassmann J (2001) The rarity of multiple mating by females in the social Hymenoptera. *Insect Soc* 48:1–13
- Suckling DM, Tobin PC, McCullough DC, Herms DA (2012) Combining tactics to exploit Allee effects for eradication of alien insect populations. *J Econ Entomol* 105:1–13
- Tabadkani SM, Nozari J, Lihoreau M (2012) Inbreeding and the evolution of sociality in arthropods. *Naturwissenschaften* 99:779–788
- Takahashi J, Akimoto S, Hasegawa E, Nakamura J (2002) Queen mating frequencies and genetic relatedness between workers in the hornet *Vespa ducalis* (Hymenoptera: Vespidae). *Appl Entomol Zool* 37:481–486
- Takahashi J, Akimoto S, Martin SJ, Tamukae M, Hasegawa E (2004a) Mating structure and male production in the giant hornet *Vespa mandarinia* (Hymenoptera: Vespidae). *Appl Entomol Zool* 39:343–349
- Takahashi J, Nakamura J, Akimoto S, Hasegawa E (2004b) Kin structure and colony male reproduction in the hornet *Vespa crabro* (Hymenoptera: Vespidae). *J Ethol* 22:43–47
- Takahashi J, Inomata Y, Martin SJ (2007) Mating structure and male production in *Vespa analis* and *Vespa simillima* (Hymenoptera: Vespidae). *Entomol Sci* 10:223–229
- Tan K, Radloff SE, Li JJ, Hepburn HR, Yang MX, Zhang LJ, Neumann P (2007) Bee-hawking by the wasp, *Vespa velutina*, on the honeybees *Apis cerana* and *A.mellifera*. *Naturwissenschaften* 94:469–472
- Tan K, Li H, Yang MX, Hepburn HR, Radloff SE (2010) Wasp hawking induces endothermic heat production in guard bees. *J Insect Sci* 10:142 <http://insectscience.org/10.142>. Accessed 25 October 2013
- Tan K, Wang Z, Li H, Yang S, Hu Z, Kastberger G, Oldroyd BP (2012a) An ‘I see you’ prey–predator signal between the Asian honeybee, *Apis cerana*, and the hornet, *Vespa velutina*. *Anim Behav* 83:879–882
- Tan K, Yang MX, Wang ZW, Li H, Zhang ZY, Radloff SE, Hepburn HR (2012b) Cooperative wasp-killing by mixed-species colonies of honeybees, *Apis cerana* and *Apis mellifera*. *Apidologie* 43:195–200
- Tan K, Wang Z, Chen W, Hu Z, Oldroyd BP (2013) The ‘I see you’ prey–predator signal of *Apis cerana* is innate. *Naturwissenschaften* 100:245–248
- Thirion C (2012) Ils vous en diront tant! A propos du frelon asiatique. *Le Sillon Belge* 02/03/2012. <http://naturamosana.be/documents/Frelon-SB-2-03-12%20vdef>. Accessed 25 October 2013
- Thomas CR (1960) The European wasp (*Vespa germanica* Fab.) in New Zealand. *N Z Dep Sci Ind Res Inf Ser* 27:5–74
- Tibbetts EA, Izzo A, Tinghitella RM (2011) Juvenile hormone titer and advertised quality are associated with timing of early spring activity in *Polistes dominulus* foundresses. *Insect Soc* 58:473–478
- Tobin PC, Berek L, Liebhold AM (2011) Exploiting Allee effects for managing biological invasions. *Ecol Lett* 14:615–624
- vanEngelsdorp D, Meixner MD (2010) A historical review of managed honey bee populations in Europe and the United States and the factors that may affect them. *J Invertebr Pathol* 103:S80–S95
- Vetter RS, Visscher PK (1997) Plasticity of annual cycle in *Vespa pensylvanica* shown by a third year polygynous nest and overwintering of queens inside nests. *Insect Soc* 44:353–364
- Vigneaud J-P (2013) Gironde : fait rarissime, un rapace dévore un nid de frelons asiatiques. *Sud Ouest* 20/08/2013. <http://www.sudouest.fr/2013/08/20/le-tueur-de-frelons-1145390-2777.php>. Accessed 25 October 2013
- Villemant C, Barbet-Massin M, Perrard A, Muller F, Gargominy O, Jiguet F, Rome Q (2011a) Predicting the invasion risk by the alien bee-hawking yellow-legged hornet *Vespa velutina nigrit thorax* across Europe and other continents with niche models. *Biol Conserv* 144:2150–2152
- Villemant C, Muller F, Haubois S, Perrard A, Darrouzet E, Rome Q (2011) Bilan des travaux (MNHN et IRBI) sur l’invasion en France de *Vespa velutina*, le frelon asiatique prédateur d’abeilles In : Barbançon J-M, L’Hostis M (eds) Proceedings of the Journée Scientifique Apicole, Arles. ONIRIS-FNOSAD, Nantes, 11 February 2011, pp 3–12
- Wilson EE, Mullen LM, Holway DA (2009) Life history plasticity magnifies the ecological effects of a social wasp invasion. *Proc Natl Acad Sci USA* 106:12809–12813
- Witzgall P, Kirsch P, Cork A (2010) Sex pheromones and their impact on pest management. *J Chem Ecol* 36:80–100
- Wray MK, Mattila HR, Seeley TD (2011) Collective personalities in honeybee colonies are linked to colony fitness. *Anim Behav* 81:559–568
- Yamane S (1974) On the genus *Vespa* (Hymenoptera, Vespidae) from Nepal. *Kontyû* 42:29–39
- Yañez O, Zheng H-Q, Hu F-L, Neuman P, Dietemann V (2012) A scientific note on Israeli acute paralysis virus infection of Eastern honeybee *Apis cerana* and vespine predator *Vespa velutina*. *Apidologie* 43:587–589
- Yoshida K (2008) Evolutionary cause of the vulnerability of insular communities. *Ecol Model* 210:403–413
- Zayed A, Packer L (2005) Complementary sex determination substantially increases extinction proneness of haplodiploid populations. *Proc Natl Acad Sci USA* 102:10742–10746