Observations on the colony activity of the Asian hornet *Vespa velutina* Lepeletier 1836 (Hymenoptera: Vespidae: Vespinae) in France

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T he Asian hornet, *Vespa velutina* Lepeletier 1836, has adapted perfectly to the environment of the south-west region of France, since its record in 2005, when several solitary queens and a first colony belonging to the variety *nigrithorax* du Buysson 1905 were officially discovered in the Lot-et-Garonne department (Haxaire et al. 2006; Villemant et al. 2006). However, the species may have arrived earlier through trade from China (Villemant et al. 2006). By the end of 2006, the hornet was recorded in eleven departments, while in 2007, it spread across 20 south-western departments (INPN 2008; Rortais et al. 2009). Numerous testimonies on the presence of nests allowed the monitoring of the species invasion. The insect became rapidly famous because of the large size of the nests, usually located in treetops, but also because of its propensity to prey on honeybees in front of hives. Now the insect eradication seems impossible, rapid solutions need to be found to stop or slow down its expansion.

While the preference of *V. velutina* for honeybees has been well described (Abrol 1994, 2006; Ken et al. 2005), its biology remains poorly documented, and its adaptation and expansion capacities in France and Europe remain unknown. Very few studies have been conducted on the insect in its natural range of distribution, in Asia, and since the environmental conditions there are different from those found in the south-west of France, the available information may not be relevant. Observations made *in situ* are essential to determine the impact of the hornet on the environment through predation and competition, in particular on other vespid species.

Given the lack of information on *V. velutina*, this study was performed to better understand the insect biology in the introduction area (France) through
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observations made on colonies daily activity, prey preferences, and non-nestmate workers acceptance.

**Material and methods**

The observations were made on several nests of *V. velutina* between June and July 2007 in the Lot-et-Garonne department. All information related to the nests is presented in table 1.

**Captive breeding conditions**

An embryo nest of *V. velutina* was removed from the roof of a shed on 25.V, near the Dordogne River, at Castillon-La-Bataille (44°50’45"N 0°0’23"W), and placed in a well-ventilated plastic box. The young colony comprised a queen and seven workers, three of which did not survive. The nest was placed in a cage (H = 163 cm, L = 104 cm and W = 100 cm) at Laplume (44°05’52"N 0°30’59"E), and a corrugated sheet metal placed 8 cm above the wooden roof of the cage to allow air to circulate. The legs of the cage were covered with glue to prevent small insects, like ants, from invading the nest. The nest was left in the open plastic box for 16 days and then placed in the cage on a branch with several twigs. The handling of the nest slightly altered the shape and caused a disturbance within the colony during two days. Food (water, icing sugar, honey, live insects such as honeybees, bumblebees, halictids, paper wasps and brachycera flies) and material for nest construction (wood fragments and pieces of old nests of *V. velutina*) were provided to the colony every day and in sufficient amounts, as previously described for the rearing of other vespids (Darchen 1964; Raveret Richter 2000).

An additional eight workers (one on 29.VI, five on 30.VI, two on 05.VII) and one male (on 07.VII) collected from nearby captive *V. velutina* nests were marked with white Tipp-ex on the thorax and introduced into the cage. The first introduced worker was caught with a honey trap near Agen (44°13’06"N 0°35’25"E), whereas all the other individuals, which were young imagos, were collected at Bon-Encontre (44°11’03"N 0°40’22"E) from a partially destroyed nest.

**Observations of colonies activities**

The daily activity of the captive colony was recorded 10 minutes every 30 minutes between 5:30 am and 10:30 pm (i.e. up to 35 observations per day), over a month (from 20.VI to 20.VII). In total, 296 observations were made.

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**Figure 1**

The captive nest at its final developmental stage (16.XI.2007).
During each of these observations, the number and types of tasks achieved by workers outside the nest were determined. The number of hornets entering and leaving the nest refers to the global activity of the colony. Tasks included sugar and water intakes, nest construction, predation, grooming and cleaning (e.g. waste removal). Local microclimatic conditions were also recorded (temperature, humidity, cloud cover, and light) during the observation sessions. Upon completion of the experiment, observations on the colony continued from August and until its death in November 2007. A large opening was made in the cage wall on 20.VII, at night, to allow the hornets to forage outside the cage.

Additional observations were made on three free-living colonies, one at Laplume (44°09’52”N 0°32’17”E) and two others at Agen (44°12’10”N 0°37’50”E; 44°12’40”N 0°36’31”E). Nests’ description and dates of observations are listed in table 1. The activity of the colony was estimated during a 10 minutes observation session at about 4:00 pm. The hornet food selection was determined from pellets made by the insect. On their return to the nest, workers from nest number 2 were captured by a net and the pellets carried in their legs were retrieved. Resistant individuals were placed in a fridge at 4 °C for a few minutes to force them to abandon their pellets. All pellets were stored in individual tubes containing alcohol (70°) for further identification.

**Results**

**Observations on the seasonal development of a colony**

While the queen worked outside the nest during the first days of observation, it stopped all external activities on 21.VI. Then workers took over with sugar intake, nest construction and predation activities. The population of the captive colony remained low until August, with a global increase of about 10 workers during the observation period.

The nest was enlarged by workers which continuously added new layers of pulp on the envelope, forming shell-like aerial chambers. Workers formed arcs of fibrous pulp which they first deposited on the nest cover, and then expanded to form a shell-like pocket. These shells often developed towards the nest entrance (which open laterally, contrary to that of *V. crabro* L. 1758), and sometimes towards the basal area. During the first few days of observation, the workers entered the nest just after gathering plant fibres, whereas, later in the season (beginning of July), they remained outside to engage in food exchange (trophallaxis) with the nestmate guarding the entrance.

![Graph](image-url)  
**Figure 2**  
Daily activity of the captive colony: average number of workers coming in or out of the nest during 10 minutes of observation per 30 mn throughout the day (N = 3950 individuals; error bars = standard deviation).
Two days after the formation of the large opening in the cage, an assortment of vegetal matter was introduced and processed, as detected by the presence of new colours on the nest envelope. Population and colony activity increased considerably from August to October when the nest reached its maximal size: 38 cm in height and 36 cm in diameter (fig. 1). Throughout the observation period, hornets ventilated the nest when temperatures reached maximum levels. Workers achieved evaporative cooling – that is, they regurgitated water from their mandibles onto the nest (sometimes soaking the nest wall), and evaporated that water through the vibration of their wings.

The flying out of sexuals began at the end of September, and while males are distinguishable from other nestmates by their long antennae, future queens and workers are difficult to discern due to their limited distinguishing features. The highest number of males seen on the nest over the second week of October may correspond to the sexual swarming peak of the
colony. After that, the number of sexuals decreased and the nest took back its normal activity. The colony survived until the first days of frost, toward the end of November, and perished rapidly thereafter, within three days.

**Daily activity of the captive colony (fig. 2)**

The daily activity began with the workers’ flights at around 6:00 am. With the exception of one day (21. VI), sugar intake never occurred before 6:30 am, even in warm conditions (16.5 °C on 14.VII and 20 °C on 17.VII at 5:30 am). When temperatures got below 10 °C (on 27.VI), no activity was recorded outside the nest.

The activity stopped at dusk (between 10:00 pm and 10:30 pm), even when outside temperatures exceeded 20 °C (on 20.VI, 14.VII and 17.VII), but the slightest nest disturbance, even at night, always triggered the colony activity (several workers walked out the nest). The number of workers entering and leaving the nest increased from 6:00 am to 11:30 am, stabilized from 11:30 am to 5:00 pm, decreased gradually between 5:00 pm and 8:30 pm, and abruptly from 8:30 pm to 9:30 pm. The average overall activity of the colony reached a maximum between 3:30 pm and 4:30 pm.

**Extranidal activity rate (fig. 3–4)**

The timing of worker tasks outside the nest varied among and within each day, in particular for predation and construction activities in spite of the continuous availability of prey items and construction materials. Overall, 76% of the activities performed by workers outside the nest were devoted to construction (16%), exploration (13%), and foraging (47%); the rest of the activities being devoted to nest guarding, cleaning, ventilation, grooming and workers interactions. Among foraging activities, sugar intake was more common (19%) than hunting (10%), and water (9%) or pulp (9%) intakes.

Sugar intake was achieved by workers from dawn to dusk, and it was in most cases preceded by water intake (fig. 3). Construction activities dominated from 10:00 am to 5:00 pm (fig. 4). Workers used mainly fragments of old nests to build the envelope of the captive nest. Wood pulp pellets, made from old nest walls, were more readily made (3 min ± 42 s, n = 6) than wood fibre pellets (4 min ± 50 s, n = 4). Attack trials lasted only a few seconds after the onset of the honeybee workers’ flights.

**Predation behaviour and prey spectrum (fig. 5, tab. 1 & 2)**

The captive colony preyed mostly on honeybees (i.e. 25 to 50 honeybees per day). Hornets attacked preferentially live honeybees, but were not always successful. Despite those failures, honeybee captures were performed at an almost constant frequency all along the day but with a variable number of trials. In average, four trials were necessary to catch a honeybee (fig. 5). After capturing its prey, the hornet worker made a flesh pellet exclusively from the protein rich honeybee thorax, by removing all the others parts of the body (i.e. legs, wings, abdomen, head and sometimes the thorax cuticle). This process lasted on average 4 min 30 s ± 55 s (n = 32 observations). In some cases, when the hornet fell down while removing the appendages, the

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**Table 1.** Nests description and observations data. The symbol “ - ” represents missing data.

<table>
<thead>
<tr>
<th>Nest number</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest situation</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Locality</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Laplume</td>
<td>Agen</td>
<td>Laplume</td>
<td>Agen</td>
<td></td>
</tr>
<tr>
<td>Human environment</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rural (breeding site)</td>
<td>Urban (garden)</td>
<td>Rural (close to a broad-leaved forest)</td>
<td>Urban</td>
<td></td>
</tr>
<tr>
<td>Habitat type</td>
<td>Cage</td>
<td>Above a veranda roof</td>
<td>Under terrace</td>
<td>Tree crown</td>
</tr>
<tr>
<td>Nest features</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Support</td>
<td>Dead branch</td>
<td>Wall</td>
<td>Inside a breezehook</td>
<td>Yew tree branch</td>
</tr>
<tr>
<td>Height/ground (m)</td>
<td>1.7</td>
<td>3</td>
<td>2.5</td>
<td>8</td>
</tr>
<tr>
<td>Entrance direction</td>
<td>NE</td>
<td>E</td>
<td>E-NE</td>
<td>NE</td>
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<tr>
<td>Observation interval</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Duration (days)</td>
<td>43</td>
<td>11</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Nest dimensions at start/ end of observations</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Height (cm)</td>
<td>7 / 14</td>
<td>15 / 25</td>
<td>-</td>
<td>- / 35</td>
</tr>
<tr>
<td>Diameter (cm)</td>
<td>8 / 13</td>
<td>25 / 31</td>
<td>-</td>
<td>25 / 31</td>
</tr>
<tr>
<td>Estimated population at end of observations</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>100</td>
<td>40</td>
<td>120</td>
<td></td>
</tr>
<tr>
<td>Activity at nest entrance for 10 minutes</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Date of observation</td>
<td>09.VII</td>
<td>03.VII</td>
<td>03.VII</td>
<td>16.VII</td>
</tr>
<tr>
<td>Number of returns</td>
<td>10</td>
<td>42</td>
<td>25</td>
<td>84</td>
</tr>
<tr>
<td>Number of departures</td>
<td>9</td>
<td>40</td>
<td>21</td>
<td>76</td>
</tr>
</tbody>
</table>
captured bee was left dying on the ground. However, these bees were collected by other hornets within a few hours when live prey items were no more available. With the exception of flies, other prey items released in the cage were rarely successfully caught and processed by the hornets.

The observed free-living nests were bigger than the one maintained in captivity and showed higher levels of activity (tab. 1), mainly predation. More than half of the workers returning to the nest carried pellets.

The pellets (n = 235) collected from nest number 2 contained either preys (71.8%) or pulp (27.2%) (tab. 2). Flesh pellets were predominantly composed of honeybee thoraxes (84.8%), but also contained fragments of various insects (11.7%), mostly halictids and brachycera dipterans, or vertebrate flesh (3.5%). Two out of the six vertebrate samples contained feathers, possibly from dead young birds.

Other hymenopterans can be attacked by *V. velutina*, as demonstrated by the capture, in natural conditions, of workers carrying pellets of a paper wasp and a bumblebee.

**Non-nestmate acceptance**

Most of *V. velutina* individuals introduced from other nests were accepted within 24 hours by the captive colony, except for two workers which never entered the nest, and died rapidly in the cage. One was an active worker, caught with the honey-trap, and attacked only once, whereas the other fell on the floor when introduced in the cage, and remained there all night before dying. The male that was introduced, although globally accepted by the colony, remained isolated most of the time and was rejected only once by a worker.

**Discussion**

**Captive colony development and activity**

As no internal colony observations were possible, data on the precise level of population structure and dynamics was not attainable. In addition to the queen, the number of workers was estimated to be about 15 during the observation period, by counting the hornets coming out the nest when shaking the nest. Within the same period, the exact size of the free-living colonies could not be determined, but the global activity and nest size suggested that these colonies were bigger than the captive one. Disturbance during transfer, confinement and insufficient food provision – likely due to under-estimation – could have limited the growth of the captive colony. Darchen (1964) observed that several captive colonies of *Vespa orientalis* L. 1771 used half of their own larvae to feed adults and the remaining brood rather than live honeybees provided in sufficient amount.

Such a trauma may explain why, when the queen stopped all activities outside the nest, the transition of

![Figure 5](image-url)

*Figure 5*  
Importance and success of hornets attacks against honeybees during 10 minutes of observation per every 30 mn (Total = 359 attacks; error bars = standard deviation).
the colony into the polyethic stage was not followed by a significant population growth, as usually observed in natural conditions (Matsuura & Yamane 1990). Such a colony development occurred just after the end of the observation period, when the opening made in the cage allowed the workers to forage freely outside. As a consequence of such captive conditions, the data obtained in this study may have been underestimated, in particular for the duration of activities because the time required to forage in the field was not taken into account. Finally, predation may have been biased by such conditions because of the lack of space and proximity of preys.

**Global activity of *Vespa velutina* in comparison with other vespids**

Contrary to what was previously observed in Kashmir (India) on free-living colonies of *V. velutina* (Williams 1988; Abrol 1994), the captive colony studied in France maintained a high level of activity all day until dusk. However, the effect of temperature on the hornet’s activity showed a similar trend in Kashmir and France. Observations made by Williams (1988) in August 1985 at Gulmarg (2700 m ASL), a place where *V. velutina* is very abundant, showed that worker’s activity started at dawn, at about 5:30 am (11 °C), and ended at 8:00 pm (11.5 °C), at sunset, with a peak of intensity when the temperature was the highest, at about 1:30 pm (25 °C).

The nests observed in natural conditions showed a rhythm of activity similar to that of the captive colony, and to the trends observed in France by Rolland (1976) on *Vespula vulgaris* (L. 1758), and *V. germanica* (Fabricius 1793). According to other authors, *Vespula* and *Vespa* colonies have the highest level of activity early in the morning. The significant flow of workers coming out of the nest may be related to the urgent need of larvae for food after their nocturnal feast and/or to the fact that removing water in the form of dew is easiest when collected early in the morning (Edwards 1980).

It is noteworthy to add that, as in most European (Edwards 1980) and Japanese (Matsuura & Yamane 1990) vespids, the activity of *V. velutina* can occur under rainy, cloudy and clear weather conditions.

**Tasks performed outside the nest**

In wasps, the time spent for diurnal foraging activities vary among species and environmental conditions making comparison with the present study difficult; however, fluid collection (i.e. nectar, tree sap and water for free living colonies) is always the dominant foraging task performed by workers (Edwards 1980).

Both adults and larvae require carbohydrates (Edwards 1980). Water intake, which precedes sugar intake, could improve sugar intake by dissolving it, as is the case with the processing of wood pellets (Raveret Richter 2000). In the field, however, hornets obtain liquid carbohydrates mostly by gnawing the bark of living trees to obtain the sap (Matsuura & Yamane 1990).

To construct the nest envelope, the worker prepares a paste by masticating wood fibres with its saliva and probably mixing it with liquid regurgitated by workers (Edwards 1980) or larvae (Sandeman 1940; Wafa et al. 1968), during trophallaxis performed inside the nest or at the entrance.

During the construction of the captive nest, the addition of new shells was the only observed activity.

<table>
<thead>
<tr>
<th>Dates</th>
<th>06 VII</th>
<th>10 VII</th>
<th>16 VII</th>
<th>18 VII</th>
<th>23 VII</th>
<th>25 VII</th>
<th>total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flesh pellets</td>
<td>32</td>
<td>13</td>
<td>12</td>
<td>33</td>
<td>19</td>
<td>62</td>
<td>171</td>
</tr>
<tr>
<td>Pulp pellets</td>
<td>-</td>
<td>0</td>
<td>17</td>
<td>11</td>
<td>18</td>
<td>18</td>
<td>64</td>
</tr>
<tr>
<td><strong>Prey spectrum</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Apis mellifera</em></td>
<td>28</td>
<td>9</td>
<td>9</td>
<td>30</td>
<td>14</td>
<td>55</td>
<td>145</td>
</tr>
<tr>
<td>Halictinae</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Other Apiformes</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Calliphoridae</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Muscidae</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Other Brachycera</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Insecta (unidentified fragment)</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Vertebrate flesh</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>6</td>
</tr>
</tbody>
</table>
However, audible scratching noises coming from inside the nest were detected. In addition, the identification of individuals coming out of the nest carrying paste pellets lead to the assumption that workers may remove material inside the nest to enlarge the envelope from outside. This behaviour has already been described by several authors (Edwards 1980; Matsuura & Yamane 1990).

Abrol (1994) at Harvang Stinagar (Kashmir) reported that predation activity of *V. velutina* reaches a maximum at 10:30 am and decreases slowly after 1:00 pm to stop at dusk at about 8:00 pm. In this study, the colony also showed a peak of prey attack in the morning; however, observations made in captive conditions must be cautiously interpreted since predation activity primarily depended on the amount of food (bees) supplied by the observer.

**Diet**

The making of flesh pellets was first described in *V. crabro* by Janet (1895). The prey spectrum determined by the analysis of pellets is an indicator of the food selection made by a colony at a given time of its development and in a given area (e.g. urban or rural area). The colony’s needs and the resources vary spatio-temporally, and hornets need to adapt their foraging habits to such changes. Therefore, samples collected later in the season or in another environment could show different trends of food selection (Matsuura & Yamane 1990). In the literature, the main preys of *V. velutina* are brachycera dipterans and social hymenopterans, mainly bumblebees and honeybees (Van der Vecht 1957; Williams 1988; Abrol 1994). However, contrary to what is reported by Abrol (1994), *V. velutina* can also attack halictids.

Repeated and sometimes severe attacks from *V. velutina* on beehives were reported in 2006 and 2007, in particular at the end of the summer and in the fall, by beekeepers from the south-west region of France. The damages caused to honeybees and colonies are widely recognized in Asia (Williams 1988; Shah & Shah 1991; Abrol 1994). Free-living honeybee colonies may also be actively attacked by *V. velutina*, as observed in Vietnamese tropical forest (Villemant 2008). However, in Asia, the autochthonous honeybee species have developed more efficient strategies to defend their colonies than the imported European honeybee (Abrol 2006; Tan *et al.* 2007).

Like what is already observed in Asia, data on the diet of *Vespa velutina* suggest that this insect could have a large impact on honeybees in France.

**Non-nestmate acceptance**

In the captive colony, aggression towards newly introduced hornets was rare and even when it occurred, it was low. The acceptance of intruders and their integration to the activity of a mature colony has never been observed in the European hornet (Ruther *et al.* 1998); in this case, it could be the demonstration of an altruistic behaviour related to the genetic proximity of *V. velutina* colonies in France. This trend has already been observed in other invasive species, such as the Argentinian ant, *Linepithema humile* Mayr 1868 (Holway *et al.* 1998), sadly famous for its impacts on biodiversity. If this hypothesis is confirmed, it could explain the success of the invasion of *V. velutina* in France, and may underpin future major impacts on the environment, in France, and elsewhere if the species expands further. The absence of aggressiveness between individuals of different nests may also be due to the young age of the individuals introduced in the cage soon after their emergence, as seen in other primitive and eusocial vespids like the Polistinae *Ropalidia marginata* Lepeletier 1836 (Arathi *et al.* 1997).

**Aggressiveness**

While *V. velutina* aggressiveness towards humans is widely recognized among the inhabitants of Java (Van der Vecht 1957) and Taiwan (Matsuura 1973; Ho *et al.* 1999), the hornet aggressiveness observed in France, at the study site, was low. During the experiment, only one case of injury by a sting was reported after the accidental destruction of a nest on a building. The hornet nest is most often located on the top of tall trees, but it can also be found in buildings (e.g. verandas, terraces, barns) where the insects remain discrete and tend to ignore humans. This lack of aggressiveness may be explained by a habituation process where colonies close to housing get used to the presence of humans. However, since the observations described in this study are only based on the early development of a colony, which in normal conditions, and at a mature stage, can reach several hundreds or thousands of individuals, the observed aggressiveness may have been underestimated. Further research is required to determine how different the aggressiveness of the species is in its home range of distribution and in France, and what factors can mitigate it (e.g. density dependent factors).

**Conclusion**

The observations described in this study covered the first part of the active period of the hornet and did not include intranidal data. These results represent preliminary information that needs to be further developed to better understand and monitor the
impact of this new invasive species. It is important to continue such studies and to increase our knowledge on the hornet biology to better predict its influence on the French fauna, and to find adequate solutions before its impact becomes too severe on beekeeping, biodiversity, and ecosystems.

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References


