A foreigner in France: the Asian hornet

In 2004 the hornet *Vespa velutina* L. was accidentally introduced into the South West region of France, probably via garden pots imported from China. Eradication of the species from France is now impossible. As this hornet is a predator of honey bees, the introduction into Europe of *V. velutina* is certainly bad news for beekeepers.

Marie-Pierre Chauzat[1] and Stephen Martin[2]

[1]Food Safety Agency, France, and [2]University of Sheffield, UK

Title image: An adult hornet. Picture: Jean Haxaire.

Since its first introduction to France in 2004, *Vespa velutina* has spread to 24 'départements' from the Charente-Maritime to the Gard (Haxaire *et al*, 2006) (Figure 1). Its introduction was first officially noticed in 2005 in Lot-et-Garonne. However field information has reported that some 'black hornets' have been observed in the vicinity of a ornamental plant seller since 2004.

The hornet has adapted well to its new environment, colonising urban, sub-urban, agricultural and wooded areas. The native range of *V. velutina* extends from north-eastern India, throughout southern and central China, as far east as Taiwan and as far south as Indonesia (Archer, 1994). When *V. velutina* occurs in tropical regions, nests are normally found in the cooler highland or upland regions that have a climate comparable to that found in Southern Europe (Starr, 1992).

The sub-species of *V. velutina* introduced into France is *V. velutina nigrithorax* (Haxaire *et al*, 2006), which is very easy to recognise since it is the only hornet or wasp that has an entirely dark brown body with only one orange band towards the end of the abdomen (4^{th} tergite). The *nigrithorax* colour form occurs in the

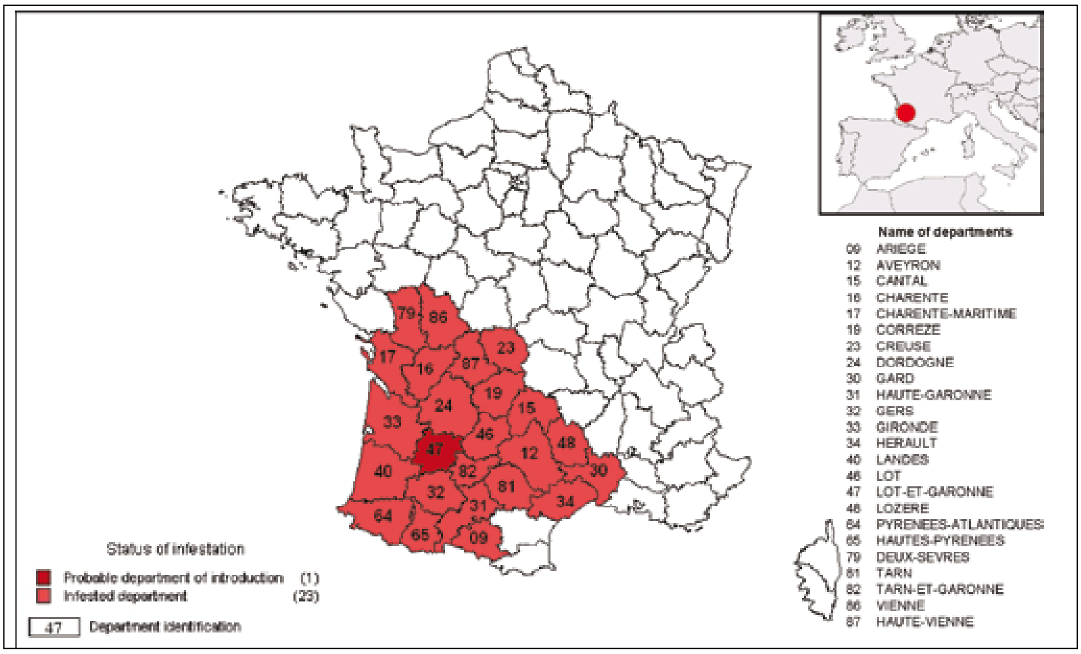


Figure 1: French departments infested with *V. velutina* in 2009.

India-China part of its distribution. The life cycle of *V. velutina* is similar to that of other hornets except that this species in its native range can produce very large colonies that can reach 75cm in length and contain up to 12,000 brood cells in 11 combs (Martin, 1995). It has a long nesting period that lasts from May to November.

The hornets (*Vespa*) consist of 23 species worldwide, and are widely distributed throughout Asia. Europe has two native hornet species: the European hornet, *V. crabro* L., which is found throughout Europe and the oriental hornet, *V. orientalis* L., which has a distribution restricted to Bulgaria, Greece and Southern Italy. Both species produce much smaller colonies than *V. velutina* and are much less aggressive despite both being larger than *V. velutina*.

In Asia, *V. velutina* is a predator that often focuses on European honey bees (*Apis mellifera* L) and to a lesser extent the Asian honey bee (*Apis cerana* Fab.). In India (Kashmir), *V. velutina* has been reported to limit colony development of European honey bees by the persistent predation of adult bees (Shah *et al*, 1991). *V. velutina* is one of the most adept hornets at catching honey bees on the wing: other species land on the hive and grab individuals that try and attack the hornet. *V. velutina* workers hover in front of the hive waiting for returning foragers (Figure 2). When the unsuspecting honey bee nears the hive the hornet swoops down, catching its victim on the wing. The head and abdomen are removed and a meatball made of the flight muscle which is fed to larvae back in its nest.

The hawking area in front of the hives is territorial as other hornets that intrude are quickly expelled. In Yunnan Province China, hornet predation levels are highest in the morning and afternoon, which corresponds with the daily rhythm of honey bee flights (Tan *et al*, 2005). If a honey bee colony becomes sufficiently deprived of workers, *V. velutina* will then enter the hive, feed on the honey and remove the brood.

Life history of *V. velutina* colonies

In France, data on the biology on *V. velutina* is still lacking although, like all hornets and wasps, their nests are made of paper and mature nests are typically built near the top of trees or on buildings – although subterranean nests have been recorded (Martin, 1995). The following information is based on direct observation from Asian *V. velutina* colonies and is supplemented by information on *V. simillima,* a hornet with a very similar biology.

Figure 2. *V. velutina* attacks honey bee foragers when they return to the hive. Picture: J. Haxaire

Figure 3: Embryo nest of *V. velutina* observed in France in a protected area. Picture: J.Haxaire

All hornets have an annual lifecycle, with the mated queens emerging from their over-wintering hibernation period in spring. The queens quickly establish a small embryo nest, usually in an enclosed and protected place, such as a wall cavity or tree hollow. In the tennis ball-sized embryo nest, the queen rears her first batch of workers.

In *V. simillima* these embryo colonies often undergo relocation when 50-100 workers are present (Dazhi *et al*, 1989), since many sites do not allow for rapid nest expansion, so forcing the colony to relocate to a new less constricting site, such as high in a tree (Figure 3). After relocation the nest expands rapidly as increasing numbers of workers help to rear more workers with the queen being restricted to egg-laying within the nest. In the autumn the colony reaches it maximum size containing over 1,000 adult workers and hundreds to thousands of 'sexuals', i.e. new queens and males. The new queens and males mate outside the colony, the males and workers die with the onset of winter due to the lack of food, while the mated queens enter hibernation. Queens hibernate alone or in groups of two or three, under the bark of trees or stones. During the over-wintering period queen mortality is high (>99%) (Archer, 1984) otherwise the population would explode since hundreds and sometimes thousands of new queens are produced by each colony.

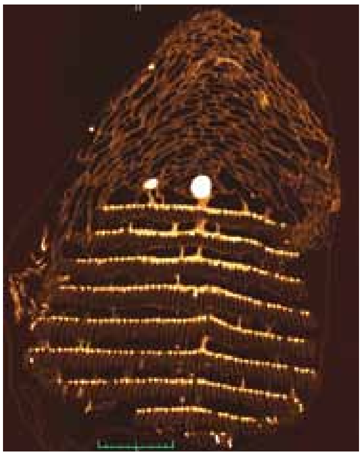
The climate can affect colony development: in France, the mild winter of 2006 allowed the continuing development of nests until late November, whereas the wet and cold spring of 2008 noticeably delayed the process. The longer the colony survives into the autumn, then the more queens are produced: there is a good correlation between the number of queens produced and colony size, so larger nests produce more queens. If the queen dies before sexual production, some of the workers will develop their ovaries within a few days and lay unfertilised (haploid) eggs. These will develop into males, and can mate with new queens if present. Queenless *V. velutina* nests have been reported in France. All nests are only ever used once and are destroyed by birds or the weather, although the same nest-sites can be used year after year.

A key characteristic of hornets such as *V. velutina* is their resilience to environmental change and their capacity to overcome difficulties. Hornet populations commonly fluctuate between years, often with a two year cycle that may be superimposed on longer fluctuations. For example, population studies on the common wasps *Vespula germanica* and *Vespula vulgaris* in the UK found a two year cycle possibly enclosed within a longer seven year cycle (Archer, 1985). It remains unknown what drives these population cycles; limited nest sites and usurpation (queen fighting) rates have been suggested (Martin, 1992) and the summer and autumn weather certainly play a role, but large fluctuations in nest numbers between years are a trait common to all hornets. It is also unknown whether *V. velutina* populations in France will follow this trend but it seems unlikely in an expanding population where nest-sites will not be limited.

Thermoregulation

One of the key factors that allows hornets to be highly successful predators is their ability to thermoregulate their nests. The horizontal combs that contain the brood are enclosed within a nest envelope that protects the adults and brood from both high and low ambient temperatures by preventing heat loss from the nest interior (Figures 4 and 5). As the size of the colony increases, the ability of workers to maintain a stable nest temperature increases, until they are able to maintain a constant nest temperature at around 30°C, despite ambient temperatures that may be up to 20°C lower (Martin, 1990).

The high nest temperature allows hornets to forage early in the morning when ambient temperatures are low and many insects are immobile. It also allows them to mount an effective attack if the nest is disturbed even during cold weather or at night when they are attracted to lights. Despite this ability to maintain a stable



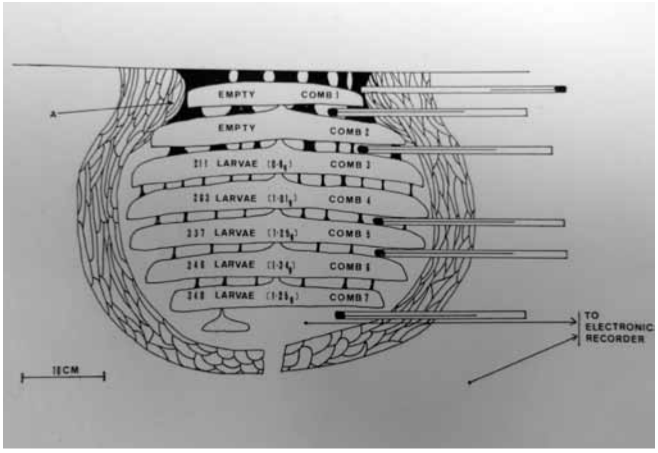


Figure 4 (left). Mature nest of *V. velutina* scanned with X rays. Picture: Eric Darrouzet **Figure 5** (right). Structure of a hornet mature nest. Picture: Stephen Martin

nest temperature hornet larvae (unlike honey bee larvae) are able to tolerate a wide range of temperatures.

Hornets and wasps feed almost exclusively on animal prey which they cannot digest directly due to their narrow waist. Therefore, the animal prey is fed to their larvae and in exchange the larvae produce larval secretions that are rich in carbohydrates and amino acids (Figure 6). These secretions fuel the foraging adult workers and allow the new queens to build up their fat bodies, prior to mating and hibernation. As the colony declines and the brood dies, the workers seek out other sources of carbohydrates and this is when they often come into contact with humans as they enter houses searching for sweet food sources. Kuo and Yeh (1990) observed that *V. velutina* was better at catching prey e.g. flies and honey bees, as it is much faster and more agile than other hornet species.

Being able to age a nest is important when studying colony development in order to assess whether a given factor affects the fitness of the population. Aging the colony is done by using young nests (50-100 days old), since the addition of new cells to the nest is low, forcing the queen to re-use cells once the brood has hatched. So by knowing the developmental time of the brood that has gone before, it is possible to age the nest, by back-calculation. This is aided by the number of meconia (hardened faecal pellets) in a cell that indicates how many times each cell has been used (Martin, 1991).

Risks to public health

In Asia, *V. velutina* is known to be exceptionally aggressive (Matsuura, 1973) especially in the vicinity of its nest. In Japan around 70 human deaths per year are attributed to hornet stings. In Malaysia and Taiwan *V. velutina* is the most feared of all hornet species. It appears that this species has a unique recruitment behaviour when intruders get too close to the colony: a worker will 'warn' the intruder by flying around him. If the intruder continues towards the nest then the hornet returns to its nest, recruits other workers and attacks *en masse* (Martin, 1995). The current apparent lack of aggression in France may be due to the low population pressure. The French Poisons Unit is currently gathering data on the toxicology of hornet stings, with data expected by mid-2009.

Impact on beekeepers

The introduction into Europe of *V. velutina* is certainly bad news for beekeepers. Eradication of *V. velutina* from France is now impossible as during the past four years it has become too well established over a large area. Therefore, a coordinated action of nest destruction is not realistic and anyway such a policy failed to work in New Zealand in an attempt to eradicate German Wasps (*Vespula germanica*). New Zealand also targeted the over-wintering wasp queens by offering a small cash reward for each queen killed. Despite thousands of queens being killed the wasp population actually increased the following year. The main problem is that each colony can produce thousands of new queens and only one needs to establish a successful nest for the population to remain stable, such is the resilience of wasps and hornets.

In Asia, the Eastern honey bee *Apis cerana* has developed two defensive behaviours against predation by hornets. First, when a hornet starts hawking in front of the colony and workers move out onto the surface of the hive and start performing Mexican waves by shimmering their wings in unison. This behaviour warns returning forgers that a hawking hornet is in the area and foraging often stops until the

Figure 6. Exchange of food between the larvae and the adult. Picture: J. Haxaire

hornet has left (Tan *et al*, 2005). Second, if a hornet attempts to enter a bee colony the bees attack the hornet by enclosing it in a ball of vibrating bees and proceed to kill the hornet by raising the temperature at the centre of the ball to 45°C (Ono, 1995). This behaviour is relatively efficient, as *A. cerana* colonies are less affected by *V. velutina* workers than European honey bee (*A. mellifera*) colonies that lack both behaviours. European honey bees can form balls but these are much less efficient at killing the hornet than *A. cerana* balls (Tan *et al*, 2005). To date there have been no reports of heat-balling or shimmering behaviours in European honey bees towards *V. velutina* in France.

In India, control strategies such as killing hornet queens in early spring, destroying hornet nests and swatting hornets at the hives' entrances have been advocated, but none of these have been reported to be effective (Shah *et al*, 1991). In France similar methods have been tried with similar results. In 2007, during September, a beekeeper in the Bordeaux area killed about 80 hornets a day during several weeks without any decrease in the hornet pressure on his honey bee colonies. Locally, beekeepers can fit entrance reducers to the hive to prevent *V. velutina* workers entering the colony but this does not prevent the hornets killing returning foragers.

V. velutina entering the nest. Picture: J.Haxaire

The future

Vespa velutina is now a well-established hornet species in Europe and eradication is not achievable. Under some circumstances the presence of *V. velutina* in France could paradoxically be beneficial, since hornets may be involuntarily involved in processes of pest control as they are quick in exploiting sudden outbreaks of (pest) insects. This is one of the reasons why *V. velutina* attacks honey bees since they are numerous and concentrated in a single place.

Studies are urgently needed to assess the impact at an ecological scale of the introduction of a new top predator such as *V. velutina* on the balance of the whole ecosystem. So far other countries that have been invaded by wasps, such as New Zealand, Australia and the islands of Hawaii, have failed to control their populations despite many attempts. These have included the introduction of parasitic nematodes, poison baits and entomopathogenic fungi (Martin, 2004). Following the example of others insects introduced in Europe e.g. *Encarcia sp.* and Chrysomelid beetles, it is highly likely that *V. velutina* will continue to spread further east in France and across Europe, and maybe even into Northern Africa.

Acknowledgments

The authors wish to thank Pascal Hendrikx for his help in drawing the map and Jean Haxaire for valuable comments on the manuscript.

Web resources

French National Museum: http://inpn.mnhn.fr/isb/servlet/ISBServlet?action=Espece&typeAction=10&pageReturn=ficheEspeceFiche.jsp&numero_taxon=433589

European website for invasive species inventories: www.europe-aliens.org/index.jsp

References

Archer M E (1984) Life and fertility tables for the wasp species *Vespula vulgaris* and *Dolichovespula sylvestris* (Hymenoptera: Vespidae) in England. *Entomol. Gener*. 9, 181-188.

Archer M E (1985) Population dynamics of the social wasps *Vespula vulgaris* and Vespula *germanica* in England. *J. Animal Eco*. 54, 473-485.

Archer M E (1994) Taxonomy, distribution and nesting biology of the Vespa bicolour group (Hym., Vespinae). *Entomologist's mon. Mag*. 130, 149-158.

Dazhi D and Yunzhen W (1989) A preliminary study of the biology of *V. velutina auraria* Smith and *Vespa tropica ducalis* Smith. *Zoological Research*, 10, 155-162

Haxaire J, Bouguet J P and Tamisier J P (2006) *Vespa velutina* Lepeletier, 1836, une redoutable nouveauté pour la faune de France (Hym., Vespidae). *Bulletin de la Société Entomologique de France*, 111, 194.

Kuo M C and Yeh W H (1990) *Ecological study of the rare wasp* Vespa wilemani. Natn. Sci. Council Res. Progm. Rep. pp 1-7. [In Chinese with English summary]

Martin S J (1990) Nest thermoregulation in *Vespa simillima*, *V. tropica* and *V. analis*. *Ecol.Entomol*, 15, 301-310.

Martin S J (1992) Colony failure in the social wasp *Vespa affinis*. *Jpn. J. Ent*, 60, 671-681.

Martin S J (1995) Hornets (Hymenoptera: Vespinae) of Malaysia. *Malayan Nature Journal*, 49, 71-82.

Martin S J (2004) Biological control of social wasps (Vespinae) using mermitid nematodes. *New Zealand Journal of Zoology*, 31, 241-248.

Matsuura M (1973) Nesting habits of several species of the genus Vespa in Formosa. *Knotyu*, 41, 286-293.

Ono M, Igarashi T, Ohno E and Sasaki M (1995) Unusual thermal defence by a honey bee against mass attack by hornets. *Nature*, 377, 334–336.

Shah F A and T A Shah (1991) *Vespa velutina*, a serious pest of honey bees in Kashmir. *Bee World*, 72, 161-164.

Starr C K (1992) The Social Wasps (Hym. Vespidae) of Taiwan. *Bulletin of the National Museum of Natural Science*, 3, 93-138.

Tan K, Hepburn H R, Radloff S E, Yusheng Y, Yiqiu L, Danyin Z and Neumann P (2005) Heat-balling wasps by honey bees. *Naturwissenschaften*, 92, 492-495.

Marie-Pierre Chauzat is studying honey bee biology and ecology in France in the Honey bee Pathology Unit at the French Food Safety Agency. Honey Bee Pathology Unit. AFSSA LERRA Les Templiers, 105 route des Chappes, B.P. 111 – F-06 902 Sophia-Antipolis cedex, France. Email: mp.chauzat@afssa.fr **Stephen Martin** has spent over 20 years studying social insects including Asian hornets, honeybees and ants throughout the world. Animal & Plant Sciences, Sheffield University, Sheffield, S10 2TN, UK. Email s.j.martin@sheffield.ac.uk.

IoB Members' Evening

Evolution: The Tempo and Mode of Speciation

Wednesday 3rd June 2009
6:15pm - 8:30pm at the Institute of Biology, London
Speaker: Dr Chris Venditti

Understanding the macroevolutionary patterns and processes that has led to the diversity we see today is of fundamental interest to biologists. The tempo and mode of speciation has been studied by evolutionary biologists from all disciplines since Simpson (1944). Traditionally the fossil record has been used to address such questions. However, the signature of a group of organisms' evolutionary past can leave its mark on a phylogenetic tree, which means it may be possible to infer these important macroevolutionary processes from such trees. Phylogenetic trees identify the genealogical relationships among a group of species and the lengths of their branches record the amount of time or evolutionary change between successive events of speciation. Using a large database of phylogenetic trees and novel statistical models we find that punctuational bursts of evolution at the molecular level are common and widespread. Further, we find that speciation appears to occur at a constant rate within a group. Our findings have implications for modelling molecular evolution and explanatory theories of speciation.

Chris Venditti is a Postdoctoral Fellow in the Evolutionary Biology Research Group at the University of Reading. His research interests include; speciation, molecular evolution, phylogenetics and trait evolution. He has recently published papers on punctuational evolution, speciation and phylogenetic inference.

Fees for IoB Members' Evenings are: £10 IoB members, £13 Non-members, £5 Students
This includes light refreshments. 30 places are available and this event may be counted as 5 IoB CPD credits.

For further details please contact Victoria Wood:
IoB, 9 Red Lion Court, London EC4A 3EF. Email: v.wood@iob.org

INSTITUTE OF BIOLOGY