

VESPA VELUTINA: CURRENT SITUATION AND PERSPECTIVES

KARINE MONCEAU (*) (°) - DENIS THIERY (**)

(*) UMR CNRS 7372 Centre d'Etudes Biologiques de Chizé, Université de la Rochelle, 79360 Villiers-en-bois, France

(**) UMR 1065 Santé et Agroécologie du Vignoble, INRA, F-33883 Villenave d'Ornon, France

(°) Corresponding author: karine.monceau@univ-lr.fr

Lettura tenuta durante la Tavola Rotonda "Avversità delle api e nuove minacce da insetti alieni per l'apicoltura italiana: *Aethina tumida* e *Vespa velutina*". Seduta pubblica dell'Accademia - Firenze, 18 novembre 2016.

Vespa velutina: Current situation and perspectives

Vespa velutina is an invasive honeybee predator introduced more than a decade ago in southwest France, followed by an impressive colonization of several areas within mainland Europe (France, Spain, Portugal, Italy, Germany, Belgium) and overseas (UK, Mallorca). The purpose of this short review is to give an overview of the basic historic of this biological invasion, to expose the current situation and to propose perspectives based on the French experience.

KEY WORDS: Alien species, domestic honeybee predator, Yellow-legged hornet.

INTRODUCTION

In the last century, the increase of human trade worldwide has largely contributed to the introduction of invasive species that are considered one of the major threats to biodiversity (VITOUSEK *et al.*, 1997; CHAPIN *et al.*, 2000). Alien species are usually characterized by their overall flexibility especially when facing disturbance (LEE & GELEMBIUK, 2008). Social hymenopteran are such highly flexible species due to eusociality: they exhibit behavioural plasticity due to their organization in castes; they also have high reproductive rates, demonstrate efficient competitive and dispersal abilities and are opportunistic foragers (MOLLER, 1996). This explains why several social hymenopterans have been successful at colonization worldwide in the last century. Vespids are of special concern because there are particularly difficult to contain when introduced; thus they have colonized several places worldwide and especially in America, Australia and New-Zealand (BEGGS *et al.*, 2011). Europe was spared until the introduction of *Vespa velutina*.

BACK TO *VESPA VELUTINA* INTRODUCTION HISTORY AND SPREAD IN EUROPE

Vespa velutina was first seen in 2004 in southwest France near Agen (RORTAIS *et al.*, 2010). The yellow-legged hornet (also called improperly Asian hornet) has been most probably introduced close to Agen (France) via boat and truck transport from China. A recent population genetic study

determined that the invasive population originated from Zhejiang or Jiangsu provinces and that a single female mated with four males was responsible for the European invasion (ARCA *et al.*, 2015). *V. velutina* has now colonized the two-third of the French territory and has reached several neighbouring countries such as Spain (LÓPEZ *et al.*, 2011) including Mallorca in Balearic Islands (GOVERN DE LES ILLES BALEARS, 2015), Portugal (Grosso-Silva & Maia, 2012), Italy (DEMICHELI *et al.*, 2013), Germany (WITT, 2015), and more recently Belgium and United Kingdom (including Channel islands such as Jersey and Alderney, UK Government, 2016).

WHY *VESPA VELUTINA* IS A MAJOR CONCERN?

V. velutina forms large colony, headed by one queen that can produce thousand individuals a year. During the growth of the colony from early July to late October, a huge amount of proteins is required to feed the brood (Fig. 1). A large part of the required proteins are obtained from honeybees that explains why *V. velutina* is known in its native range as a pest for beekeeping (MATSUURA & YAMANE, 1990; SHAH & SHAH, 1991). Following the first observations in France, the predation on beehives was soon noticed. Typically, *V. velutina* workers stay in stationary flight, back to the hive entrance to catch honeybee foragers coming back to the hive (TAN *et al.*, 2007; MONCEAU *et al.*, 2013a). In Asia, *V. velutina* prey on Asian honeybees, *Apis cerana*, but also on *A. mellifera*, the European honeybee, which has been introduced into Asia

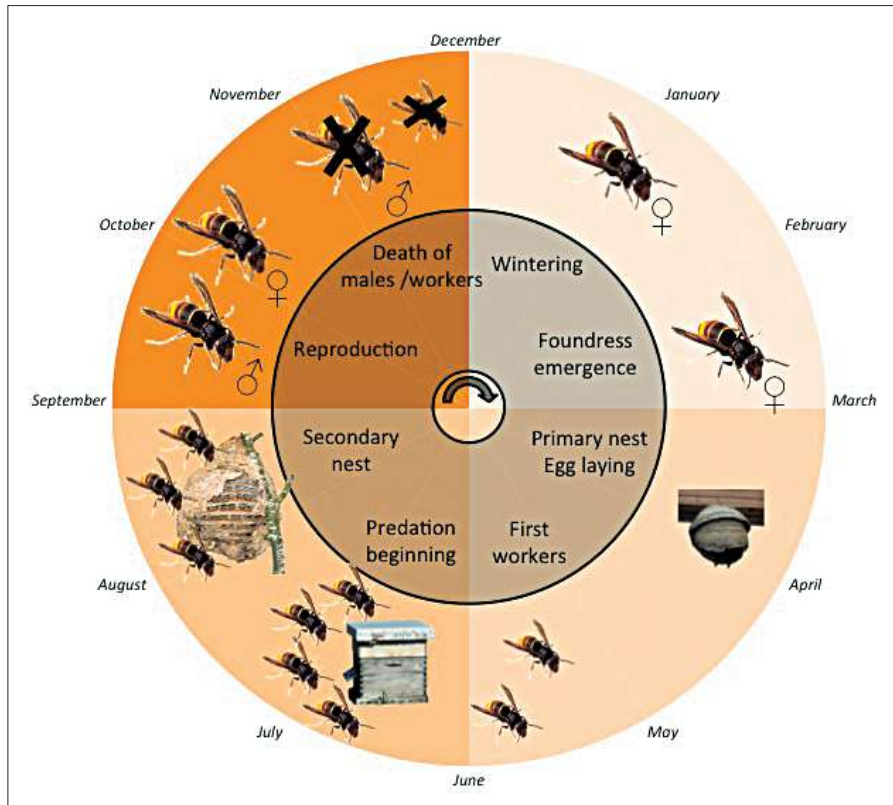


Fig. 1 – *Vespa velutina* life cycle (from MONCEAU *et al.*, 2014).

(KEN *et al.*, 2005; YANG, 2005). The predation on *A. cerana* is less intense than in *A. mellifera* because the former is able to efficiently defend its colony against *V. velutina* due to coevolution. *A. cerana* is able to display the so-called “beecarpet”, the heat-balling and shimmering behaviours while *A. mellifera* only displays the beecarpet and balling behaviours (KEN *et al.*, 2005; TAN *et al.*, 2010, 2012, 2013). In Europe, where *V. velutina* is the invasive and *A. mellifera* the native species, the situation is similar and the European honeybee does not defend efficiently against its predator (ARCA *et al.*, 2014).

IMPACT OF *VESPA VELUTINA*

The impact of *V. velutina* should be viewed at three different levels: i) the ecological impact on biodiversity, ii) the economic impact on beekeepers and citizens and iii) the sanitary impact.

The ecological impact

As previously said, the major impact of *V. velutina* is the predation on hives and other insects (MONCEAU *et al.*, 2013a, b). Direct impact on the entomofauna and indirect impact on plant biodiversity by reducing pollinator populations are thus expected. Hornet workers prey on honeybee foragers but the presence of the hornets by itself is also an important stressor for the bee colony in reducing the number of exit for the foragers, thus

decreasing the opportunity to collect food for storage and thus leading to the collapse of the hive during winter (ARCA, 2012). Additionally, studies realized in China have shown that the predation pressures of the hornet impact the learning ability of the honeybees (WANG *et al.*, 2016) and that neonicotinoid pesticides reduce predator avoidance (TAN *et al.*, 2014). The effects on domestic honeybees are probably the most conspicuous part of the impact of *V. velutina* on biodiversity but they represent only one to two-third of its diet depending on the environment (VILLEMANT *et al.*, 2011). So the impact of the huge predation on honeybee hives should be analogous on wild pollinators and other insects and should be investigated soon.

Finally, *V. velutina* is potentially a direct competitor of the native European hornet species, *V. crabro* which is considered a beneficial insect in agriculture. First studies, however, did not clearly evidence any negative impact of *V. velutina* on this species (MONCEAU *et al.*, 2015a, b) but investigations should be pushed forward.

The economic impact

Beekeeping activities have been challenged for a long time with different threats targeting honeybees such as parasites, virus, pesticides, habitat loss and/or fragmentation that weakened bee colonies (GOULSON *et al.*, 2015). *V. velutina* is an additional source of stress but its effects are difficult to dissociate from the others. According to the local section of the beekeeper union in southwest France

(Union Nationale pour l'Apiculture Française), 30% of the hives were destroyed/weakened in Gironde in 2010 due to *V. velutina*. No real assessment of the overall impact on honey production exists at this point but should be necessary.

From the citizen point of view, *V. velutina* could also represent a cost. Although French beekeepers are able and largely contribute to the destruction of nests for free, some private companies destroy nest for a cost up to several hundreds of euros depending of the conditions.

The sanitary impact

The last level to consider in this biological invasion is the sanitary problems. First of all, *V. velutina* is a venomous animal that can sting several times and thus injecting venom at each sting contrary to honeybees. In its native range, this hornet species is considered highly aggressive (MARTIN, 1995). A first assessment of the number of envenomation due to *V. velutina* was realized from 2007 to 2010 but the authors concluded that the number of accidents did not increase during this period corresponding to the proliferation of the hornet in southwest France (DE HARO *et al.*, 2010). There are, however, several accidents that ended dramatically by the death of the patient but the number of cases (although it is always too much) is low (less than 20 in 12 years). The frenzy surrounding each accident contributes to increase the phenomenon and also reinforces the fear of hornets (native and invasive species).

V. velutina can also be a vector of different parasites species. For example, it can host 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, no report of such virus has been done in *V. velutina*. It could also be a host for the parasitoid *Conops vesicularis* (DARROUZET *et al.*, 2015a) and the nematode *Pheromermis vesparum* (VILLEMANT *et al.*, 2015) which are both quite generalists and rare (see below).

The invasion by *V. velutina* poses several problems. Thus, it is urgent to control its expansion to a larger extent within Europe.

WHAT TO DO AGAINST *VESPA VELUTINA*?

Several techniques have been used to contain invasive vespids during past experiences in New Zealand for instance (BEGGS *et al.*, 2011). However, to date, there is no plug-and-play method that allows controlling efficiently *V. velutina* expansion. Different ways have been considered; some of them are potentially of major interest but this is not the case for all of them.

Trapping

Trapping is probably the first method that has ever been used to fight against invasive vespids. It can be performed at different step of the life cycle of *V. velutina* (Fig. 1): during the spring for catching foundresses and during the summer and autumn to catch workers and new emerging gynes (MONCEAU *et al.*, 2014). To date, only traps baited with food have been used. This is quite controversial for queen spring trapping for instance because of the lack of specificity, *V. velutina* foundresses representing a small percentage of the overall catches (MONCEAU *et al.*, 2012). Side effect on local entomofauna is sometimes impressive with the obvious potential consequences on population dynamics for non-target species. Additionally, there is a lack of evidence of the efficiency of such method as a mean of regulation of the invasive hornet species (MONCEAU & THIÉRY, 2016). An acute assessment of the real impact and efficiency of queen spring trapping should be done.

During the growth of the hornet colony, trapping can be used to locally decrease the predation pressure in apiaries. Three phases could be observed (Fig. 2): in June/July the late phase of the gynes, followed in early August by the dramatic increase of the predation due to the need of proteins to feed the brood and lastly in late October, the emergence of the gynes and males and the end of the colony. For these three phases, different food baits are efficient: the sugar-based baits for the first and last, and protein-based baits (fish) for the intermediate part (MONCEAU *et al.*, 2013b, 2015b). This kind of trapping has limited side effect on local entomofauna because most of the insects in apiaries at this time are either honeybees (that avoid these traps) or invasive hornets.

Toxic baits (growth inhibitor, insecticide) have also been used unofficially but the release of such molecules is problematic especially in regard to honeybee health and the current concerns about pesticides.

Inbreeding depression

As suggested by the population genetic study by ARCA *et al.* (2015), a single queen mated by four males is at the origin of the invasive population in Europe, thus with high level of inbreeding, as expected in most biological invasion. As a result, diploid males have been observed in several colonies of *V. velutina* (ARCA 2012; DARROUZET *et al.*, 2015b). Basically, in hymenopterans, females are diploid and males are haploid (haplodiploidy). However, sex is also determined by a locus, a phenomenon called complementary sex determination (CSD, see LIEBERT *et al.*, 2010). By definition, inbreeding increases the probability of an individual to be homozygous for a given locus.

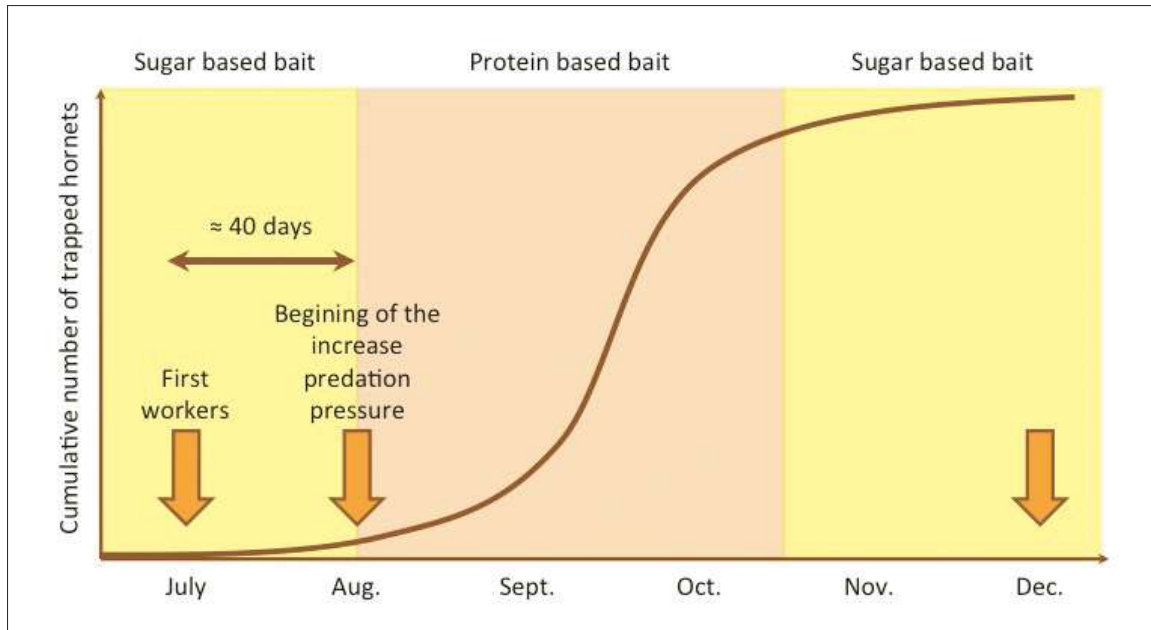


Fig. 2 – The three phases of trapping from July to December (from MONCEAU *et al.*, 2013b, 2015b).

Thus, in inbred populations like in the case of *V. velutina*, diploid females can be homozygous at CSD locus that is perceived like haploid individuals and are thus males. These diploid males represent a cost for the colonies because of their sterility and could lead to a vortex of extinction (ZAYED & PACKER, 2005). In the case of *V. velutina*, inbreeding is present since the introduction and did not seem to limit the expansion of the population through Europe, so it is unlikely that this could naturally drive the extinction of the invasive hornet. Moreover, *V. velutina* gynes are polyandrous and this mating system is known in social insects to be advantageous to increase offspring genetic diversity (JENNIONS & PETRIE, 2000) that could counteract the effect of inbreeding.

Natural enemies

As above, *V. velutina* can host different pathogens. Those recently described (DARROUZET *et al.*, 2015a; VILLEMANT *et al.*, 2015) are however unlikely to be involved in biological control because they are generalist pathogens. One predator species has been identified too, the honey buzzard, *Pernis apivorus*. Although this species is a potential predator of hymenopterans, a single observation of an individual feeding on a *V. velutina* nest has been done to date (see details in MONCEAU *et al.*, 2014).

The potential for natural enemies in a biological control context is quite restricted but some interesting perspectives from the side of entomopathogenic fungus that are often used for controlling insect pests may arise.

Nest destruction

Systematic nest destruction is probably the most effective method to control social insects (THOMAS, 1960; SPRADBERY, 1973) because the nest ensures the survival of the colony (HÖLLDOBLER & WILSON, 2008). During the queen colony phase (i.e., before the emergence of the first workers, Fig. 1), the nest is of the size of a gulf ball. Therefore, finding these little nests is often like searching for a needle in a haystack. Then, later in the cycle, the huge nests are often at the top of the trees but remain cryptic until leaves fall. Some methods are currently under development to increase our ability to detect early with harmonic radar (MILANESIO *et al.*, 2016) and nest destruction with drones for instance.

Pheromones

Due to their involvement in intraspecific communication, pheromones are probably the major way to investigate. Indeed, exploiting these naturally emitted molecules would be a clean way to enhance the specificity and attractiveness of the traps. For example, sex pheromones are used to disrupt mating in several agricultural pests like the grapevine pest, *Lobesia botrana* (IORATTI *et al.*, 2011). Recent neurobiological works on *V. velutina* showed the presence of several macrostructures in the antennal lobe of the males, which are probably linked to sex pheromones (COUTO *et al.*, 2016). To date, no sex pheromone has been clearly identified in hornets although a biological activity has been demonstrated in different *Vespa* sp. (ONO & SASAKI, 1987; SPIEWOK *et al.*, 2006). Future researches are thus required to identify candidate molecules in this way.

CONCLUSION AND PERSPECTIVES

Vespa velutina has become of major concern in the last decades, but it took ca. eight years before the French government legislated on this species. However, eradication was not possible anymore at this time. Early warning such as the system proposed by UK seems to work, as the reaction to the first observation of *V. velutina* in September 2016 lead to the destruction of the nest (although nobody at this time cannot know if there was only one nest). The main problem with biological invasion is that since the eradication step is exceeded, the establishment of a management program will be costlier and costlier as in several other examples (SIMBERLOFF *et al.*, 2013). Now, *V. velutina* has been implemented on the European alien list with 36 other invasive species but it still questions how and who will be mandated to coordinate the efforts of all the European research teams, beekeeper unions and citizens involved in the fight against the invasive bee predator.

REFERENCES

- 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., MOUGEL F., GUILLEMAUD T., DUPAS S., ROME Q., PERRARD A., MULLER F., FOSSUND A., CAPDEVIELLE-DULA, C., TORRES-LEGUIZAMON M., CHEN X.X., TAN J.L., JUNG C., VILLEMANT C., ARNOLD G., SILVAIN J.F., 2015 – *Reconstructing the invasion and the demographic history of the yellow-legged hornet, Vespa velutina, in Europe*. - Biol. Invasions, 17: 2357-2371.
- ARCA M., PAPACHRISTOFOROU A., MOUGEL F., RORTAIS A., MONCEAU K., BONNARD O., TARDY P., THIÉRY D., SILVAIN J.F., ARNOLD G., 2014 – *Defensive behaviour of Apis mellifera against Vespa velutina in France: testing whether European honeybees can develop an effective collective defence against a new predator*. - Behav. Proc., 106: 122-129.
- BEGGS J.R., BROCKERHOFF E.G., CORLEY J.C., KENIS M., MASCIOCCHI M., MULLER F., ROME Q., VILLEMANT C., 2011 – *Ecological effects and management of invasive Vespidae*. - Biocontrol, 56: 505-526.
- 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.
- CHAPIN F.S.III, ZAVALA E.S., EVINER V.T., NAYLOR R.L., VITOUSEK P.M., REYNOLDS H.L., HOOPER D.U., LAVOREL S., SALA O.E., HOBBIÉ S.E., MACK M.C., DIAZ S., 2000 – *Consequences of changing biodiversity*. - Nature, 405: 234-242.
- COUTO A., LAPEYRE B., THIÉRY D., SANDOZ J.-C., 2016 – *Olfactory pathway of the hornet Vespa velutina: new insights into the evolution of the hymenopteran antennal lobe*. - J. Comp. Neurol. 524: 2335-2359.
- DARROUZET E., GÉVAR J., DUPONT S., 2015a – *A scientific note about a parasitoid that can parasitize the yellow-legged hornet, Vespa velutina nigrithorax, in Europe*. - Apidologie, 46: 130-132.
- DARROUZET E., GÉVAR J., GUIGNARD Q., ARON S., 2015b – *Production of early diploid males by European colonies of the invasive hornet Vespa velutina nigrithorax*. - PLoS ONE, 10: e0136680.
- 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.
- DEMICHÉLIS 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>.
- GOULSON D., NICHOLLS E., BOTIAS C., ROTHERAY E.L., 2015 – *Bee declines driven by combined stress from parasites, pesticides, and lack of flowers*. - Science 347: 1435-1444
- GOVERN DE LES ILLES BALEARS, 2015 – *S'ha detectat una nova espècie invasora a les Illes Balears, la vespa asiàtica*. <http://www.caib.es/govern/pidip/dadesComunicat.do?lang=ca&codi=8827670>
- GROSSO-SILVA J.M., MAIA M., 2012 – *Vespa velutina Lepeletier, 1836 (Hymenoptera, Vespidae), new species for Portugal*. - Arquivos Entomol., 6: 53-54.
- HÖLLDOBLER B., WILSON E.O., 2008 – *The Superorganism*. W.W. Norton & Company, New York.
- IORIATTI C., ANFORA G., TASIN M., DE CRISTOFARO A., WITZGALL P., LUCCHI A., 2011 – *Chemical ecology and management of Lobesia botrana (Lepidoptera: Tortricidae)*. - J. Econ. Entomol., 104: 1125-37.
- JENNIONS M.D., PETRIE M., 2000 – *Why do females mate multiply? A review of the genetic benefits*. - Biol. Rev., 75: 21-64.
- KEN T., HEPBURN H.R., RADLOFF S.E., YUSHENG Y., YIQIU L., DANYIN Z., NEUMANN P., 2005 – *Heat-balling wasps by honeybees*. - Naturwissenschaften, 92: 492-495.
- LEE C.E., GELEMBIUK G.W., 2008 – *Evolutionary origins of invasive populations*. - Evol. Appl., 1: 427-448.
- LIEBERT A.E., WILSON-RICH N., JOHNSON C.E., STARKS P.T., 2010 – *Sexual interactions and nestmate recognition in invasive populations of Polistes dominulus wasps*. - Insect. Soc., 57:457-463.
- LÓPEZ S., GONZÁLES M., GOLDARAZENA A., 2011 – *Vespa velutina Lepeletier, 1836 (Hymenoptera: Vespidae): first records in Iberian Peninsula*. - Bull. OEPP/EPPD Bull., 41, 439-441.
- MARTIN S.J., 1995 – *Hornets (Hymenoptera: Vespinae) of Malaysia*. - Malay. Nat. J., 49: 71-82.
- MATSUURA M., YAMANE S., 1990 – *Biology of vespine wasps*. Springer-Verlag, Berlin.
- MILANESIO D., SACCANI M., MAGGIORA R., LAURINO D., PORPORATO M., 2016 – *Design of an harmonic radar for the tracking of the Asian yellow-legged hornet*. - Ecol. Evol., doi: 10.1002/ece3.2011
- MOLLER H., 1996 – *Lessons for invasion theory from social insects*. - Biol. Conserv., 78: 125-142.
- MONCEAU K., ARCA M., LEPRÉTRE L., MOUGEL F., BONNARD O., SILVAIN J.-F., MAHER N., ARNOLD G., THIÉRY D., 2013a – *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., 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., BONNARD O., THIÉRY D., 2014 – *Vespa*

- velutina: a new invasive predator of honeybees in Europe. - J. Pest Sci., 87: 1-16.
- MONCEAU K., MAHER N., BONNARD O., THIÉRY D., 2013b – *Predation dynamics study of the recently introduced honeybee killer Vespa velutina: learning from the enemy.* - Apidologie, 44: 209-221.
- MONCEAU K., MAHER N., BONNARD O., THIÉRY D., 2015b – *Evaluation of competition between a native and an invasive hornet species : do seasonal phenologies overlap?* - Bull. Entomol. Res., 105: 462-469.
- MONCEAU K., MOREAU J., POIDATZ J., BONNARD O., THIÉRY D., 2015a – *Behavioral syndrome in a native and an invasive hymenoptera species.* - Insect Sci., 22: 541-548.
- MONCEAU K., THIÉRY D., 2016 – *Vespa velutina nest distribution at a local scale: An 8-year survey of the invasive honeybee predator.* - Insect Sci., doi: 10.1111/1744-7917.12331
- 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.
- 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: Atlas of biodiversity risks-from Europe to the globe, from stories to maps, Settele J. Ed., Pensoft, Sofia, p. 11.
- SHAH F.A., SHAH T.A., 1991 – *Vespa velutina, a serious pest of honey bees in Kashmir.* - Bee World, 72: 161-164.
- SIMBERLOFF D., MARTIN J.-L., GENOVESI P., MARIS V., WARDLE D.A., ARONSON J., COURCHAMP F., GALIL B., GARCÍA-BERTHOU E., PASCAL M., PYŠEK P., SOUSA R., TABACCHI E., MONTSERRAT V., 2013 – *Impacts of biological invasions: what's what and the way forward.* - Trends Ecol. Evol., 28: 58-66.
- 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 J.P., 1973 – *Wasps: an account of the biology and natural history of social and solitary wasps.* University of Washington Press, Seattle.
- TAN K., CHEN W., DONG S., LIU X., WANG Y., NIEH J.C., 2014 – *Imidacloprid alters foraging and decreases bee avoidance of predators.* - PLoS ONE, 9: e102725.
- TAN K., LI H., YANG M.X., HEPBURN H.R., RADLOFF S.E., 2010 – *Wasp hawking induces endothermic heat production in guard bees.* - J. Insect. Sci., 10: 142 <http://insectscience.org/10.142>
- TAN K., RADLOFF S.E., LI J.J., HEPBURN H.R., YANG M.X., ZHANG L.J., NEUMANN P., 2007 - *Bee-hawking by the wasp, Vespa velutina, on the honeybees Apis cerana and A.mellifera.* – Naturwissenschaften, 94: 469-472.
- TAN K., WANG Z., CHEN W., HU Z., OLDROYD B.P., 2013 – *The 'I see you' prey-predator signal of Apis cerana is innate.* - Naturwissenschaften, 100: 245-248.
- TAN K., WANG Z., LI H., YANG S., HU Z., KASTBERGER G., OLDROYD B.P., 2012 – *An 'I see you' prey-predator signal between the Asian honeybee, Apis cerana, and the hornet, Vespa velutina.* - Anim. Behav., 83: 879-882.
- THOMAS C.R., 1960 – *The European wasp (Vespula germanica Fab.) in New Zealand.* - N. Z. Dep. Sci. Ind. Res. Inf. Ser., 27: 5-74.
- UK Government, 2016 - <https://www.gov.uk/government/news/asian-hornet-identified-in-gloucestershire>
- 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 : Proceedings of the Journée Scientifique Apicole, Arles, Barbançon J.-M. & L'Hostis M., Eds., ONIRIS-FNOSAD, Nantes, 11 February 2011, pp 3-12.
- VILLEMANT C., ZUCCON D., ROME Q., MULLER F., POINAR G.O., JUSTINE J.-L., 2015 – *Can parasites halt the invader? Mermithid nematodes parasitizing the yellow-legged Asian hornet in France.* - PeerJ, 3: e947.
- VITOUSEK P.M., MOONEY H.A., LUBCHENCO J., MELILLO J.M., 1997 – *Human domination of Earth's ecosystems.* - Science, 277: 494-499.
- WANG Z., QU Y., DONG S., WEN P., LI J., TAN K., MENZEL R., 2016 – *Honey bees modulate their olfactory learning in the presence of hornet predators and alarm component.* - PLoS ONE, 11: e0150399.
- WITT R., 2015 – *Erstfund eines Nestes der Asiatischen Hornisse Vespa velutina Lepeletier, 1838 in Deutschland und Details zum Nestbau (Hymenoptera, Vespinae).* - Ampulex, 7: 42 53.
- 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
- YANG G.-H., 2005 – *Harm of introducing the Western honeybee Apis mellifera L. to the Chinese honeybee Apis cerana F. and its ecological impact.* - Acta Entomol. Sinica, 48: 401-406
- ZAYED A., PACKER L., 2005 – *Complementary sex determination substantially increases extinction proneness of haplodiploid populations.* - Proc. Natl. Acad. Sci. USA, 102:10742-10746.