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Twenty years of attempting to control the *Vespa velutina* invasion: will we win the battle?

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Eusocial insects are among the most successful invaders worldwide. Among them, Vespine species are particularly prone to invasion due to sociality (Rankin 2021). The invasion by *Vespa velutina* is probably the most emblematic of the problem that Vespine wasps may pose. The yellow-legged hornet has been introduced accidentally into France near Agen in 2004 through a single queen as demonstrated by Arca et al. (2015). Twenty years later, the whole French territory is invaded as well as neighboring European countries. In 2023, *V. velutina* entered the US in Georgia. Although there have been several attempts to coordinate all actors, the lack of a global European strategy both from stakeholders but also among scientists probably contributed to the success of the invasion. With 20 years' hindsight on this invasion, we can take stock of the illusions and disillusions in the fight against this highly effective invader.

1 Illusions and disillusions

Early predictive models of distribution – Predictive models of distribution are classically used to identify areas at major invasion risk. This has been also done for *V. velutina* at an early stage of the invasion based on climatic suitability but the extent to which their special plasticity could not be predicted. From a practical point of view, this may have led decision-makers to neglect the systematic dimension that is required for such an invasion.

Nests and individuals mapping – Several databases exist, sometimes overlapping sometimes not, and may have limited our ability at coordinating a global strategy against *V. velutina*. Among the most popular methods, spring trapping is largely used to catch queens although controversial due to huge impact on non-target species. Even with no numeric relations between queen trapping and local population, matching such data with the number of nests detected or destroyed the previous year may be practically used to drive the control efforts. Nevertheless, no spatial model has been produced

to understand short and long-distance dispersal strategies, as queens can be highly explorative (Monceau et al. 2015). One may also consider that low dispersal abilities in queens may contribute to 1) increase nest density locally and 2) reducing nearest neighbour nest distances (see next section).

Competition between foundresses and nest usurpation was probably misleading – Although common among Vespidae such as *Polistes sp.*, there is no cues for this mechanism to exist in *V. velutina* as a potential regulative process. Considering the high density of nests in some French areas e.g., 12 to 19 nests per km² (Cotentin, France) with minimal distances of ca. 150 m between the nearest colonies (Monceau & Thiéry 2017), this competition appears unlikely, especially for a species foraging usually at ca. 1000 m or few kilometers (Poidatz et al. 2018a).

Population management based on chemical ecology is still a dream – Mating disruption with pheromones is a success story in crop protection mostly against moths. For purpose, pheromone dispensers release high amounts of synthetic sex pheromone nearby mating sites. The idea has thus emerged to control *V. velutina* with the identification of a sex pheromone produced by the queens. However, as mating seems to occur close to the nest, it would require first to locate them. If this is possible removing the nests when it is found would be more efficient. Several attempts to isolate specific attractants from plants (e.g., *Saracenia sp.*) have harvested poor results so far. One future option could be the intriguing attraction of males often observed on ivy. Trapping males could thus be an option, but it has first to be confirmed that visiting ivy occurs before mating.

The story of diploid males and population collapse? – In *V. velutina*, sex determination occurs both with ploidy (males are from unfertilized eggs and are haploid and females are from fertilized eggs and are diploid) and a complementary sex determination gene. Due to founder effect, the probability to be homozygous for this gene increases (genetic drift), making homozygous diploid individuals which should be females developing into males. These males can either be

sterile or produce diploid sperm that will result in triploid sterile offspring, either of which places a heavy burden on the colony and has been suggested as a possible cause of population collapse. Although there was a lot of buzz about this possible regulation, 10 years later the *V. velutina* population is still expanding, calling this hypothesis into question. This idea of a natural population collapse was probably harmful in the period when efforts should have been done to develop control techniques.

2 Future routes of research

Protecting the hives – Recent advances have been done with the development of non-baited electric traps placed close to the hives in summer. Several works congruently revealed a decrease of the predation intensity (Thiéry et al. 2023). These traps have little adverse effect on biodiversity since they are not based on a food source that may attract non target species.

The resistance of honeybees, defence mechanisms – *V. velutina* is a selective pressure that would naturally select resistant honeybee colonies. Protecting honeybees against the predator contributes to preserve maladapted colonies from the predation point of view. While research efforts to fight *Varroa destructor* have been partly dedicated to the selection of resistant honeybee lineages or at least the selection of hygienic behaviours, this has been poorly run in the case of *V. velutina*. As for varroa, the solution to limit *V. velutina* cost on honeybees should be integrative and should not only focus on trapping methods.

The high potential of micro-organisms as biological control agents – So far, we have very little examples of parasitism or predation of *V. velutina*. However, micro-organisms could represent a control option. The replicative Deformed Wings Virus was identified in hornets as a result of predating infected honeybees (Mazzei et al. 2018). A natural infection of a foundress by the entomopathogenic fungi *Metharizium robertsii* was also observed. Cross contamination of individuals by contact was successfully realized and death of infested workers was observed after 5–6 days post infection (Poidatz et al. 2018b). Viruses or fungi could thus reveal promising in a near future. The pioneer work comparing the immunocompetence of the two castes and the comparison with *V. crabro* (Cappa et al. 2021) will help applied research in this field.

Why honeybees? – One missing point is understanding why *V. velutina* starts to predate in summer honeybees. This is a dangerous resource, and one may expect that specific molecules are important during the larval development of next year gynes. Investigating the role of such molecules for reproductive capacities but also for the immunocompetence of wintering queens is probably a key point.

3 Conclusion

In this opinion paper, we tried to identify future research actions. For 20 years, several findings which made rather intense buzz were not confirmed or corroborated. Also, a rather fair number of promises of possible eradication were published or produced. We have now probably a million colony (estimate) that started 20 years ago with one colony. There is no more chance to eradicate this predator, and the reasonable objective of science will be now to produce methods able to limit the populations. Beekeeping will have to live with that new scourge in addition to varroa, pesticides and viruses.

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