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Rapid Communication

With a little help from the natives: a first report on a novel ecological interaction between yellow-legged hornet *Vespa velutina* Lepeletier, 1836 (Hymenoptera, Vespidae) and bumblebee wax moth *Aphomia sociella* L. (Lepidoptera, Pyralidae)

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Abstract

Invasive alien species often benefit from a lack of natural enemies in their introduced range. However, over time, native organisms can exploit these newcomers. Here, we report a novel ecological interaction between the invasive yellow-legged hornet (*Vespa velutina*) and the native bumblebee wax moth (*Aphomia sociella*) in Flanders, Belgium. In 2024, larvae of *A. sociella* were found in nine degrading primary nests of *V. velutina*. In five cases, the species identity was confirmed through DNA barcoding or adult moth emergence, while in four other nests larvae were present but not definitively identified. The caterpillars were observed feeding on nest materials and brood, indicating active parasitism. This constitutes the first known record of *A. sociella* exploiting *V. velutina* nests in its invasive European range. Spatiotemporal analysis of occurrence data across Flanders revealed that *A. sociella* and *V. velutina* co-occurred in 9.1% of shared 1 km^2 grid cells during the same year. However, all infestations were observed in primary nests early in the season, coinciding with the moth's phenology. While parasitism by *A. sociella* can affect individual nests, potentially disrupting early colony development, the overall impact on the hornet population is likely to be limited. Further research is needed to assess the extent to which *A. sociella* may influence hornet population dynamics or potentially contribute to biological control.

Key words: invasive alien species, ecological interactions, parasitism, parasite acquisition

Introduction

The spread of invasive species is one of the most critical ecological challenges of our time, contributing significantly to global biodiversity loss and ecosystem disruption (Roy et al. 2023). Invasive species often thrive in new environments where they may encounter fewer natural predators or competitors compared to their native range, allowing them to proliferate. This release from enemies reduces top-down control and allows species to

experience rapid growth and spread because they escape the native ecological interactions such as predation, diseases or parasitism (Torchin et al. 2003; Colautti et al. 2004; Liu and Stiling 2006; Roy et al. 2011). Combined with a reduced competition, enemy release increases the species' fitness, facilitating invasion success. Over longer-time frames, however, new biotic interactions may emerge in the invasive range, and eventually slow down or completely reverse the invasion (Roy et al. 2011; Dunn and Perkins 2012; Gendron et al. 2012; Schultheis et al. 2015; Westby et al. 2019; Sarabeev et al. 2022; Baso et al. 2025). Native species may acclimate and/or genetically adapt to exploit invaders, as demonstrated by various examples: invasive Asian house geckos (*Hemidactylus frenatus* Schlegel, 1836) are attacked by native pentastomes (*Woodycephalus* spp.) (Barnett et al. 2018), the emerald ash borer (*Agrilus planipennis* Fairmaire, 1888), invasive in North America, is preyed upon by several native woodpecker species (Jennings et al. 2016), and the Chinese mitten crab (*Eriocheir sinensis* Milne-Edwards, 1853), invasive in Europe, is consumed by larger benthic-feeding fish species such as eels, perch, and roach (Soes and Bouma 2010).

The yellow-legged hornet (*Vespa velutina* Lepeletier, 1836), introduced to Europe in 2004, provides a clear example of an invasive insect proliferating outside its native range. Since its arrival, *V. velutina* has spread rapidly across Western Europe arriving in Flanders (northern Belgium) in 2017 (Schoonvaere et al. 2020). The hornet's invasion success is attributed to its high dispersal ability, high reproductive rate, non-selectivity of habitat, and access to a rich abundance of prey (Rome et al. 2015; Arca et al. 2015). Indeed, *V. velutina* is especially profiting from the mass-abundance of domesticated, protein-rich bees (*Apis mellifera* Linnaeus, 1758) (Perrard et al. 2009; Monceau et al. 2013). As an invasive species, *V. velutina* may have an impact on native biodiversity as they also prey on other important pollinators, mainly flies, social wasps as well as other arthropods (van der Vecht 1957; Stainton et al. 2023; Pedersen et al. 2025).

Recently, there are increasing reports of *V. velutina* encountering natural enemies in its invasive range, with predation by birds and mammals being reported. For example, in southwestern Europe, the European honey buzzard (*Pernis apivorus* Linnaeus, 1758) has been documented preying on *V. velutina* nests (Macià et al. 2019; Rebollo et al. 2023; Martín-Ávila et al. 2024; Martín Ávila et al. 2025), and in Korea, where the species is also invasive (Lima et al. 2022), *V. velutina* was one of the wasp species identified in fecal samples of yellow-throated marten (*Martes flavigula* Boddaert, 1785) (Kim and Choi 2021). Additionally, a recent study documented the emergence of parasites—*Pyralis regalis* (Denis & Schiffermüller, 1775) and *Hypsopygia mauritialis* (Boisduval, 1833), both pyralid moths—from nests of *V. velutina* in Korea. Furthermore, in Taiwan, facultative interactions are observed where *V. velutina* is predated on by birds such as *Dicurus*

marcocercus (Vieillot, 1817) (https://www.inaturalist.org/observations/93873664) and spiders such as *Trichonephila clavata* (Koch, 1878) (https://www.inaturalist.org/observations/106321206) (Poelen et al. 2014). Overall, these observations indicate that a range of native organisms is beginning to exploit this new host (Shin et al. 2023).

Pathogenically, *V. velutina* harbours most common hymenopteran enteropathogens and shares a parasite profile very similar to that of the native *Vespa crabro* (Linnaeus, 1758) (Gabín-García et al. 2021). Several viruses frequently detected in honey bees and other hymenopterans have also been found in *V. velutina*, including Israeli acute paralysis virus (IAPV), aphid lethal paralysis virus (ALPV), black queen cell virus (BQCV), acute bee paralysis virus (ABPV), chronic bee paralysis virus (CBPV), deformed wing virus (DWV), Kashmir bee virus (KBV), and Sacbrood virus (SBV) (Yañez et al. 2012; Mazzei et al. 2019; Dalmon et al. 2019; Marzoli et al. 2021; Cilia et al. 2024; Shantal Rodríguez-Flores et al. 2024). In addition to these viruses, infections by entomopathogenic fungi (*Beauveria* and *Metarhizium*), a mermithid nematode (*Pheromermis* sp.), and a parasitoid fly (*Conops vesicularis* Linnaeus, 1761) have been reported in France (Darrouzet et al. 2015; Villemant et al. 2015; Poidatz et al. 2018). More recently, the strepsipterans *Xenos moutoni* (du Buysson, 1903) and *X. oxyodontes* (Nakase & Kato, 2013) were observed parasitizing *V. velutina* in South Korea, marking the first report of stylopization in this invasive species (Kim et al. 2025).

In this article, we report the first documented case of larvae from the bumblebee wax moth (*Aphomia sociella* Linnaeus, 1758) invading and feeding on brood in nests of the invasive yellow-legged hornet (*V. velutina*) in Europe, highlighting a novel biological interaction with this invasive hornet. *Aphomia sociella* is native to Europe, parts of Asia, and has also been reported in North America. It is mainly parasitic in the nests of bees and bumblebees, but also vespine wasps (Thomas 1960; Matsuura and Yamane 1990; Martin 1992; Gambino 1995; Yamane et al. 2022). The larvae are known to consume nest materials such as wax, pollen, meconia (larval fecal matter left in brood cells) and stored food, as well as immature brood stages of their hosts (Gambino 1995; Goulson et al. 2018a, b). Infestations often lead to the destruction of entire colonies, particularly in bumblebees, where mortality rates of up to 80% have been observed in urban gardens in Southern England (Schweiger et al. 2022). The larvae spin dense silk tunnels within the nests, obstructing movement and disrupting colony structure, providing physical protection from host aggression (Schweiger et al. 2022). *Aphomia sociella* is often observed in already weakened colonies, suggesting that it may act opportunistically, exploiting environmental or biological stressors within the nest (Gambino 1995; Krams et al. 2025). Despite the commonness and importance of these moth-wasp/bee interactions, studies

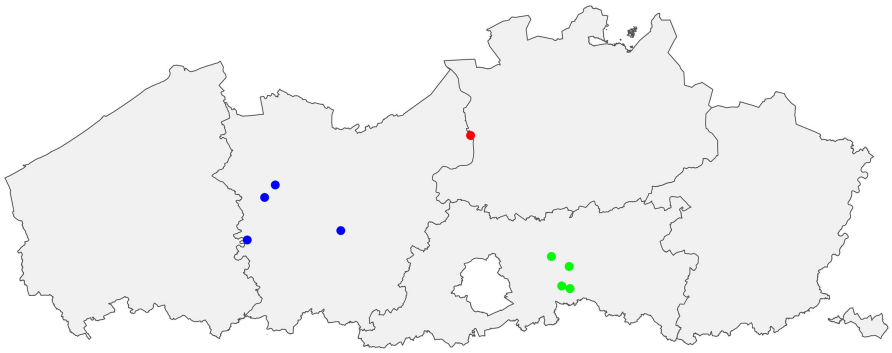

Figure 1. Distribution of nests in Flanders (Belgium) being parasitized by a moth species in 2024. In red, the sample which was identified as *A. sociella* through DNA barcoding. In green, the samples which were identified through pupation. In blue, the samples where larvae were present, but the species remained unidentified.

Table 1. Overview of reported primary nests with parasitic wax moths inside.

Nest ID	Lat	Long	Date of observation	Moth larvae
1	50.835667	4.665864	06/08/2024	*Aphomia sociella*, confirmed with pupation
2	50.882261	4.694405	04/08/2024	*Aphomia sociella*, confirmed with pupation
3	50.829358	4.697452	31/07/2024	*Aphomia sociella*, confirmed with pupation
4	50.906053	4.626517	22/07/2024	*Aphomia sociella*, confirmed with pupation
5	51.077099	3.573035	20/07/2024	Present, but unidentified
6	50.945580	3.466078	10/07/2024	Present, but unidentified
7	50.967992	3.822989	08/07/2024	Present, but unidentified
8	51.047222	3.532396	08/07/2024	Present, but unidentified
9	51.195321	4.318142	05/07/2024	*Aphomia sociella*, confirmed with barcoding

on the impact of parasitic moth on their hosts, their development, and ecology are scarce. To assess the potential for occurrence of this novel interaction, we explored the spatio-temporal niche overlap between *A. sociella* and *V. velutina* across Europe (Adriaens et al. 2008).

Materials and methods

Sampling

In Flanders (Belgium) in 2024, several caterpillars from one *V. velutina* nest (Nest ID 9 in red in Figure 1; Table 1) were collected. They were preserved in absolute ethanol for DNA barcoding, and sent to two separate laboratories independently to ensure accurate species identification. The sampling was not systematic but aimed at rapid identification of the specimens. In addition, caterpillars from nests 1–4 (in green in Figure 1; Table 1) were sampled for indoor pupation and observed until they emerged as adult moths.

DNA extraction and barcoding

A first molecular analysis was conducted at the Genetic Diversity lab (Research Institute for Nature and Forest). A caterpillar was divided into two parts. DNA was extracted from each part using the DNeasy Blood &

Tissue Kit (Qiagen) and eluted in 100 µl AE buffer. The integrity of DNA was assessed on 1% agarose gel using serial dilution and the concentration with the Quantus fluorometer with the QuantiFluor ONE dsDNA kit (Promega). A 658 bp fragment of the cytochrome c oxidase subunit I (COI) gene was amplified using degenerated Folmer primers dgLCO1490 (5'-GGTCAACAAATCATAAAGAYATYGG-3') and dgHCO2198 (5'-TAA ACTTCAGGGTGACCAAARAAYCA-3') primers (Meyer 2003). Reactions were performed in a total volume of 25 µl containing 2.60 µl of 10 × Taq buffer with 500 mM KCl (Thermo Fisher Scientific), 2.08 µl $MgCl_2$ (25 mM), 0.52 µl dNTP (10 mM), 1.04 µl of the primer set (10 µM), 0.8 U Taq DNA polymerase (Thermo Fisher Scientific), 12 µl of diluted DNA (5 ng/µl), and 7.60 µl DEPC water. The temperature cycle was 94 °C for 2 min, then 35 cycles of 94 °C for 30 s, 52 °C for 40 s and 72 °C for 1 min, and finally a single cycle at 72 °C for 5 min.

PCR products were checked on 1% agarose gels and purified using PureIT ExoZAP PCR CleanUp (Ampliqon). Bidirectional sequencing was performed using the BigDye Terminator v3.1 Cycle Sequencing Kit (Thermo Fisher Scientific) in a 32 µl volume containing 2 µl of purified PCR product, 1.6 µl of primer (10 µM), 8 µl Ready Reaction mix, 4 µl of 5x Sequencing buffer and 14.8 µl DEPC water. The PCR profile consisted of the following steps: 96 °C for 1 min, 35 cycles each with10 s at 96 °C, 5 s at 50 °C and 4 min at 60 °C. After purification with the BigDye XTerminator Purification kit (Thermo Fisher Scientific) products were analyzed on an ABI 3500 genetic analyzer (Applied Biosystems). After a visual check of overall quality, a consensus sequence from both directions was generated for each specimen using Geneious Prime v2019.2.3 (Biomatters Ltd.). It was compared with sequences in databases provided by NCBI (accessed December 2024) using the BLAST tool in Geneious Prime and in the database of BOLD (https://www.boldsystems.org, accessed December 2024).

A second molecular analysis was conducted at the University of Florence (Florence, Italy). DNA was extracted using a non-destructive protocol. Raw reads were demultiplexed using the Pacific Biosciences SMRT Link software. Consensus sequences were generated with the PacBio Amplicon Analysis (pbaa) tool. Primer trimming, translation and stop codon checking were performed using Geneious Prime 2024.0.1. Consensus sequences were made available in the BOLD database (Ratnasingham and Hebert 2007).

Screening for A. sociella occurrences in the dataset

The Vespawatch database (https://nesten.vespawatch.be/#/) was searched to identify additional records of wax moth occurrences. The search was performed by filtering the notes using keywords such as "wax moth", "parasite", "parasitized", and "caterpillar".

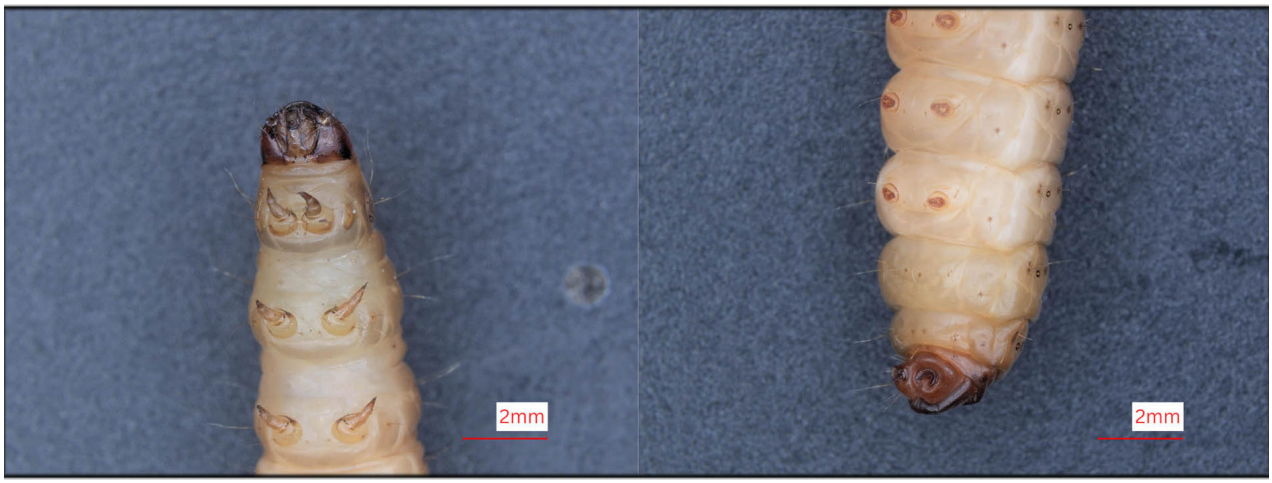

Figure 2. Photographs of a caterpillar from the bumblebee wax moth (*A. sociella*). ©Heleen Van Ransbeeck.

Co-occurrence

We assessed the spatiotemporal co-occurrence of *V. velutina* and *A. sociella* using presence-only observation data across Europe. Occurrence records for *V. velutina* were retrieved from the Global Biodiversity Information Facility (GBIF; download key: 0010917-250426092105405), while records for *A. sociella* were obtained from Waarnemingen.be, the nature information website of Natuurpunt and Stichting Natuurinformatie, reference number INBODATAVR-428 (data delivered on 3 June 2025), which provide more regionally complete data for Flanders. Records were cleaned, harmonized, and converted to spatial objects in WGS84 using R (v4.3.0) (R Core Team 2024) and the sf, raster and dplyr packages (Pebesma 2018; Wickham et al. 2023; Hijmans 2024).

To quantify co-occurrence, observations were aggregated per 1 km² grid cell using a CHELSA-based European raster layer. Spatial subsetting was performed using administrative boundary polygons for Flanders and Belgium. We assigned each observation to a raster cell and grouped them by cell and year. A cell-year combination was scored as (1) both species present, (2) only *V. velutina* present, or (3) only *A. sociella* present. Co-occurrence was expressed as the proportion of grid cells containing *V. velutina* where *A. sociella* was also detected as calculated in Adriaens et al. (2008).

Results

In 2024, a total of nine primary hornet nests were identified in Flanders as being parasitized by the caterpillars of a wax moth species (Table 1; Figure 1). In five of these nests the caterpillars were identified as the larvae from the bumblebee wax moth (*A. sociella*). According to the BLAST and BOLD search results, the consensus sequence of a caterpillar in one nest (Nest ID 9 in red in Figure 1; see also Figure 2) held a pairwise identity of 99.8% with *A. sociella* (accession number GU093027) and a 100% identity match with the same species (Process ID: IBLPY063-11) belonging to BIN BOLD:AAA5606, respectively. These results were independently confirmed by the laboratory of

Figure 3. Caterpillars from the bumblebee wax moth (*A. sociella*) from nest 1: a) feeding on brood and meconia within a *V. velutina* nest; b) kept in a separate container, showing their size, coloration, and number of individuals ©Tom Vrancken.

prof. Leonardo Dapporto at the University of Florence, who analyzed subsamples from Nest ID 9 using COI barcoding and obtained consistent identification of *A. sociella* (99.7% identity match on BOLD).

The species in four other nests (in green) was identified based on the pupation of larvae and the subsequent identification of the adult moths. The four remaining nests (in blue) contained unidentified caterpillars, which are highly suspected to be the same species based on their morphological characteristics and the conditions of the nests. However, as no specimens were preserved or sequenced from these cases, we cannot exclude the possibility of other wax moth species (eg. *Galleria mellonella* Linnaeus, 1758), although this species has not previously been recorded from *V. velutina* nests. Based on the congruence in morphology and timing with the confirmed cases, we consider it most likely that these infestations also involved *A. sociella*, but acknowledge that this remains unconfirmed.

In the region around Leuven, a local eradicator surveyed approximately 30 hornet nests during the hornet activity season in 2024 and reported finding clear signs of wax moth infestation in at least four nests (corresponding to Nest ID's 1–4), indicating a minimum infection rate of 13% among inspected nests (pers. comm. Tom Vrancken).

The caterpillars were feeding on the hornet brood and meconia, and in each case the hornet nest was in a clearly degrading stage, meaning that brood combs were partially damaged or consumed. However, some of these nests were still functionally active at the time of collection. For example, nest 3, the most heavily infested, consisted of two combs; the brood in the upper comb was almost completely taken over by caterpillars, with no pupae present, only a few larvae and eggs. Despite this, the nest still contained 79 workers and a queen, and appeared externally intact and active. In the other infested nests, the brood was also affected to varying degrees.

Caterpillars from nests 1–4 (Figure 3) successfully pupated by February 2025 and emerged as adults. The adult moths were confirmed to be *A. sociella* through morphological identification (Figure 4).

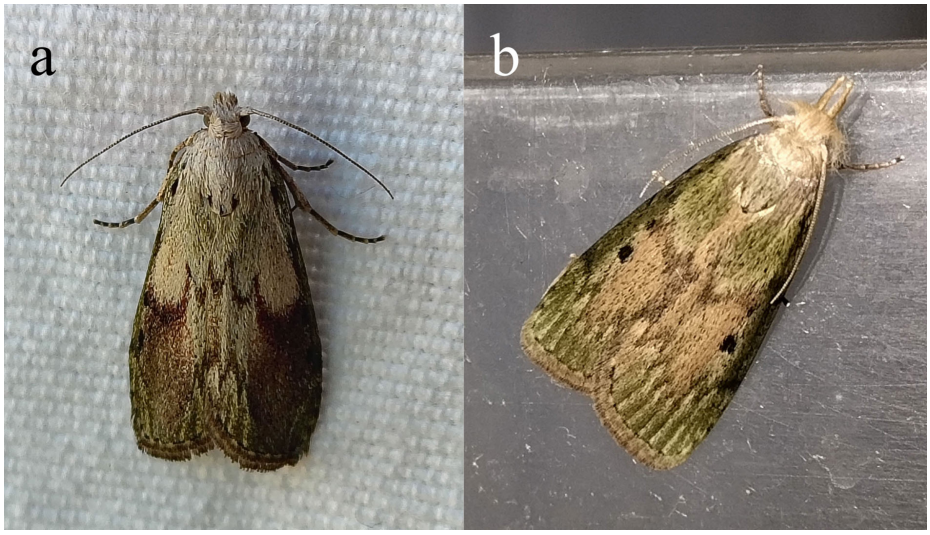

Figure 4. Pictures of the bumblebee wax moth (*A. sociella*) after pupation: a) male; b) female ©Tom Vrancken.

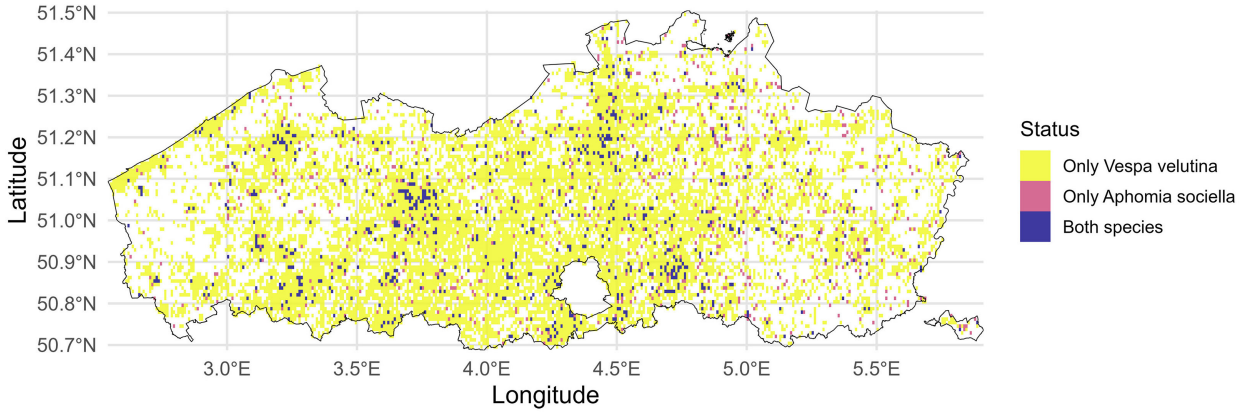

Figure 5. Co-occurrence map of *V. velutina* and *A. sociella* in Flanders (Belgium).

The spatiotemporal co-occurrence analysis for Flanders indicates that *A. sociella* is found in approximately 9.12% of the 1 km^2 grid cells where *V. velutina* was also observed in the same year (Figure 5). For Belgium this ratio is 7.24% and in Europe 2.83%. These values are based on cell-year combinations, meaning that observations of both species had to occur within the same 1 km^2 grid cell and calendar year to be considered co-occurring.

Discussion

The presence of larvae from the bumblebee wax moth (*A. sociella*) was confirmed in several degrading primary nests of *V. velutina* in Flanders during 2024. To our knowledge, this represents a first report of this species as a parasite of *V. velutina* in its European invasive range. Larvae of the moth were clearly feeding on brood and causing damage to the nests, indicating that the moth uses this novel host to fulfil at least part of its lifecycle. Hence, this constitutes a novel biotic interaction which may represent an example of parasite acquisition by an invasive species in its new habitat (Tompkins et al. 2011). According to the parasite acquisition

framework, invasive species can pick up local parasites from the new environment, with potential ecological consequences depending on the relative competence of the invader as a host (Schatz and Park 2021). In this case, it remains unclear whether *V. velutina* acts as a more or less competent host for *A. sociella* compared to its native hosts. If *V. velutina* is less competent, this could lead to a dilution effect, reducing the parasite's overall impact. However, if *V. velutina* proves to be a more competent host, *A. sociella* populations could increase within hornet nests, potentially leading to spillback towards its primary hosts, thereby amplifying infection pressure on native pollinators (Levi et al. 2016), or other hornet species like *V. crabro* which is a competitor of *V. velutina* (Cini et al. 2018; Cappa et al. 2021; Carisio et al. 2022). A likely consequence of such spillback is apparent competition, an indirect negative interaction in which native species experience increased parasite pressure not because of direct competition, but due to the invader's role in sustaining higher parasite densities (Holt and Bonsall 2017).

The observed infestation pattern also suggests that environmental or phenological constraints may shape this interaction. It is probable that the infestation only could take place in nests that are already degrading, either due to unfavorable weather conditions in 2024 or because colonies were naturally relocating from primary to secondary nests. In Belgium, this relocation typically takes place in July for 70% of the nests (Monceau et al. 2014; Bunker 2019). All confirmed infestations by *A. sociella* were found in primary nests between early July and early August, which is consistent with the moth's phenology: adults fly from April to July, with a peak in May and June (Figure 6). Whether the feeding by *A. sociella* on *V. velutina* brood affects colony success or whether the moth rather opportunistically occupies nests at the end of their lifetime remains unknown and merits further investigation. The fact that early nests are affected is a promising indicator for population control, as the survival of primary nests plays a more critical role in the hornet's life cycle than secondary nests. Parasitism at this stage may thus have a stronger impact on population dynamics, warranting further investigation through stage-structured modeling.

In addition to phenological and ecological overlap, spatiotemporal patterns of co-occurrence provide further insight into the potential for interaction. The results from the spatiotemporal co-occurrence analysis suggest a limited but non-negligible spatiotemporal overlap between *A. sociella* and *V. velutina* across different geographic scales. In Flanders, co-occurrence was observed in approximately 9.12% of 1 km^2 grid cells where *V. velutina* was recorded within the same year. This proportion decreases to 7.24% in Belgium and 2.83% across Europe. These values are likely conservative estimates due to potential sampling biases. *Vespa velutina* is a high-profile invasive species, subject to targeted monitoring and public reporting, leading

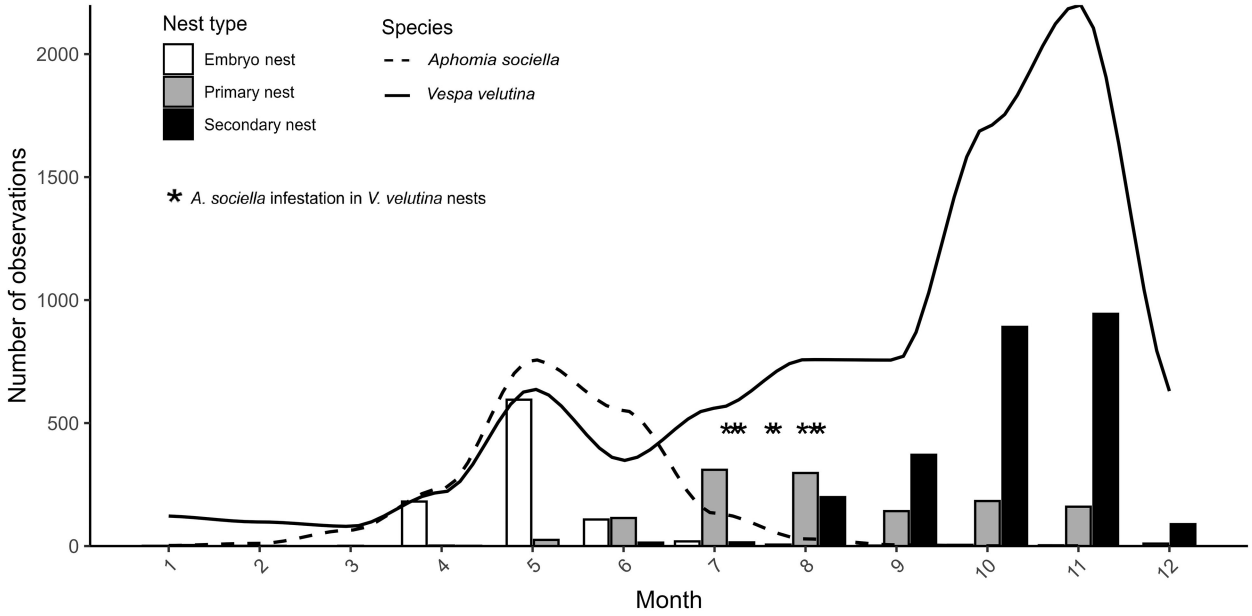

Figure 6. Phenology of *Aphomia sociella* and *Vespa velutina* in 2024 in Flanders. The solid line represents smoothed monthly observations of *V. velutina* nests (Vespawatch database). The dashed line represents smoothed monthly observations of *A. sociella* individuals (Waarnemingen.be, INBODATAVR-428). Bars indicate the number of observed *V. velutina* nests by type: embryo (white), primary (grey), and secondary (black) (note: nest type not yet validated by the VespaWatch administrators). Asterisks mark records of *A. sociella* infestation in *V. velutina* nests; their placement along the x-axis reflects the chronological order of these records within each month.

to relatively dense and geographically broad data coverage. In contrast, *A. sociella* is a native species not typically targeted in monitoring schemes, resulting in fewer and potentially underreported observations. Consequently, true co-occurrence rates are likely to be higher than reported, as absences of *A. sociella* in the dataset may reflect under-sampling rather than true absence. Furthermore, the univoltine life cycle of *A. sociella* restricts its phenological overlap with *V. velutina* to a narrow seasonal window, which may further reduce observed co-occurrence. Despite these limitations, the detected overlap suggests the potential for ecological interaction, particularly in regions where both species are present and conditions favor synchrony in their life cycles.

Current management strategies for *V. velutina* are primarily focused on nest destruction with biocides, such as permethrin, diatomaceous earth, etc. (Turchi and Derijard 2018) or mechanical methods like vacuum extraction. While these methods are effective, they are labor-intensive and in case of the biocides harmful to the environment. The recent observation of *A. sociella* larvae feeding on *V. velutina* brood suggests that native species might exert some degree of natural pressure on hornet populations. Although the idea of using *A. sociella* in augmentative biological control is theoretically interesting, its practical application appears unlikely. The moth's natural impact on hornet populations is probably strongest during its peak activity in May and June, particularly in years with poor weather conditions. The observed co-occurrence ratio of approximately 9.12% in

Flanders suggests that *A. sociella* has the potential to contribute to natural population regulation, although the extent of this effect requires further investigation.

In conclusion, the documentation of *A. sociella* parasitizing *V. velutina* nests introduces a new facet to the ecology of this invasive hornet in Europe. It highlights the importance of monitoring emergent interactions between invaders and native species – not only for understanding invasion biology but also for identifying potential natural checks on invasive populations.

Authors' contribution

HVR: writing – original draft and editing; JH: writing – editing; KC: methodology – DNA barcoding; TV: methodology – sample collection; DS: writing – review; GB: writing – review; AC: writing – review; AB: methodology – DNA barcoding; DdG: writing – review; DB: writing – review; TA: writing – original draft and editing, sample collection.

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Ethics and permits

The sampling pertaining to this article was performed under the derogation of the research Institute for Nature and Forest (INBO), in accordance with Article 19 of the Species Decree of 15 May 2009, issued by the Agency for Nature and Forest (ANB), permit number ANB/BL-FF/V19-00209-212. No ethics approvals were required.

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