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ORIGINAL PAPER

Predation of the invasive Asian hornet affects foraging activity and survival probability of honey bees in Western Europe

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Abstract

Introduced in France more than a decade ago from China, the invasive Asian hornet *Vespa velutina* preys on honey bee *Apis mellifera* foragers at hive entrances and is a major concern for Western European beekeepers and governmental policies. Asian hornet predation is suspected to weaken honey bee colonies before the winter season. In this study, we assessed the risk of winter colony losses related to hornet-induced disturbances by combining field observations and model system simulations. We provide empirical evidence in bee foragers' homing failures and bee foraging paralysis behaviour of the colony related to the predator–prey relationships between the hornet and the honey bees nearby colonies' entrances. Our model-based assessment confirms concerns of beekeepers and governmental policies that these hornet-induced disturbances affect honey bee colony dynamics and winter survival. Simulations reveal that the foraging paralysis behavioural response of honey bee colonies is an important mechanism underlying winter colony collapse. We provide recommendations of beekeeping management to mitigate potential detrimental effects from hornets to ensure bee colony survival, such as the control of the hornet-induced foraging paralysis of Western European honey bee colonies that may be viewed as an unadapted behavioural response to the invasive predator.

Keywords Alien species · Biological invasion · Honey bee colony collapse · Mechanistic modelling · Predator–prey relationship · Yellow-legged hornet

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Key message

- The Asian hornet is a new (invasive) threat to honey bees in Western Europe.
- The Asian hornet affects bee foragers' homing failures and colony foraging paralysis.
- In this study, two main honey bee colony collapse mechanisms were evidenced.
- Low hornet loads affect bee population size of previously weakened colonies.
- High hornet loads cause foraging paralysis and honey reserve overconsumption.
- The Asian hornet decreases the survival probability of honey bee colonies in Western Europe.

Introduction

The yellow-legged hornet *Vespa velutina* (also named Asian hornet and called hornet hereafter) is the first effective exotic invasive Vespidae in Europe (Beggs et al. 2011; Monceau et al. 2014). First observed in 2004 in Southwest France (Haxaire et al. 2006), this species has rapidly spread across most of the French territory (Rome et al. 2015; Robinet et al. 2017). Between 2010 and 2017, it has also successfully established itself in six neighbouring countries: Belgium, Germany, Italy, the Netherlands, Portugal, Spain (Rome and Villemant 2018), and has crossed the English Channel to also settle in the UK (Keeling et al. 2017). The hornet is expected to eventually spread further in Europe (Villemant et al. 2011; Fournier et al. 2017; Barbet-Massin et al. 2018; Robinet et al. 2018), and under future climate change scenarios, its expansion may increase even more rapidly than in the past 10 years (Barbet-Massin et al. 2013). Wherever it is encountered, one of the hornet's main sources of prey is honey bees. In Asia—its native distribution range (Arca et al. 2015)—the hornet hunts both the native *Apis cerana* and the introduced *A. mellifera* honey bee, with a higher frequency and success rate on the latter when both species are present in the same apiary (Tan et al. 2007). In Europe, predation activity of hornets on *A. mellifera* increases during summer and reaches its maximum in October, when hornets feed their sexual brood (Monceau et al. 2013; Villemant et al. 2014). At this time, the percentage of *A. mellifera* in the hornet diet can reach a maximum of up to 70% (Villemant et al. 2014). The period of preferential diet also corresponds to the critical pre-wintering season for *A. mellifera* as they store honey and breed winter bees to prepare for overwintering (Winston 1994).

Western European honey bees (*A. mellifera,* called bee hereafter) are currently declining. Their decline is manifested by high bee colony losses during winter (Neumann and Carreck 2010) and is probably due to a combination of multiple stresses, i.e. from parasites, pesticides, and lack of flowers, all of which weaken bee colonies before winter (Potts et al. 2010; Goulson et al. 2015). The current hornet invasion is of great concern to Western European beekeepers and governmental policies, as this predator may represent an additional risk factor involved in the loss of bee colonies. The hornet captures foraging bees, which increases their overall probability of homing failure (HF) (Monceau et al. 2013). Another impact is the disruption of colony foraging activity (called "foraging paralysis of the colony", FP) in response to the presence of hornets hovering in front of beehives (Monceau et al. 2018). Such impacts have the potential to greatly increase the risk of bee colony mortality over winter. Based on this assumption and given that no study has yet quantified this risk, the invasive hornet has been and is still considered as a "harmful species" by French governmental policies, a decision supported by beekeepers. Specifically, the hornet has been registered both as a "second category sanitary hazard" in 2012 and as an "invasive alien species" in 2013, respectively, under the French Rural Code (MAAF 2012) and under the French Environmental Code (MEDDE 2013). Since 2015, *V. velutina* is also included in the Europe's risk-assessment list of invasive alien species and is targeted by EU legislation to coordinating a plan of invasion control (European Commission 2016; Rome and Villemant 2016).

The overarching objective of this study was to assess the risk of hornet predation to bee colony collapse. To overcome the challenge of designing such an experiment in the field (which is the reason that no risk assessment has been done yet), we used a combination of field observations and model simulations. In the first step, we carried out a large-scale survey in France over 5 years to measure FP with respect to hornets hovering in front of beehives. Associated with these visual observations, we also relied on video surveillance (based on computer vision algorithms) to track the flights of both bees and hornets in the surrounding area of the beehive entrance in order to census the success of hornet predation (i.e. the number of bees caught). In a second step, we used the BEEHAVE model—a mechanistic model of bee colony dynamics (Becher et al. 2014)—to test whether the impacts of hornet disturbance, i.e. the FP and HF, on colony dynamics, leading to direct or indirect effects on winter colony mortality. Mechanistic ecological modelling has matured over the last decade and leads to more predictive and flexible models, which are increasingly used for solving a wide range of applied problems (Stillman et al. 2016). This modelling approach also aims to identify and to understand potential mechanisms of colony collapse (Rumkee et al. 2015; McMahon et al. 2016; Henry et al. 2017). We tested the following hypotheses:

1. FP and HF increase with hornet loads hovering at the beehive entrance before colony overwintering. These two impacts can disturb bee colony dynamics and lead to winter colony mortality according to two mechanisms:
2. At low FP intensity, the HF related to hornet predation decreases the size of adult population of the colony during the period of predation and can lead to winter mortality by colony depopulation.
3. Conversely, a high FP intensity increases the population size because foragers no longer leave the colony to forage. As a consequence of larger population size, the reduction of food supply due to the FP and the overconsumption of food by larger number of adult bees in the colony can deplete food reserves prepared in anticipation of the overwintering, thus leading to winter colony mortality through food shortage.

Materials and methods

Assessment of colony foraging paralysis (FP) by visual surveys

Visual observations were performed at the entrance of beehives to quantify FP associated with the presence of the hornet at the beehive entrance. Visual observation was deemed a robust and effective method to measure the number of hornets flying in the vicinity of the colony entrance. A total of 131 bee colonies were observed in 75 apiaries

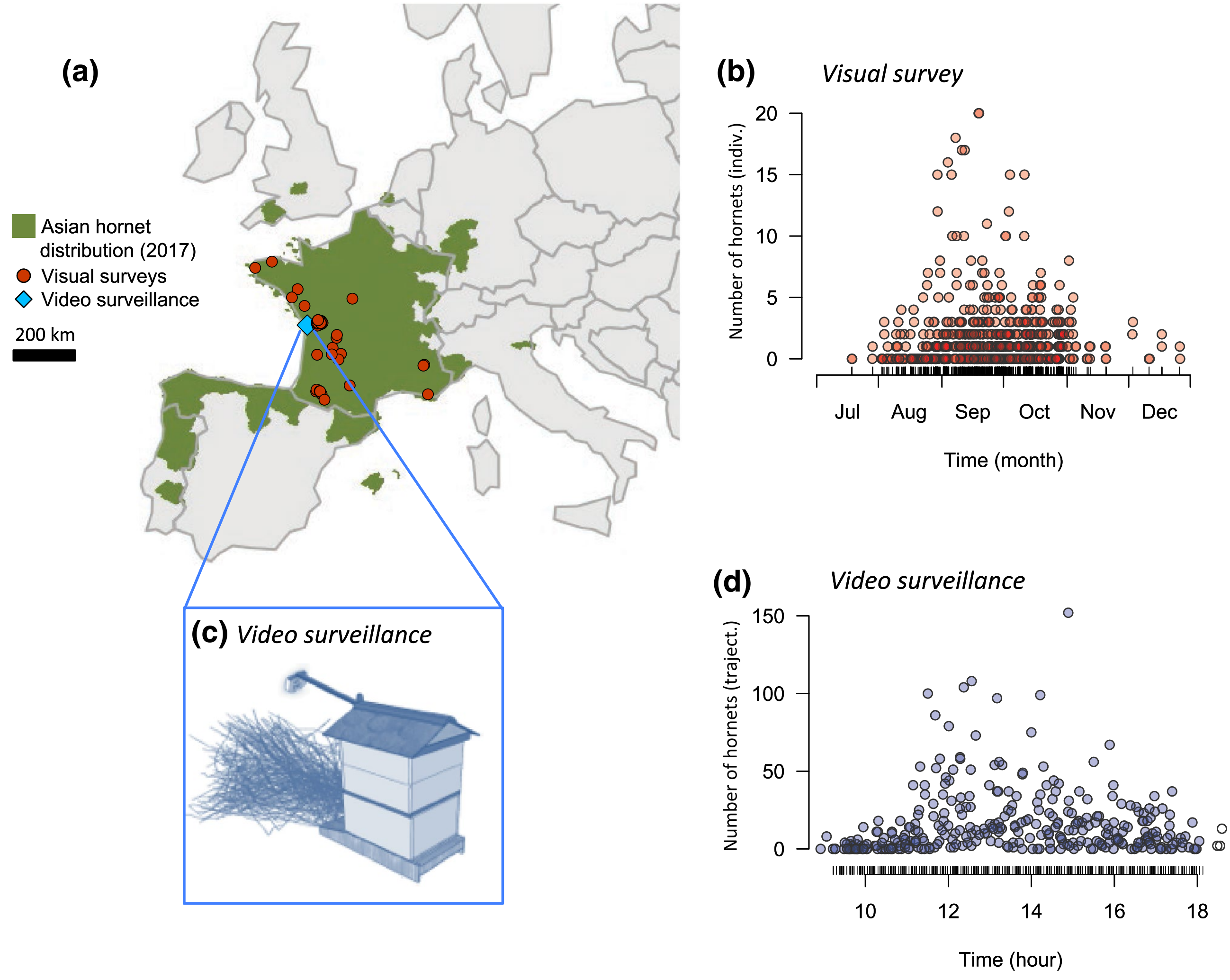

Fig. 1 Large-scale visual survey and video surveillance to track the predator–prey relationships between Asian hornets and Western European honey bees nearby colonies' entrances. **a** The spatial distribution of visual observations and video surveillance is shown as well as the current distribution of the invasive Asian hornet over Western Europe (Rome and Villemant 2018). **b** Seasonal variations hornet loads observed in front of visually monitored beehives. **c** Video surveillance device to track the light trajectory of honey bees and hornets at the entrance of a beehive. **d** Daily flight activity of hornets recorded in front of video-surveyed beehives

distributed in the area of presence of the hornet observed in France (Fig. 1a, see also the Electronic Supplementary Material ESM1). From 2012 to 2016 and during the complete period of hornet predation in Western Europe, i.e. from July to December, 603 observations were performed (Fig. 1b). A single person carried out the observations to mitigate any observer effect. Each observation consisted in 17 min of visual observation from a distance of 3–5 m to the beehive entrances. The first 15 min were dedicated to record the maximum number of hornets hovering in front of the beehive at the same time and the number of successful predations, i.e. the catch of a honey bee forager by a hornet. The two last minutes were dedicated to evaluate the flight activity of the bee colonies by counting the number of returning bees. The FP was estimated as the relative flight activity of bee colonies compared to their maximum level of flight activity (see data analysis).

Assessment of forager homing failure (HF) by video surveillance

A stereovision camera (G3 Evo 3, TYZX®) connected to a computer (for video storage) was mounted on the top of a beehive (Fig. 1c) to track the flights of bees and hornets in the surrounding area of the beehive entrance. Video surveillance was deemed a robust and effective method to measure the number of honey bees at the entrance of the colony. The experimental beehive was located nearby the town of La Rochelle (46°8′N, 1°8′W, Fig. 1a), 200 km away from where the hornet was introduced in 2004 (Haxaire et al. 2006; Villemant et al. 2011). The camera was placed 50 cm above the flight board of the beehive to ensure the non-trivial trade-off between the device intrusiveness (no nearby source of disturbance), the image definition (at least eight pixels per bee on the board) and observed volume (must include at least the 50 cm wide flight board) (Requier et al. 2016). The video surveillance was carried out in 2015, from October 16 to October 25, i.e. during the peak period of the hornet predation (Fig. 1b). Given that honey bees and hornets are diurnal insects, the 10 consecutive days of video tracking were performed without interruption from 9 to 18 h (Fig. 1d), providing in total 90 h of recorded activity. We then summarized the records of video surveillance per slot of 15 min ($n = 255$). Based on Chiron et al. (2013), we computed the trajectories of all the insects flying in front of the beehive. The details on target size/depth ratio in RGB-D images (such as provided by stereo-cameras) are available in Requier et al. (2016). A total of 603,259 trajectories were extracted, and, following Chiron et al. (2015), we distinguished the flight trajectories between bees and hornets using a clustering approach based on flight dynamics (e.g. max speed) and appearance features (e.g. the body size). A total of 5181 trajectories were found to be from the hornet. Each video slot for which both hornet(s) and honey bee(s) were detected was manually reviewed in order to census successful predation of a hornet on a bee (i.e. the number of bees caught). We considered a predation to be successful when a hornet catches a bee and flies away with its caught prey, given the limit of our video screen (about 1.5 squared metre around the beehive entrance). Each video was reviewed twice to confirm predation. Whenever predation success was unclear, that event was excluded. In the end, a total of 126 successful predation events were recorded. The probability of HF related to hornet predation was estimated for each 15-min slot as the ratio of number of bees caught reported to the total number of (incoming) bee trajectories.

Mechanistic modelling of bee colony dynamics

The hornet-induced colony collapse risk was assessed by a modelling approach using the mechanistic BEEHAVE model (Becher et al. 2014). We performed 1000 colony simulations with BEEHAVE to predict the colony daily growth from the beginning of January to the end of May of the following year, to include a complete winter season. We calibrated the model following Becher et al.'s (2014) initial colony settings along with random variations of four key parameters to ensure realistic simulation stochasticity: (i) the maximal egg-laying rate of the queen was randomly drawn from 1900 to 2300 eggs per day, (ii) the initial adult population size from 10,000 to 14,000 bees, (iii) the initial *Varroa destructor* infestation from two to four mites and (iv) the prevalence of virus-infected mites from 0 to 100% on the first day of simulation. We also included the typical beekeeping management practices using the ad hoc options, including *Varroa* treatments and honey harvests. After implementing a gradient of hornet impacts into the simulations (see data analysis), we exported and analysed the simulation outputs with a particular focus on five core colony traits recorded on a daily basis: (i) "Adult population" as the total number of adult bees alive including drone and the whole cast of workers, (ii) "Larvae population" as the total number of worker larvae (including the pupal stage), (iii) "Honey reserve" as the total amount of honey storage in the beehive, (iv) "Pollen storage" as the total amount of pollen storage in the beehive and (v) "*Varroa* load" as the number of *Varroa* mites alive.

Data analysis

All statistical analyses were performed using the R Project for Statistical Computing version 3.3.3 (R Development Core Team 2018).

Hornet impacts on bee colonies and foragers

To estimate the effect of the hornet on FP, we tested the correlative link between the number of incoming bees and the maximum number of hornets hovering in front of the beehive in the same time, using generalized linear mixed-effects models (GLMM) and a Poisson error structure (*glmer* function in the *lme4* R-package). The region and year of observations were specified as random variables in a nested design (region within year) to account for the spatio-temporal dependence of the repeated measurements. The FP was then predicted and expressed as the per cent flight activity of bees relative to its maximal value. We also tested the correlative link between the proportion of HF and the number of flying bees (incoming or outgoing) using binomial GLMM with a logit-link function. Likewise, hour and date of recording were specified as random variables in a nested design (hour within date) to account for the temporal dependence of repeated measurements. The model residuals were extracted and inspected against fitted values (residuals vs. fitted plot and normal Q–Q plot) to ensure that residual normality and the homoscedasticity assumptions were fulfilled.

Risk assessment of bee colony mortality

To simulate hornet impacts in BEEHAVE, we implemented HF and FP within the model by altering the two corresponding parameters: the forager mortality and the maximal foraging distance allowed for the colony. We varied these parameters in our simulations only during the main predation activity observed (see results), i.e. from day 240 (August 28th) to day 310 (November 6th). Across the 1000 computed simulations, we gradually decreased the maximal foraging distance allowed for the colony from the default value of 7299 km per day down to 0 (no foraging activity), and we increased the forager mortality rate from the default value of 1.00e−05 to 2.00e−05 per second foraging. Thus, each simulation involved a level of hornet impact scaled on the field observations, ranging from low to high impact. Simulations were further classified based on whether they predicted colony collapse during winter. Collapse events were defined using two thresholds (Becher et al. 2014): (i) simulations that predict a population size smaller than 4000 adult bees during winter and (ii) simulations that predict a complete depletion of honey stock during winter.

Mechanism underlying bee colony mortality

We used path analyses (Shipley 2009) to test causal hypotheses on the chain of demographic processes linking hornet-based disturbance with honey bee colony collapse events throughout the winter period. Path analysis helps to disentangle the most plausible direct and indirect links in multivariate datasets by assessing conditional independence among indirectly linked variables. We applied the path analysis to the colony simulation outputs (at day 310) using the *PiecewiseSEM* R-package (Lefcheck 2016). We first built a basic path model that reproduced the mechanistic structure of the BEEHAVE colony model, with the corresponding links among the core colony traits (Becher et al. 2014). We then implemented the hornet-induced effects as a proximal disturbance variable affecting the FP and HF. Each causal link in the path model was depicted as a linear model (LM) or a generalized linear model (GLM), depending on the nature of the involved variables. We used a GLM with a logit-link function for the binary colony collapse occurrence and LMs with Gaussian error structure for other variables. All variables were standardized using Z scores, and the normal distribution of residuals of each model was checked. We then identified the simplest path model structure that did not deviate from the conditional independence expectations while including only significant links. (Detailed P values for direct links and conditional independencies are available in the ESM2 and ESM3).

Early warning indicators of bee colony mortality

Conditional inference tree models (*ctree* function in the *party* R-package) were used to characterize the demographic profile of colonies with higher hornet-based collapse risks. Cluster tree models use nonparametric regressions and binary recursive partitioning to identify the most influential explanatory variables and associated thresholds underlying the variations of the response variable (Hothorn et al. 2006). Herein, the colony collapse occurrence was taken as the response variable, and the five core colony traits at the end of the impact period (i.e. day 310) as the explanatory variables.

Results

Hornet impacts on bee colonies and foragers

The visual observations returned a range of 0–20 hornets hovering at beehive entrances between July and December (Fig. 1b), with occurrences of more than five hornets being recorded only between August 28 and November 6. Flight activity of the bee colonies was negatively impacted by hornet loads hovering at the entrance of the beehives ($Z = -20.65$, $P < 0.001$, Fig. 2a), with complete bee foraging paralysis theoretically expected for at least 12.6 hornets simultaneously hovering in front of the beehives (see the prediction 95% confidence interval in Fig. 2a). The video surveillance showed hornet daily activity at the beehive entrance ranging from 0 to 152 tracked flight trajectories

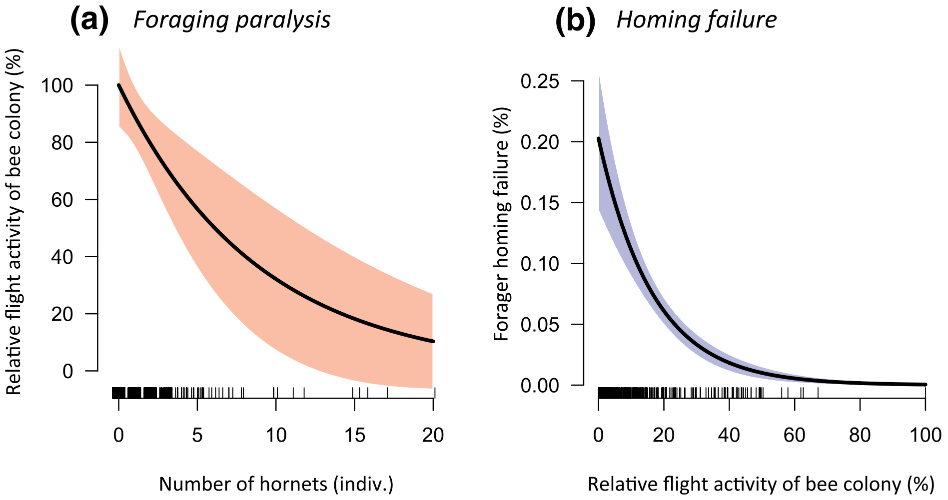

Fig. 2 Impacts of the invasive Asian hornet on Western European honey bees. **a** The hornet loads in front of beehives triggers foraging paralysis (FP), with a sharp decrease in honey bee flight activity. **b** As flight activity decreases, hornets increase their bee capture success, increasing the risk of homing failure (HF) due to hornet predation. Thick lines show the model predictions with shaded areas indicating the 95% confidence interval

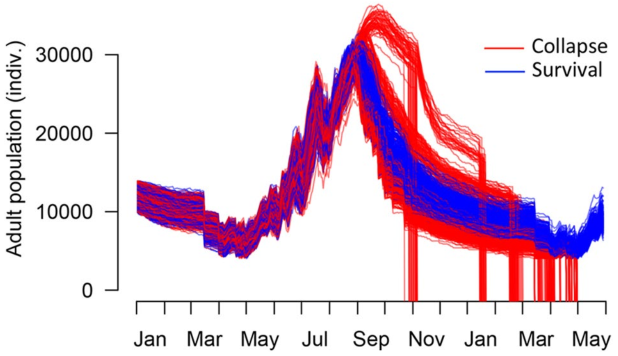

Fig. 3 Temporal pattern of the honey bee colony population size simulated with the BEEHAVE colony model parameterized with a range of hornet impact levels. Collapsing lines show simulated colonies that reached the endpoint (see text), with vertical lines pointing to the collapse date

over a typical day (9:06–18:08; Fig. 1). The hornet-based HF was significantly dependent on the flight activity of the bee colony ($Z = -5.37$, $P < 0.001$, Fig. 2b). Thus, the HF is maximal under condition of very low flight activity of the bee colony, and quickly decreases with the increase of the flight activity of the bee colony (Fig. 2b).

Risk assessment of bee colony mortality

A prior validation step excluded seven simulations that reached the endpoint before the implementation date of the hornet impacts, and among the 993 remaining simulations, 55.3% eventually reached the endpoint at some time following the hornet activity period (Fig. 3). A low number of simulated colonies collapsed during the period of hornet predation (i.e. 24 colonies representing 2.5% of remaining simulations), while collapse events mainly occurred during winter, from January 13 to May 1 (Fig. 3).

Mechanism underlying bee colony mortality

Because the effect of hornets on bee colony dynamics was clearly nonlinear (ESM4), we used the threshold of 13.3 hornets simulated to discriminate the scenario of “low hornet loads” that maintained a high ratio of food storage availability per bee (more than 0.5 g per bee, $n = 657$ simulations) vs. the scenario of “high hornet loads” which reduced the food storage availability per bee (less than 0.5 g per bee, $n = 336$).

At low hornet loads, the path analysis depicted consistent causal links between hornet predation, honey bee colony dynamics and the colony mortality in winter with indirect links that did not significantly deviate from conditional independency requirements (Fisher’s $C = 1.68$, $k = 32$, $P = 0.432$; Fig. 4). The main links are graphically represented in ESM5. Coefficients and detailed P values underlying the path analysis are presented in ESM2. The most notable effects were the negative effect of hornet loads (number of hornets simulated, from 0 to 13.3 hornets) on bee core traits at the end of the hornet impact period, such as the honey reserve and the adult population. Following the causal links, the implemented impacts of hornets then disturbed the relationship among core colony traits. For instance, the honey and pollen stores were both negatively affected by an increase in the adult population size. On the other hand, the larvae population size was positively affected by an increase in the adult population size. Winter colony survival was mainly explained by a direct effect of the adult population size at the end of the hornet impact period, where larger adult population size colonies survived the winter better. The amount of pollen stored at the end of the hornet impact was also positively correlated with the winter survival of colonies, while the indirect negative effect of the hornet to winter colony survival was not tightly correlated.

At high hornet loads, path analysis also identified a consistent chain of causal links between hornet predation,

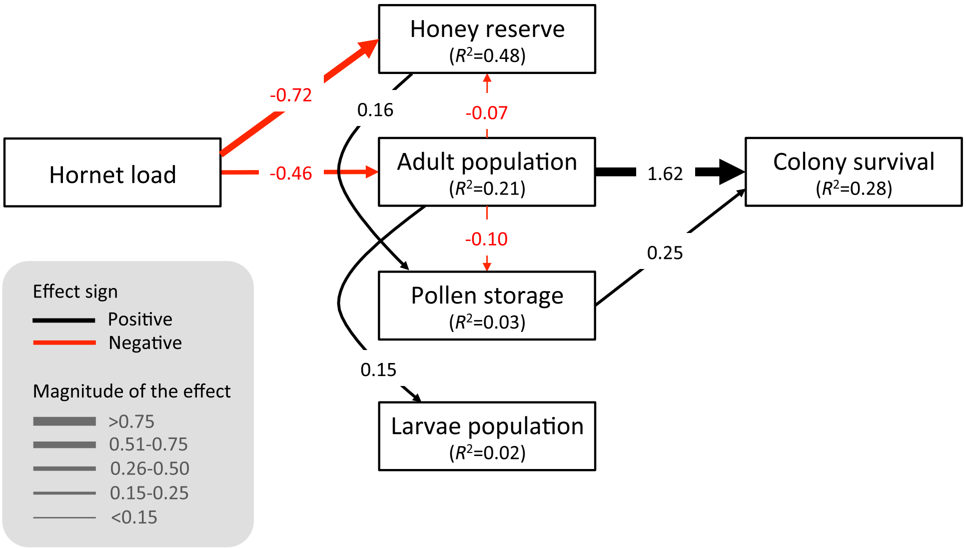

Fig. 4 Path analysis revealing the process of bee colony depopulation in situation of low hornet loads (< 13.3 hornets), leading to higher winter colony mortality. Only significant links are shown. See ESM2 for detailed statistical properties of the path model and links. Total explained variance (R^2) is indicated in the box for each response variable. The thickness of an arrow represents the magnitude of the (standardized) effect, and the colour shows the effect sign (positive or negative)

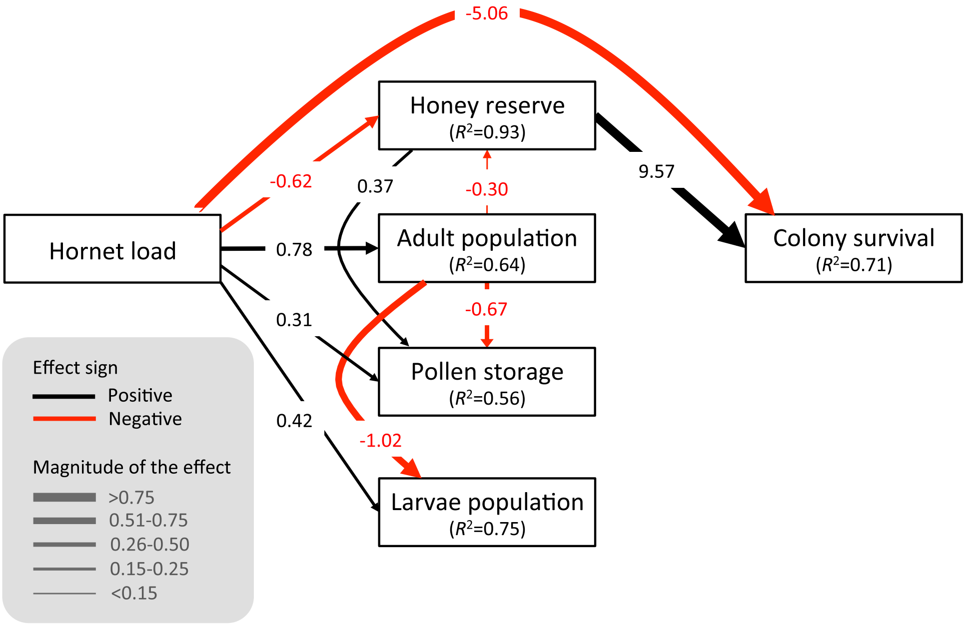

Fig. 5 Path analysis revealing the process of bee colony depopulation in situation of high hornet loads (> 13.3 hornets), leading to higher winter colony mortality. Only significant links and effects > 0.15 are shown. See ESM3 for detailed statistical properties of the path model and links. Total explained variance (R^2) is indicated in the box for each response variable. The thickness of an arrow represents the magnitude of the (standardized) effect, and the colour shows the effect sign (positive or negative)

honey bee colony dynamics and colony mortality in winter (Fisher's $C = 2.45$, $k = 32$, $P = 0.293$; Fig. 5). Raw data for significant links are provided in ESM6, and estimates of all paths (including missing path coefficients) along with the corresponding *P* values are given in ESM3. With high numbers of hornets (from 13.3 to 20 hornets), hornet loads had a positive effect on the adult population size, larvae population and pollen storage at the end of the impact period, and a negative effect on the honey reserves stored. The implemented hornet impacts involved disturbances in the relationships among core colony traits with cascading costs and feedback effects. For example, an increase in adult population size had a negative effect on honey and pollen reserves. Moreover, the increase in adult population size had a negative effect on larvae population. Larvae population was positively correlated with pollen and honey reserves. Winter colony survival was improved by the amount of honey reserves stored at the end of the hornet activity period and negatively affected by hornet loads during the period of predation.

Early warning indicators of bee colony mortality

Conditional inference tree models identified three main colony profiles associated with high hornet-based risks of bee colony collapse (> 50%) during the winter following hornet activity period. These profiles are well described using the core colony traits "Larvae population", "Adult population" and "Honey reserve". As a first risk profile (simulation set A in Fig. 6,

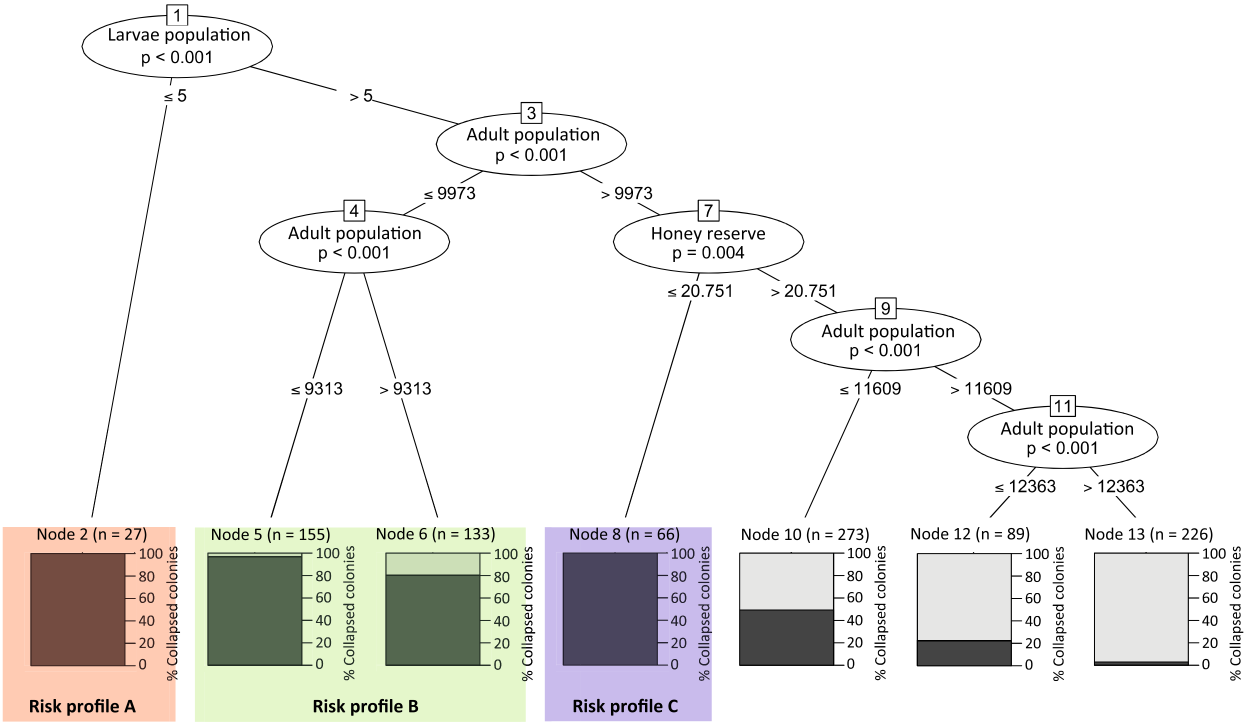

Fig. 6 Mortality risk profiles for bee colonies subject to hornet predation, as depicted by the conditional inference tree model. For each inner node, the Bonferroni-adjusted *P* value is given along with the name of the corresponding discriminatory variable. The proportion of collapsed overwintering colonies (in dark grey) is displayed for each terminal node

$n = 27$, $\chi^2 = 28.78$, $P < 0.001$), colonies with a larvae population size of less than five individuals at the end of the hornet predation period suffered a 100% winter mortality. As a second risk profile (simulation set B in Fig. 6, $n = 288$, $\chi^2 = 72.32$, $P < 0.001$), colonies with larvae population size higher than five individuals and an adult population size of less than 9950 individuals at the end of the hornet impact period suffered 80.5–96.8% mortality. The third risk profile is related to colonies with larvae population size > 5 individuals, adult population size > 9950 and a honey reserve storage ≤ 21 kg at the end of the hornet impact period which also to 100% of probability of winter mortality (simulation set C in Fig. 6, $n = 66$, $\chi^2 = 11.72$, $P = 0.004$).

The three risk profiles corresponding to simulation sets A, B and C displayed a similar decreasing larvae population size throughout the hornet impact period (Fig. 7a). However, the adult population size followed different trajectories among risk profiles (Fig. 7b). Adult population size sharply decreased in profile B (down to − 19,732 individuals), while adult population size increased in profile A (up to + 4874 individuals). In line with the adult demographics, honey reserves sharply decreased in the populated colonies of profile A (Fig. 7c, down to − 26.8 kg), while reserves stabilized at high levels in the depopulated colonies of profile B (+ 12.3 kg). Profile C colonies displayed intermediary population and reserve trajectories.

Discussion

Hornet predation can lead to winter mortality of Western European honey bee colonies

In Western Europe, the yellow-legged hornet concerns beekeepers and governmental policies because it poses a significant collapse risk on wintering honey bee colonies. This study is a first attempt to estimate the risk of bee colony mortality related to two different observed hornet impacts, namely the predation of individual foragers and the colony foraging paralysis. Through large-scale visual surveys of bee colony behaviour, we identified predating hornets and confirmed seasonal predation activity spanning from July to December, with an activity peak during September and October (Monceau et al. 2013). Hornet loads at colony entrances disturbed bee foraging activity and were associated with a behavioural response called foraging paralysis (FP). This behaviour is commonly observed across the hornet distribution area (Monceau

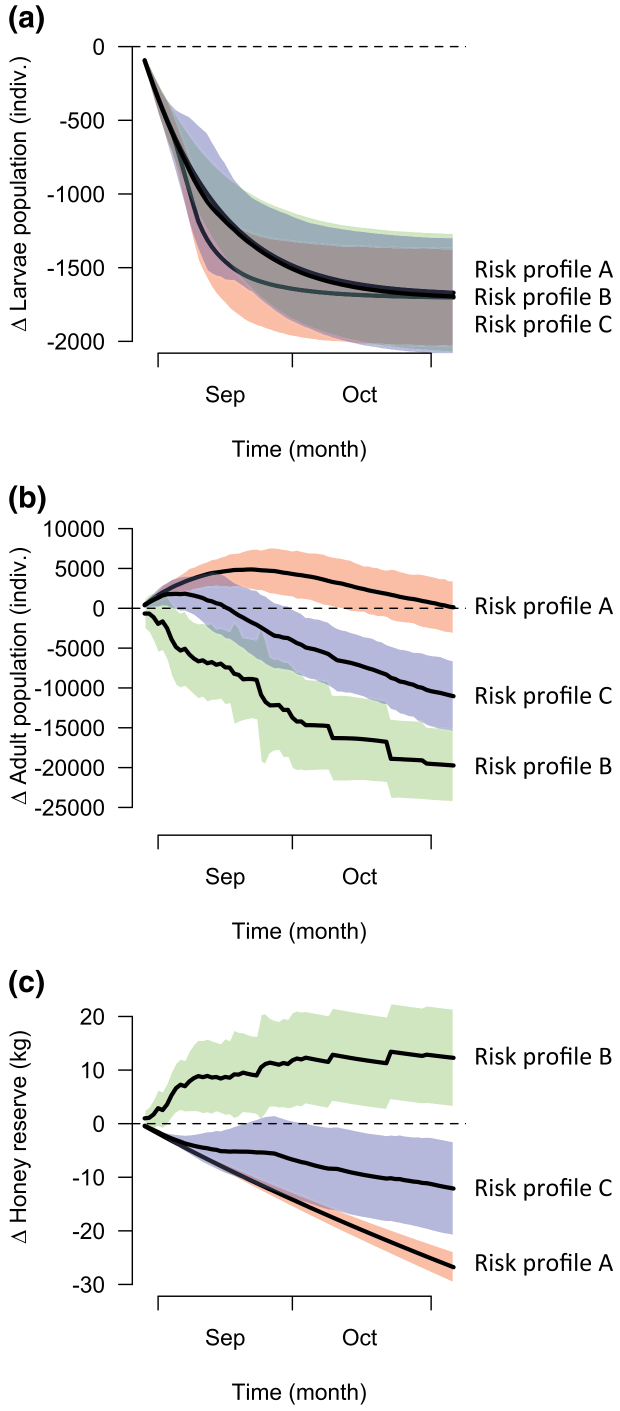

Fig. 7 Response of simulated honey bee colonies to hornet predation in the three categories of colonies with high-risk profile of hornet-based colony collapse. For each simulation matching a high-risk profile, we estimated the temporal changes in **a** larvae population size (Δ population size), **b** adult population size (Δ population size) and **c** honey reserves storage (Δ honey reserve). Changes are computed on a daily basis, with day 240 (August 28) being the reference date. The horizontal dotted line shows the no-change value. Thick lines show the average value of the change at day *d* with shaded areas indicating the 95% confidence interval

et al. 2018). During the most severe foraging paralysis events, bees completely cease their flight traffic at the hive entrance.

We further explored a second impact, i.e. the predation per se, using video recording, confirming the previously established daily activity pattern of hornets at hive entrances from 9 a.m. to 6 p.m. (Monceau et al. 2013). During this time frame, hornets catch returning bees, which translates into an increased probability of forager homing failure (HF) in simulations. When implemented in the BEEHAVE bee colony model (Becher et al. 2014), these two hornet impacts were expected to disturb bee colony dynamics, eventually precipitating collapse during winter in a substantial proportion of simulations. Collapse events were rarely evidenced during the period of predation itself (i.e. during pre-wintering), suggesting a carry-over effect on winter colony survival. This first risk assessment supports the registration of the invasive hornet as the “harmful species” and “second category sanitary hazard” by governmental policies in France (MAAF 2012; MEDDE 2013), as well as within the Europe’s risk-assessment list of invasive alien species by the European Commission (European Commission 2016; Rome and Villemant 2016).

Our simulation-based approach can be considered conservative as hornet activity was simulated only during a restricted period of time (i.e. September and October instead of the whole July to December activity period). Moreover, the two simulated impacts, FP and HF, can be considered as conservative themselves. The HF estimate was constrained by the screen size of the camera as it is possible that hornets can catch foragers outside of this screen. Furthermore, the screen size restriction led to a maximal number of hornets simultaneously hovering at the entrance of the beehives of four individuals while visual observation survey measured a maximal number of 20 individuals (Monceau et al. 2018). Finally, the simulation approach could also be considered as conservative given that the BEEHAVE model (Becher et al. 2014) does not consider the need for colonies to breed winter bees with higher lipid contents, based on lipid-rich pollen diet, to face overwintering (Winston 1994). Colonies may therefore suffer lipid dietary deficiency, along with winter bee lifespan reduction, whenever hornets trigger excessive FP during pre-wintering seasons (Winston 1994). However, additional homing failure assessments obtained from different environmental contexts would be welcome to refine current colony simulations. Our Asian hornet predation datasets are scarce due to the difficulty to properly census predation events (herein carried out at a single beehive during a single season). This appeals for caution about generalizing from the current models without further exploring potential environmental variabilities.

The foraging paralysis: an unadapted behavioural response underlying colony collapse

Interestingly, empirical data showed that two impacts of hornets were not independent of each other as HF increased with FP. In other words, FP enhanced the predation success of the hornet, which was more efficient at preying on returning bees in conditions of reduced bee traffic at hive entrances. This suggests that the behavioural response of the Western European bee colonies is poorly adapted to its recently introduced predator. In Asia, the long-term predator–prey relationship between the Eastern honey bee, *A. cerana,* the yellow-legged hornet and several other hornet species led to the development of a peculiar defensive response against these predators. For instance, facing a hovering hornet, Eastern honey bees increase the number of defenders at the entrance of the beehive, forming a carpet on the flight board (similarly to FP). When a hornet is captured by a defending bee, a group of workers quickly engulf the intruder into a ball. Then, they increase the temperature inside the ball through non-shivering thermogenesis and kill the predator by heat stroke (Ono et al. 1995; Ken et al. 2005). Several decades after its introduction in Asia, *A. mellifera* also became able to perform the same balling and killing behaviour as *A. cerana* although less efficiently (Tan et al. 2007; Abrol 2006). Similarly, *A. mellifera cypria* in Cyprus forms a ball to kill its local predator, the Oriental hornet *Vespa orientalis*, even though the underlying killing mechanism (asphyxia) is different (Papachristoforou et al. 2007). Nevertheless, our observations as well as others made in the field in France showed that *A. mellifera* is not yet able to cope with hornet attacks and that when hornets congregate in front of the beehive, the bee colony stops flight activity, leading to foraging paralysis behaviour (Monceau et al. 2013; Arca et al. 2014).

Recommendations for beekeeping management to mitigate risk of colony mortality

This study shows that *V. velutina* is an additional factor to be considered in bee colony decline, beyond existing threats such as the ectoparasite *Varroa destructor*, pesticides, and the lack of flowers which remain major threats to beekeeping. Many researchers working on invasive social wasps around the world point out that locating and destroying nests or trapping hornets in mass cannot sustainably reduce the populations of these invaders (Beggs et al. 2011; Turchi and Derijard 2018). Home-made syrup traps and poisoned baits, because not specific, remain a threat to numerous species of the local entomofauna (Rome et al. 2011). Trapping hornets in autumn inside the apiary may be considered with caution, as long as syrup traps and poisoned baits specific to *V. velutina* have not been developed (Couto et al. 2014; Goldarazena et al. 2015; Turchi and Derijard 2018). Moreover, we demonstrate that the hornet-based risks of bee colony collapse could be, in some cases, indirectly related to hornet predation, for which traditional destroying and trapping methods would be ineffective. Hornet-based risk of colony mortality during the period of predation was very low, while carry-over effects on winter colony survival were much probable through results of disturbances in colony dynamics. In such conditions where traditional methods may present detrimental effects on the environment, we suggest the need to use environment-cared alternative methods involving beekeeping to safeguard bee colony overwintering.

At low hornet loads and in the absence of FP, hornet-based risks of bee colony collapse weaken colonies' population size. Given the low efficiency of traditional trapping methods and their detrimental effects on biodiversity, we suggest using common beekeeping methods to reinforce bee colony population instead of controlling the hornet loads around the beehives. For instance, merging little colonies before overwintering can help to mitigate risk of winter mortality. Moreover, supplementary feeding using "bee bread", i.e. a mixture of pollen and honey, could also be tested, under situations of low hornet loads, to mitigate the lack of pollen storage and subsequent decrease in larvae production. At high hornet loads, the hornet-based risk of bee colony collapse results from an unadapted behaviour of colony defence to the predation resulting in FP and subsequently an overconsumption of honey stocks reserved for overwintering. In such conditions, controlling the hornet loads around the beehives is recommended to decrease the number of hornets overflying and to help bee colonies to conserve their foraging activity. Based on the current existing options for the biological and physical control of the Asian hornet in Europe (Turchi and Derijard 2018), the use of beehive muzzles may be recommended, even not yet fully evaluated, to prevent bees from FP response and therefore limit the impacts of predators. Beehive muzzles consist in grid sheds that keep hornets away from the flight board of the beehive, which reduces the behavioural stresses and prevent foraging paralysis. Supplemental feeding during pre-wintering or wintering periods may also be considered whenever food provisioning is suspected to be deficient due to excessive or recurrent FP. Feeding bee colonies with supplementary sugar syrup is a common practice in professional beekeeping to compensate for floral resource scarcity in agricultural landscapes during summer (Requier et al. 2017). It may also help compensate the lack of honey reserves after hornet activity period, though caution in supplemental feeding methods is required to avoid any disturbance in bee colony thermoregulation during the critical period of overwintering.

Detecting hornet nests and assessing the load rate of hornets can be challenging in the field and for professional beekeepers (Rome et al. 2015; Milanesio et al. 2016;

Kennedy et al. 2018). Therefore, we provided early warning indicators of bee colony mortality to help beekeepers to detect hornet-induced disturbance in colony dynamics during the predation period. An increase in honey reserve associated with a decrease in adult population could be the result of low hornet loads and imply reinforcement of population size of the colony before overwintering to mitigate risk of winter mortality. Conversely, a stagnation of population size (or an increase) associated with a sharp decrease in honey reserves could result from high hornet loads and FP, for which a thorough hornet control (e.g. trapping hornets) around beehives would be recommended, and associated with supplemental feeding for the colony. Overall, these recommendations do not compensate the need to develop monitoring and control networks to prevent the settlement of hornets and to provide early warning and rapid responses against new introductions (European Parliament, Council of the European Union 2014).

Author contribution statement

FR, QR and MH conceived the idea and designed methodology; QR, GC and FM collected the data; GC, MM and SM analysed the videos; FR analysed the data and ran the simulations; F.R. wrote the first version of the manuscript; FR, QR, DD, CV and MH contributed critically to the drafts; and all authors gave final approval for publication.

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Compliance with ethical standards

Conflict of interest All authors declare that there is no conflict of interest.

Human and animals rights All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

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