A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

NeoBiota 101: 25–44 (2025)
DOI: 10.3897/neobiota.101.148570

Research Article

Public reporting is essential for controlling the invasive yellow-legged hornet: a novel model simulating the spread of *Vespa velutina nigrithorax* and timescales for control in Great Britain

Daniel A. Warren[1], Richard Budgey[1], Nigel Semmence[2], Eleanor P. Jones[3,4], Ben Jones[3]

1 *Animal and Plant Health Agency, York Biotech Campus, Sand Hutton, York, North Yorkshire, YO411LZ, UK*
2 *National Bee Unit, Animal and Plant Health Agency, York Biotech Campus, Sand Hutton, York, North Yorkshire, YO411LZ, UK*
3 *Fera Science Ltd, Biotech Campus, York, North Yorkshire, YO411LZ, UK*
4 *School of Natural and Environmental Sciences, Agriculture Building, King's Road, Newcastle University, Newcastle upon Tyne, NE14LB, UK*
Corresponding author: Daniel A. Warren (daniel.warren@apha.gov.uk)

Abstract

The invasive yellow-legged hornet (*Vespa velutina nigrithorax*) was introduced into France in 2004 from China and has now spread across western Europe and into Great Britain. Between 2016 and 2022, 13 *V. velutina nigrithorax* nests were sporadically found and destroyed in England. In 2023, 72 nests were found and destroyed by the Animal and Plant Health Agency's National Bee Unit (NBU) inspectors across southern and northern England. In 2024, 24 nests were found and destroyed. To better understand the potential establishment of *V. velutina nigrithorax* in Great Britain, a model was developed to simulate its dispersal and the associated control efforts. We simulated public reporting based on the realistic distribution of observers in the landscape, the genetic load due to the presence of diploid males, and continued incursions into a freely breeding population. We estimated the number of years before officials tasked with locating and destroying nests became overwhelmed by the number of nests in the landscape. In the absence of reporting, an undetected population would be large enough to overwhelm control efforts after three to seven years (i.e. the person-days required to locate and destroy nests would exceed those available). When nests were reported by members of the public and beekeepers, control efforts could continue for at least 10 years before becoming overwhelmed – depending on the national reporting probability, the abundance of observers in the landscape, and the annual incursion rate.

Key words: Spread control, *Vespa velutina*

Academic editor: Victoria Lantschner
Received: 4 February 2025
Accepted: 6 August 2025
Published: 16 September 2025

Citation: Warren DA, Budgey R, Semmence N, Jones EP, Jones B (2025) Public reporting is essential for controlling the invasive yellow-legged hornet: a novel model simulating the spread of *Vespa velutina nigrithorax* and timescales for control in Great Britain. NeoBiota 101: 25–44. https://doi.org/10.3897/neobiota.101.148570

Introduction

The yellow-legged hornet (*Vespa velutina nigrithorax*) is believed to have been introduced to France in 2004 from China (Haxaire et al. 2006; Villemant et al. 2011; Arca et al. 2015). This invasive hornet has now established itself across much of western Europe and continues to spread eastward (CABI 2025) and southward, causing concerns for beekeepers and governments due to its detrimental impacts on pollinators (Monceau et al. 2013; Requier et al. 2019; O'Shea-Wheller et al. 2023). Whilst adult hornets primarily feed on carbohydrate sources such as nectar, tree sap, larval secretions and fruits, they adeptly hunt a range of arthropods for dietary protein, which is fed to developing brood within their nest (Monceau et al. 2014).

European honey bees (*Apis mellifera*) constitute a major naïve prey species for this hornet, lacking the natural defence behaviours exhibited by the Asian honey bee, *Apis cerana* (Tan et al. 2012; Arca et al. 2014). Predation on *A. mellifera* can be so intense that foraging flights are significantly diminished, causing a depletion of colony food reserves and eventual colony death (Laurino et al. 2019; Requier et al. 2019).

The invasive population in France is genetically depauperate and congruous with derivation from a single queen (Arca et al. 2015). Yet this population likely acted as the propagule for the rest of Europe, as evidenced by new incursions being characterised by further genetic bottlenecks, a shared allelic pool, and a single mtDNA haplotype or very closely related haplotypes (Arca et al. 2015; Budge et al. 2017; Granato et al. 2019; Jones et al. 2020; Dillane et al. 2022; Quaresma et al. 2022; Herrera et al. 2023). This remarkable colonisation has likely been aided by several promotive life-history traits, including its dispersal ability (Faria et al. 2016), diverse prey diets (Rome et al. 2021; Stainton et al. 2023; Pedersen et al. 2025), and polyandry. The foundress queen introduced into France is estimated to have mated with between three and four drones (effectively the founder males), from which the remaining European genetic diversity derives (Arca et al. 2015).

Eusocial Hymenoptera typically exhibit arrhenotoky and single-locus complementary sex determination (sl-CSD) (Cook and Crozier 1995; Heimpel and De Boer 2008; Darrouzet et al. 2015; Leung and van der Meulen 2022). Unfertilised haploid eggs become males, and fertilised diploid eggs become females when heterozygous at the CSD locus. Anomalous diploid males are produced when fertilised offspring are homozygous at the CSD locus (Cook and Crozier 1995). These diploid males incur a high genetic load, as they are generally infertile or sire sterile triploid offspring (Harpur et al. 2013; Darrouzet et al. 2015; Leung and van der Meulen 2022). In small or isolated populations, especially those with founder effects, the proportion of diploid males is expected to increase due to reduced allelic richness at the CSD locus, leading to a purported extinction vortex (Zayed and Packer 2005). Diploid males have been discovered in high numbers from the nests of *V. velutina nigrithorax* in France and Great Britain (GB) (Darrouzet et al. 2015; Jones et al. 2020), and although this species has successfully invaded Europe, the repressive effect of diploid males within its expansion range has not been explicitly modelled (Villemant et al. 2011; Barbet-Massin et al. 2013, 2018, 2020; Keeling et al. 2017; Robinet et al. 2017, 2019; Hassall et al. 2024).

Thirteen *V. velutina nigrithorax* nests were discovered and destroyed in GB between 2016 and 2022 (NBU 2025a) by the Animal and Plant Health Agency's National Bee Unit (NBU) inspectors. In recent years, the NBU has developed improved methods for detection of *V. velutina nigrithorax* nests. Search efforts are initiated by NBU inspectors following public reports of flying hornets in the landscape. Traps are then deployed around the areas of the sightings, and a capture-mark-release system is employed to track flight paths of hornets and triangulate nest locations using bespoke software. Traps are moved in the direction of the flight paths until the nests are located and destroyed. The existing traps are subsequently monitored for five days of suitable weather for flying hornets, and any further hornets or public reports initiate further searches. In 2023, 72 nests were discovered and destroyed following almost 21,000 public reports in England and Wales. In 2024, 24 nests were found and destroyed (NBU 2025b). Microsatellite analysis of lone-caught hornets and nest hornets revealed the infrequent presence of hornets that did not allocate to any of the 72 nest genotypes, indicating the pres-

ence of unreported nests (NBU 2025b). Additionally, reproductive castes (haploid males and new gynes) were found within and outside nests, consistent with some nests having entered their reproductive phase before they were destroyed – suggesting a local population could become at least temporarily established.

Similar national eradication or mitigation strategies have been deployed across Europe and GB, where *V. velutina nigrithorax* nests have been found. Control efforts commonly rely on public reporting of hornets before attempts are made by relevant authorities to locate and destroy nests via tracking captured hornets or the poisoning of queens and adults via baits (Turchi and Derijard 2018; Jones et al. 2020; Leza et al. 2021; Pazos et al. 2022).

The extent of spread or probability of eradication of *V. velutina nigrithorax* in GB is sensitive to the probability of nest discovery and subsequent destruction by humans (Keeling et al. 2017; Robinet et al. 2017). Concurrently, the likelihood of nest detection should increase with proximity to towns, cities and other population zones – with larger populations further increasing the probability of detections.

Our aim is therefore to parameterise the most current information and likely reporting rates for *V. velutina nigrithorax* nests found in GB. We model the spread of *V. velutina nigrithorax* in GB and predict how long before NBU inspectors tasked with the detection and destruction of nests are overwhelmed and the hornet population can no longer be eradicated. Notably, we uniquely parameterise 1) reporting probabilities based on proximity to and size of population zones in GB, 2) diploid male production and consequent mating, based on the estimated number of CSD alleles entering GB from the European continent, and 3) continued incursions into a breeding population.

Methods

Software specifications

The model was developed and run in the R statistical programme (version 4.4.0; R Core Team 2022), using the RStudio integrated development environment (version 2022.12.0; Posit Team 2022). Outputs generated from the current model were visualised using ArcGIS Pro (version 3.1.0; Esri Inc. 2022).

Model overview

Here, we provide a general overview of the model's structure and functionality. A detailed description of model functionality and a complete list of parameters and values is provided in Suppl. materials 1, 2: section S1 and table S1; see Table 1 for key parameters. *Vespa velutina nigrithorax* nests act as entities within the landscape, from which individual hornets are generated, the traits of which are dependent on the characteristics of the donor nests from which they are produced.

The primary aim of this model is to simulate the spread of *V. velutina nigrithorax* nests across GB under various invasion and reporting scenarios and to estimate the timescales within which inspectors may become overwhelmed, that is, when the time required to locate and destroy nests exceeds the capacity available, rendering eradication unfeasible. The model specifically addresses three main questions. First, how does the spatial distribution of human observers in relation to nests, and the probability of their reporting sightings of hornets, influence the success of nest detection

Table 1. Summary of input parameters, including description of purpose, input value(s), and sources.

Parameter description	Value	Source
Annual incursion rate	1, 2, 3, 5, 8, 10, 25 *	
National public reporting probability	0.001%, 0.003%, 0.005%, 0.007%, 0.009%, 0.01%, 0.015%, 0.02%, 0.03%, 0.05%, 0.07%, 0.09%	In the absence of appropriate source data, a wide range was chosen such that the true rate was likely to have been included.
Minimum diploid population size (per nest) **Note: this does not include diploid workers.**	100	Rome et al. 2015; Poidatz et al. 2018
Mean diploid population size (per nest) **Note: this does not include diploid workers.**	300	Villemant et al. 2011
Maximum diploid population size (per nest) **Note: this does not include diploid workers.**	500	Jung 2012; Rome et al. 2015
Diploid-haploid ratio (per nest)	1	Meiborg et al. 2023
Minimum number of mates per gyne (new incursions)	1*	
Maximum number of mates per gyne (new incursions)	3*	
Probability of multiple matings	0.63636 (1 mate) *	
	0.27273 (2 mates) *	
	0.09091 (3 mates) *	
Probability of matings by haploid/diploid males	0.90909 (haploid) *	
	0.09091 (diploid) *	
Maximum number of mates per gyne (established nests)	3–8	Minimum estimate based on GB data. Maximum estimate based on French data (Arca et al. 2015).
Average number of mates per gyne (minimum)	1.4 *	
Average number (maximum)	4.6	Arca et al. 2015
Proportion of migrant males	0.6	
Maximum breeding range of migrant males	30 km	Sauvard et al. 2018
Minimum overwintering survival rate for fertilised gynes	0.01	Assumes a 1% survival rate
Maximum overwintering survival rate for fertilised gynes	0.05	Archer 1984
Minimum dispersal range of fertilised gynes	0.5 km	Lioy et al. 2019
Maximum dispersal range of fertilised gynes	200 km	Rome et al. 2009
Mean annual dispersal range of fertilised gynes	78 km	Derived from Sauvard et al. 2018
Unsuitability threshold	0.72	R. Hassall UKCEH, pers. comm.
Nest establishment penalty factor	10	Applied to regions which have a suitability index below the threshold of 0.72.
Maximum dispersal range for foraging workers	30 km	Sauvard et al. 2018
Probability of beekeeper reporting	50%	
Secondary detection radius	5 km	Estimate based on current management protocols by GB government officials. Consistent with previous research (Lioy et al. 2019).
Maximum number of potential nests removed per annum, before inspectors become overwhelmed	180 nests per year	Based on the number of inspectors in operation at the time of model development.

* Estimate based on historical GB data up to 2022.

and subsequent control efforts? Second, how does the production of diploid drones influence the overall quality and composition of nest populations, and does this affect the broader spread of *V. velutina nigrithorax*? Third, how do the rate of population growth and spatial expansion respond to different levels of annual incursions?

Model inputs

To ensure the model serves as a realistic proxy for natural processes and patterns, it requires input parameters reflecting *V. velutina nigrithorax* behaviour, biology, dispersal, and life-history traits (Table 1). These parameter values were either drawn

from an extensive review of the current scientific literature or, for the specific case of GB, derived from empirical data collected between 2016 and 2022, since the first documented incursion. Additionally, six national-scale geospatial datasets were incorporated. These describe: (1) the probable geographic establishment range of *V. velutina nigrithorax*; (2) habitat composition; (3) habitat suitability; (4) total human abundance at the administrative level; (5) the probable spatial distribution of human observers based on land use and habitat types; and (6) the distribution of registered apiaries. Full details of these datasets are provided in Suppl. material 1: sections S2, S3.

Model structure

The model comprises a series of six integrated sub-modules (Fig. 1), each of which simulates the following biological and control effort processes:

1. Incursion Module – simulates the introduction and establishment of new nests within the landscape. Incursions can be a singular or annual event and can be simulated using defined coordinates (i.e. historical occurrences) or based on a probabilistic process, taking into account the suitability of a given area and the density of active, previously established nests.
2. Nest Population Module – simulates the development of established nest populations, based on the genetic makeup of nest parents, specifically the combinations of six hypothetical sl-CSD alleles from a single founder queen and four founder males in the continental population (Arca et al. 2015). By simulating genetic inheritance and tracking the distribution of parental alleles through genetic crossing, this module determines the composition of individual nest populations, deriving the ploidy of individual hornets.
3. Detection Module – simulates the detection, reporting and removal of nests from the landscape using a probabilistic process which considers the likely distribution of human observers within the landscape, their proximity to individual nests and the fixed probability that individuals file a report, having observed a hornet in flight (this probability is known as the national reporting probability and is applied uniformly across GB). Multiple reports can arise from each nest, and each triggers an attempt at nest destruction by NBU inspectors, the success of which is dependent on the distance of the observation to the nest.
4. Dispersal Module – simulates the dispersal of males between neighbouring nests present within a 30 km radius (see Sauvard et al. 2018). Male dispersal is an inverse distance-weighted process which determines where males migrate to and the number that successfully arrive at neighbouring nests.
5. Breeding Module – simulates breeding of male and female hornets and post-copulatory overwintering survival of fertilised gynes. Mating is a stochastic process, with females capable of mating with multiple males, regardless of their ploidy.
6. Spread module – simulates the spread of fertilised gynes within the landscape and the subsequent establishment of new, next-generation nests. Much like the Incursion Module, spread is simulated using a probabilistic process, based on environmental suitability and the density of existing nests present within an average radius of 78 km (Sauvard et al. 2018), up to a maximum radius of 200 km (Rome et al. 2009). Neither competition with other species of hornets

(i.e. interspecific), competition amongst *V. velutina nigrithorax* (i.e. intraspecific), nor predation on *V. velutina nigrithorax* are considered (Cini et al. 2018; Martín-Ávila et al. 2025). The mechanism for spread assumes natural dispersal only and does not account for long-range human-mediated dispersal.

The structure and functionality of each sub-module is described in full in Suppl. material 1: section S1.

Model scheduling

The model operates on an annual timestep (T), with all sub-modular processes occurring within a 1-year period, in the order provided above. In certain situations, such as the complete elimination of all nests, either as a consequence of reporting or unsuccessful breeding, sub-modules may be bypassed, causing the modelling process to return to the incursion module as the timestep advances by one ($T + 1$). Depending on the outcomes of a given timestep, the model will either continue to the next timestep or terminate if NBU inspectors are overwhelmed. The overwhelming point was defined using a national limit of 180 nests remaining undetected at the end of a given year, as population growth would always exceed subsequent control efforts. This threshold represented the maximum number of nests that could be found and destroyed in a single year, based on the number of available inspectors (n = 60 inspectors, each available for 75 workdays) and the time required to locate and destroy nests (a team of five inspectors taking a total of five days per nest, amounting to 25 person-days per nest; N. Semmence NBU, pers. comm.).

Upon the completion of a model simulation, either having reached the total simulation period or terminated based on a defined criterion, the next simulation will automatically commence, unless all predefined simulations have successfully finished. The duration of simulations was up to 50 years.

Model testing

Validation

To validate the model, thereby ensuring that parameters, processes and associated assumptions were appropriate, we ran a validation model using data describing the historical spread of *V. velutina nigrithorax* across France, a country in which *V. velutina nigrithorax* is widely distributed and well established. This dataset, obtained from the French Museum of Natural History (INPN 2025), detailed the reported locations of *V. velutina nigrithorax* nests over a 5-year period, from the initial incursion event in 2004 up to 2009 (Suppl. material 1: table S2). For consistency, the validation model was run for the same timespan (2004–2009). Model validation was conducted using visual inspection and simple statistical inference, comparing the distribution of simulated and observed data with respect to: a) the overall distribution of *V. velutina nigrithorax* nests, summarised at a 5 × 5 km resolution; b) changes in annual nest density, also summarised at 5 × 5 km resolution; c) the annual rate of spread, relative to the initial incursion; and d) the total area covered by new nests established year-on-year, represented using minimum convex polygons (MCP). For further details regarding input parameters, geospatial datasets, assumptions and analyses, refer to Suppl. material 1: table S1 and section S2.

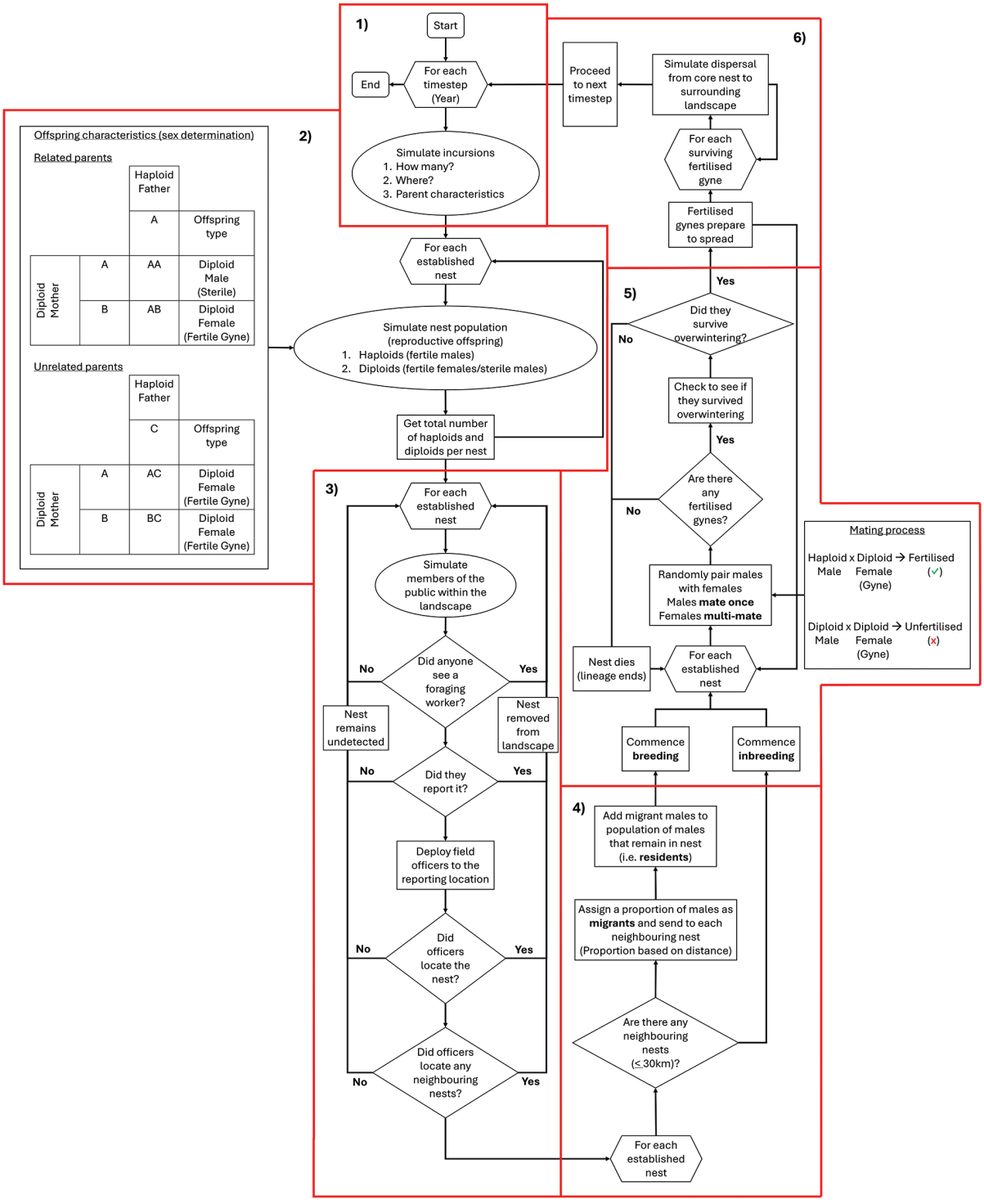

Figure 1. Conceptual diagram showing the structure of the model. The red boxes show which processes are performed in 1) the incursion module, 2) the nest population module, 3) the detection module, 4) the dispersal module, 5) the breeding module, and 6) the spread module.

Scenarios

Having validated the model using empirical data, we developed a series of scenarios designed to model the potential spread of *V. velutina nigrithorax* populations within GB under different annual incursion rates (the number of new nests founded by queens from overseas) and different levels of public reporting. For these scenarios, we considered seven hypothetical incursion rates (1, 2, 3, 5, 8, 10 and 25 incursions

per year), representative of historical nest incursion patterns recorded in GB up to 2022 (NBU 2025a), and 13 national reporting probabilities (0% (i.e. uncontrolled spread), 0.001%, 0.003%, 0.005%, 0.007%, 0.009%, 0.01%, 0.015%, 0.02%, 0.03%, 0.05%, 0.07%, and 0.09%). As there is considerable uncertainty about the different components that together determine the probability a member of the public will report a hornet, we set the range of national reporting probabilities to be sufficiently wide such that the true reporting probability was likely to be included. The number of true positive reports of hornets received by the public for the 85 nests found between 2016 and 2023 was 178, or 2.1 reports per nest (N. Semmence, pers. comm.). Between national reporting probabilities of 0.001% and 0.007%, the model estimated between 2.0 and 2.4 reports, on average, per nest.

A second process determined the probability that observations and reports were made by beekeepers at apiary locations. Following detection, a constant beekeeper reporting probability of 50% was used, analogous to the national public reporting probability but reflecting the higher awareness of the beekeeping community. For further details on the observation and reporting process for the public and beekeepers, see Suppl. material 1: section S1.4.

Please refer to Suppl. material 1: table S1 and section S3 for details regarding input parameters, geospatial datasets, and assumptions.

Resource modelling and search efficiency

Beyond the scenarios described above, additional simulations were conducted in which inspector resourcing and/or efficiency was altered, reflecting either an increase or decrease in the total number of nests that could be managed annually. A summary of predictions based on different resourcing strategies can be found in Suppl. material 2: section S4.

Sensitivity analysis

Sensitivity analysis was conducted to assess how variations in key input parameters might influence the simulated outputs of the model, thereby evaluating its robustness and identifying the most influential (or confounding) variables. The analysis focussed on the following 11 parameters: 1) annual incursion rate, 2) national reporting probability, 3) maximum number of male mates *per capita* female (β_0), 4) mean number of male mates *per capita* female (β_0), 5) diploid nest population size (minimum/maximum), 6) male dispersal success parameter (β_1), 7) overwintering survival rate for fertilised gynes (minimum/maximum), 8) dispersal range of fertilised gynes (β_0), 9) public detection parameter (β_1), 10) expert removal parameter (β_1), and 11) secondary detection parameter (β_1 – see Suppl. material 1: table S4 for summaries of parameter ranges). These parameters were selected based on their assumed potential importance to model performance or predictions or high uncertainty due to limited evidence or knowledge regarding associated mechanisms/processes. Each parameter was varied across a predefined range based on available data, where possible, with parameter ranges assumed to follow a uniform distribution. For those parameters provided as an upper/lower parameter limit (e.g. minimum/maximum diploid population size and overwintering survival rate), from which an input parameter was derived based on sampling, each range limit (i.e. minimum/maximum) was provided as a fixed value, thereby eliminating the effect of stochastic sampling. A Latin Hypercube Sampling approach (LHS) was conducted using the *lhs* package (version 1.2.0;

Carnell 2024), generating 100 parameter combinations, with each parameter range sampled evenly and efficiently across the hyperparameter space. Each parameter combination was used as input for individual simulation runs, with model outputs for each run recorded and analysed to determine the effect of input parameter variations on key performance outputs, namely 1) the maximum number of nests in the landscape, 2) the proportion of diploid female offspring produced per nest, 3) the mean number of viable nests established, 4) the duration of effective management (i.e. inspector limits), 5) the proportion of nests detected/removed, and 6) the proportional contribution of public reporting to overall reporting. Model sensitivity was analysed using partial rank correlation coefficients (PRCCs), calculated using the *epiR::epi.prcc* function (version 2.0.75, Stevenson and Sergeant 2024), to quantify the influence of each input parameter on model outputs, capturing non-/linear relationships.

Results

Validation of population spread

Our simulations of five years of uncontrolled spread in France predicted a similar geographical distribution of nests to that reported five years after the initial incursion in 2004 (INPN 2025; see Fig. 2 for overall coverage and Fig. 3a–e for example simulations). Analysis found no statistically significant difference between historical and simulated data with regard to the distribution, density, spread rate or invasion range of *V. velutina nigrithorax* nests in France ($p > 0.05$ for all; see Suppl. material 2: section S1 for details). The number of observed nests reported to the French authorities equated to 28% of that simulated (2,243 nests reported vs 8,086 simulated; Suppl. material 2: table S1). We acknowledge that our simulated number of nests is an average across 50 simulations, with considerable variation that increases over time. However, we expect the number of nests in the landscape to be higher than that reported. A case study in southwest France found that only 37% to 48% of nests were reported (Franklin et al. 2017; Keeling et al. 2017). Additionally, some control efforts were deployed in France in the years following the initial incursion, although it is unclear what intensity of control was employed (Monceau et al. 2014; Franklin et al. 2017; Robinet et al. 2017; Barbet-Massin et al. 2020). A complete summary of the validation model, including associated figures, can be found in Suppl. material 2: section S1.

Uncontrolled spread in GB

In the absence of reporting by both beekeepers and the public, and any associated control efforts, the model predicted widespread establishment in GB. An undetected population would be large enough to overwhelm subsequent control efforts after three to seven years (i.e. the person-days required to locate and destroy nests exceeds that available) across all annual incursion rates (Table 1, national reporting probability = 0%).

Controlled spread in GB

Reporting

As 1) the abundance of people within 30 km of nests increased, and 2) the national reporting probability increased, more reports were made, and the likelihood of

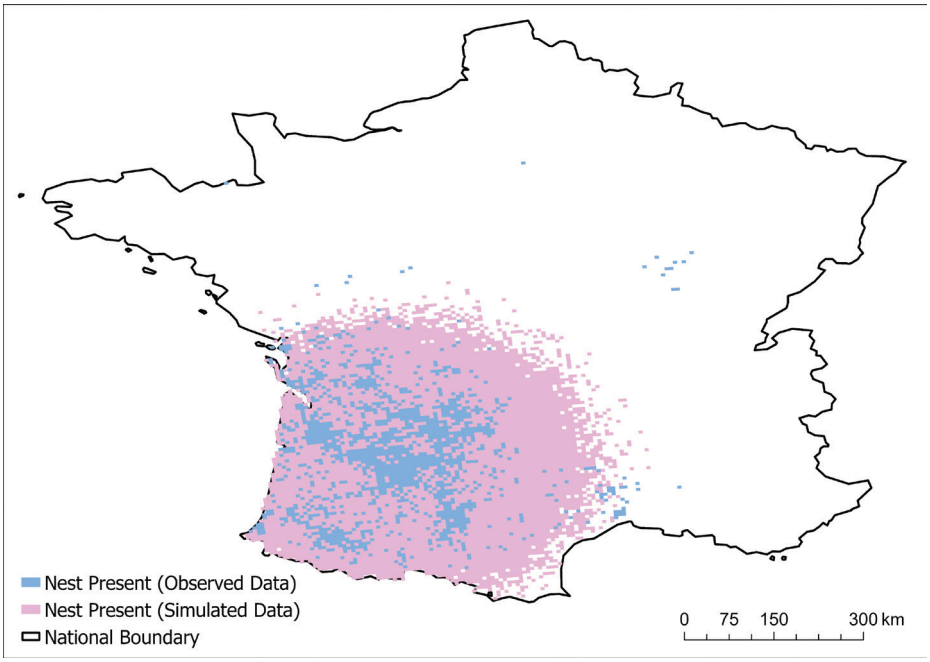

Figure 2. A map of France showing the distribution of *V. velutina nigrithorax* nests at 5km² resolution, observed between 2005 and 2009 (blue grid cells), and simulated across the same period (pink grid cells). Note: pink cells represent the distribution of simulated nests across all 50 simulations combined. Distributions are derived from natural dispersal processes only and do not account for human-mediated movement.

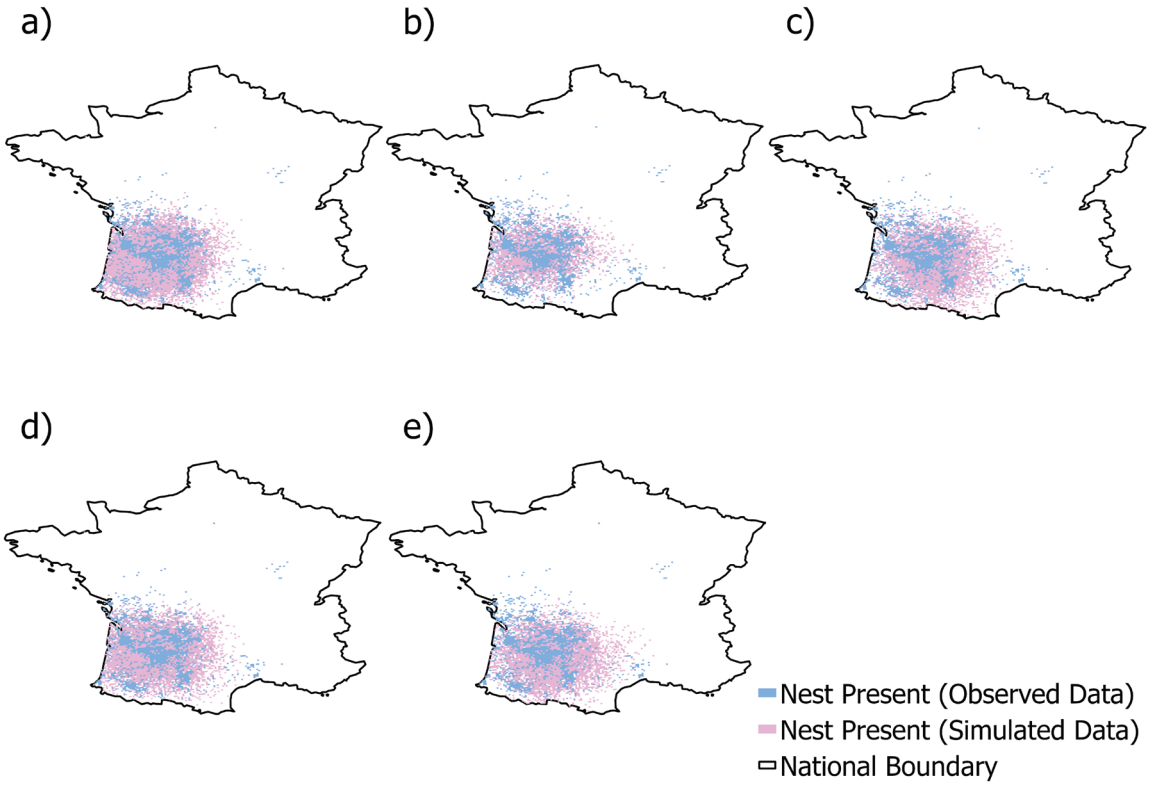

Figure 3. A series of maps showing the distribution of *V. velutina nigrithorax* nests at 5 km² resolution, observed between 2005 and 2009 (blue grid cells), and simulated across the same period (pink cells), for simulation seed 9935 (**a**), simulation seed 8776 (**b**), simulation seed 7620 (**c**), simulation seed 7080 (**d**), and simulation seed 5875. Note: distributions are derived from natural dispersal processes only and do not account for human-mediated movement.

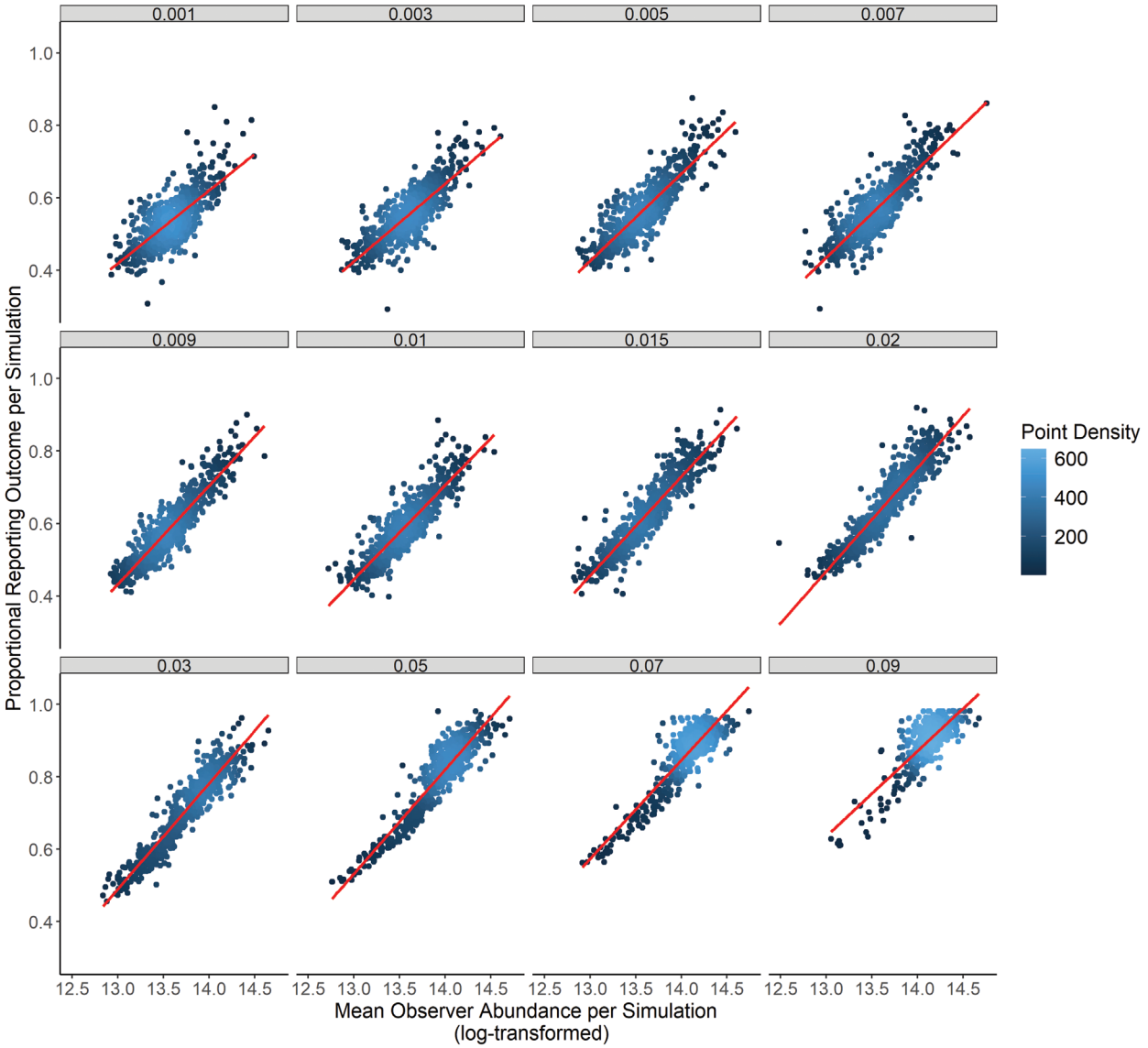

Figure 4. Relation between the proportional success (proportion of nests destroyed) associated with beekeeper and public reporting and the total abundance of observers (log-transformed) situated within a 30 km radius of each nest. Individual plot panels show the relationship under different national reporting probabilities. Each individual point indicates a single estimate, generated for each simulation across each scenario. Each point is coloured according to the number of neighbouring points (i.e. simulations) which share a similar predicted outcome, with lighter colours indicating a greater clustering of points and darker colours indicating lower clustering of points.

nest destructions increased (Fig. 4). As the national reporting probability increased from 0.001% to 0.09%, the number of reports increased from approximately two to seven reports per destroyed nest (Suppl. material 2: table S2). There is now data from public reports submitted in GB and the number of nests found and destroyed that might allow an approximate determination of the true reporting probability, albeit with a high degree of uncertainty. The number of true positive reports received for the 85 nests found between 2016 and 2023 was 178, giving a combined general public and beekeeper reporting rate of 2.1 reports per nest. This is within the range of values included in our model at national reporting probabilities between 0.001% and 0.007% (Suppl. material 2: table S2), corresponding to inspectors becoming overwhelmed between 18.80 and 40.51 years, depending on the incursion rate (Table 2).

Table 2. Mean ± standard error number of years before which management of *V. velutina nigrithorax* nests becomes ineffective, with NBU inspectors expected to become overwhelmed. Estimates are derived from all simulations, generated for each incursion/reporting scenario.

National reporting probability (%)	Annual Incursion Rate						
	1	2	3	5	8	10	25
0.000	7.4 ± 0.1	6.3 ± 0.1	5.8 ± 0.1	5.1 ± 0.0	4.4 ± 0.1	4.1 ± 0.0	3.0 ± 0.0
0.001	43.7 ± 1.0	36.7 ± 1.3	32.8 ± 1.2	24.4 ± 0.9	18.6 ± 0.6	17.9 ± 0.7	9.9 ± 0.3
0.003	45.5 ± 0.9	38.1 ± 1.3	34.9 ± 1.2	29.1 ± 1.1	21.4 ± 0.8	18.8 ± 0.6	10.2 ± 0.2
0.005	44.5 ± 1.0	40.5 ± 1.2	37.6 ± 1.2	30.3 ± 1.1	23.0 ± 0.9	21.1 ± 0.8	11.6 ± 0.3
0.007	45.2 ± 1.0	40.0 ± 1.2	37.7 ± 1.2	32.5 ± 1.3	25.5 ± 1.1	22.4 ± 0.8	13.3 ± 0.4
0.009	45.3 ± 0.9	42.9 ± 1.1	40.7 ± 1.1	34.7 ±1.2	29.0 ± 1.1	23.1 ± 0.9	13.8 ± 0.5
0.010	46.7 ± 0.8	44.7 ± 0.9	41.1 ± 1.2	36.60 ± .2	31.0 ± 1.2	24.9 ± 1.0	13.1 ± 0.4
0.015	47.6 ± 0.7	46.4 ± 0.8	42.9 ± 1.2	37.5 ± 1.2	32.6 ± 1.2	30.0 ± 1.2	16.1 ± 0.6
0.020	48.9 ± 0.5	46.5 ± 0.9	47.2 ± 0.8	42.30 ± .1	33.7 ± 1.3	33.7 ± 1.2	20.4 ± 0.9
0.030	50.0 ± 0.0	48.0 ± 0.6	47.9 ± 0.7	45.5 ± 0.9	42.8 ± 1.0	42.2 ± 1.1	26.9 ± 1.2
0.050	49.5 ± 0.3	49.8 ± 0.2	49.5 ± 0.3	48.6 ± 0.5	47.9 ± 0.6	46.8 ± 0.8	38.2 ± 1.1
0.070	50.0 ± 0.0*	50.0 ± 0.0*	50.0 ± 0.0*	49.4 ± 0.3	49.4 ± 0.3	49.4 ± 0.3	46.9 ± 0.8
0.090	50.0 ± 0.0*	50.0 ± 0.0*	50.0 ± 0.0*	50.0 ± 0.0	49.9 ± 0.1	49.9 ± 0.1	49.2 ± 0.4

Note: Asterisks (*) indicate all simulations successfully ran to completion, without inspectors becoming overwhelmed within the specified time limit (i.e. 50 years).

Timescales

The number of years before NBU inspectors became overwhelmed in all scenarios is reported in Table 2. As the national reporting probability increased and the annual incursion rate decreased, the model predicted a gradual increase in the number of years before NBU inspectors were overwhelmed.

As the national reporting probability increased and the annual incursion rate decreased, the model predicted an increase in the proportion of nests removed and a concurrent reduction in the mean number of nests in the landscape. The proportion of nests removed and total numbers of nests are given in Fig. 5 for the lowest (0.001%) and highest (0.09%) national reporting probabilities and the lowest (1) and highest (25) annual incursion rates. Full results are reported in Suppl. material 2: figs S4–S10A–L.

At the lowest national reporting probability and an incursion rate of one new nest per year, the mean number of nests in the landscape remained below 50 for over 40 years before NBU inspectors became overwhelmed in the majority of simulations (Fig. 5A). At an incursion rate of 25 nests per year, the lowest national reporting probability resulted in over 150 nests in the landscape after 10 years of control efforts (Fig. 5C). At the highest national reporting probability, the number of nests in the landscape remained negligible at an incursion rate of one new nest per year (Fig. 5B) and below 50 when subjected to a simulated incursion rate of 25 nests per year (Fig. 5D).

Considering the example of two incursions per year – the average number of nests per year found in GB between 2016 and 2022 – the lowest (0.001%) and highest (0.09%) national reporting probabilities resulted in a respective 77-fold (2.95 nests) and 1,196-fold (0.19 nests) decrease in nest numbers, compared to uncontrolled spread (227 nests) after six years (Fig. 6A–C).

Diploid males

To determine the percentage of nests containing diploid males, we replicated the sampling methods used to assess their presence in nests found in GB by randomly

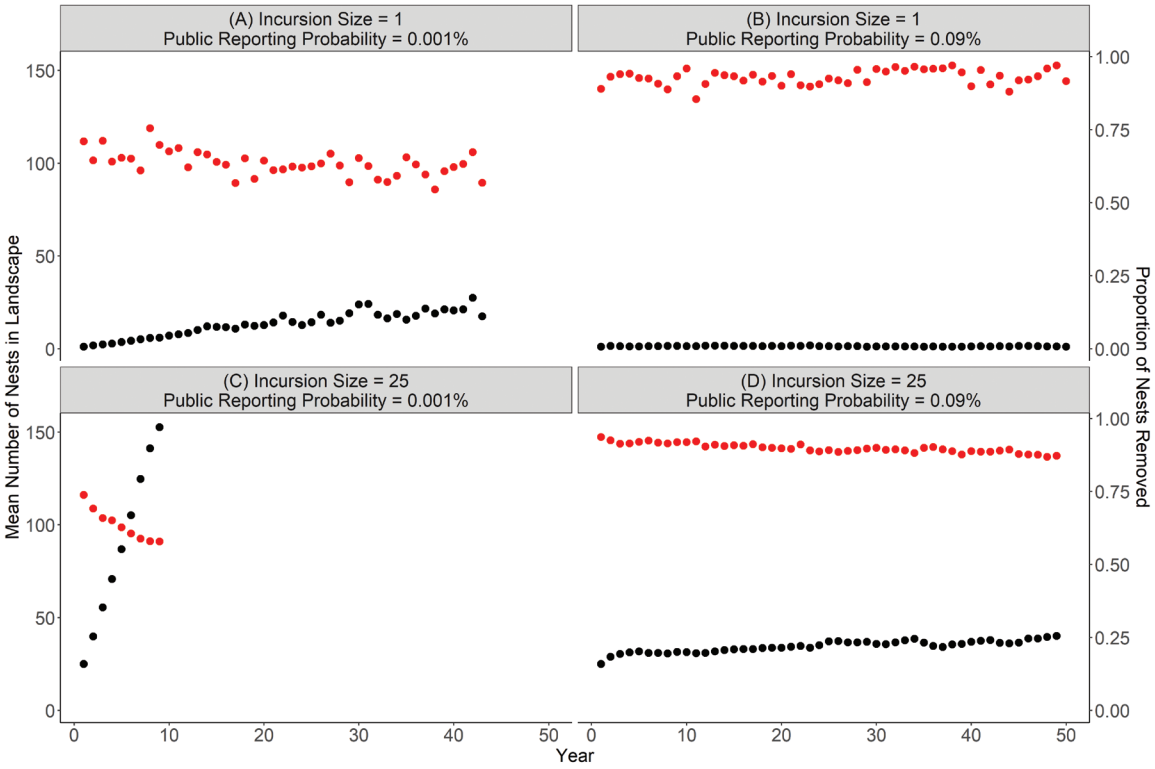

Figure 5. The mean number of nests in the landscape (black) and the proportion of nests removed (red) per year under annual incursion rates of one and 25 nests and national reporting probabilities of 0.001% (**A, C**) and 0.09% (**B, D**).

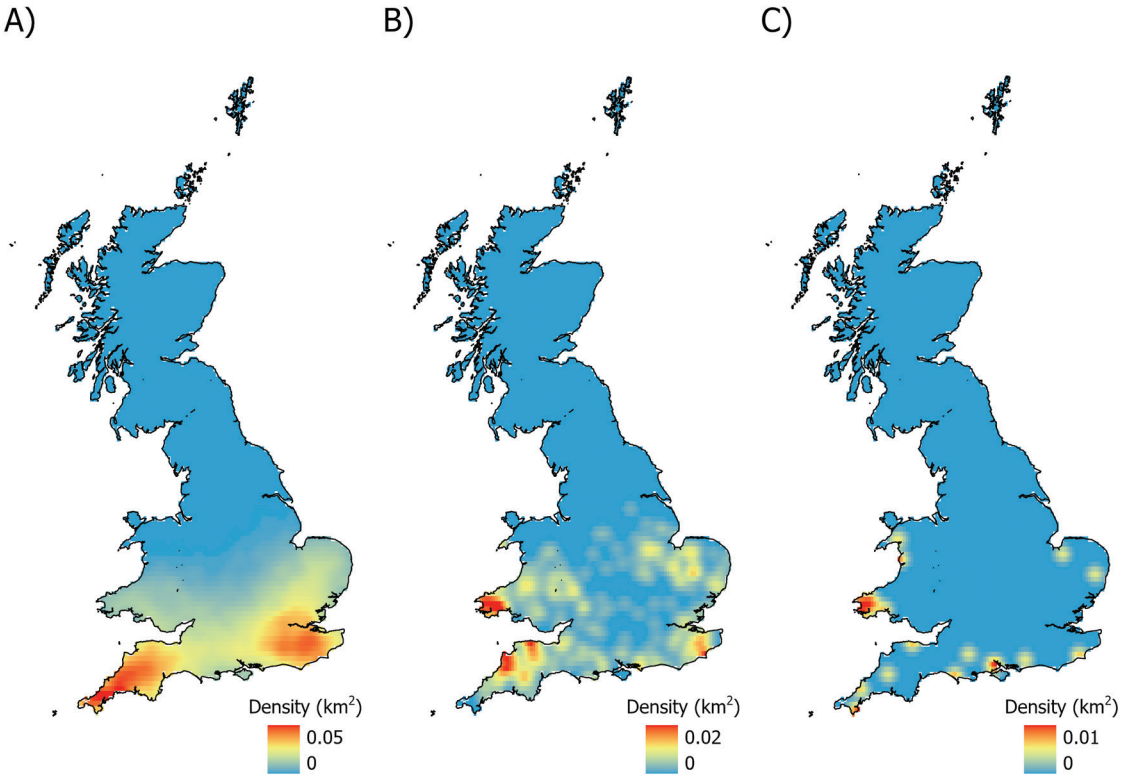

Figure 6. Maps of GB showing the mean density of undetected nests (per km^2), estimated at year six for scenarios involving two incursions per year. Maps show the average density in scenarios where control is absent (i.e. zero reporting; 227.2 nests in GB, **A**), under the lowest national reporting probability (0.001%; 2.95 nests in GB, **B**) and highest national reporting probability (0.09%; 0.19 nests in GB, **C**). For each scenario, mean density was estimated across all 100 simulations.

sampling 10 males from each nest. The mean percentage of nests containing diploid males across all national reporting probabilities and annual incursion rates was 67.1% ± 21.6% (SD), which falls within the 48% to 72% range observed in France (calculated from Darrouzet et al. 2015). During the first year of incursions into GB, the mean percentage of nests predicted to contain diploid males was 38.8% ± 6.35% (SD), closely matching the observed minimum of 31% in GB in 2023. The overall mean percentage of nests sired by a single diploid male – and thus producing only non-viable, triploid gynes – was generally consistent or decreased over time, remaining between 9% and 25% across all scenarios (Suppl. material 2: table S3).

Sensitivity analysis

Sensitivity analysis identified several parameters that, when varied, consistently influenced model predictions. These included: i) the size of the diploid nest population; ii) annual incursion size; iii) maximum overwintering survival rate; and iv) public reporting probability. Parameters related to the successful detection of nests by observers and their subsequent removal by experts also affected model predictions. For further details regarding the sensitivity analysis and associated outputs, please refer to Suppl. material 2: section S3.

Discussion

Here we model the spread of *V. velutina nigrithorax* in GB when subject to control efforts by government officials (NBU inspectors) and continued incursions from continental Europe. Our simulations terminate when the time required to locate and destroy nests exceeds that which is available, identifying the year in which NBU inspectors become overwhelmed and the current control strategy becomes ineffective.

Under current available resources equivalent to 60 NBU inspectors dedicating 50% of their time to searching for and destroying nests, control efforts could continue for 10 years before becoming overwhelmed under our worst-case scenario (Fig. 5C). In our best-case scenario (Fig. 5B), the number of nests in the landscape remained negligible. Further, the overwhelming point did not significantly alter, regardless of the number of person-days available to find and destroy nests, when the number of annual nest incursions was relatively low (between 10 and 25). At a high annual nest incursion rate (75), however, the time to overwhelming altered significantly depending on whether the person-days were halved or doubled, providing a potential threshold for resource planning in the field if new nest incursions can be distinguished from progeny nests in GB (Suppl. material 2: section S4).

Sensitivity analysis highlights that the values of biological parameters have a large effect on the spread and detectability of hornet nests. Values or ranges of model input parameters were selected after extensive expert consultation and literature review. However, small changes in the choice of values for parameters such as incursion rate, diploid population size and overwintering survival led to large differences in outcomes – emphasising the need for accurate biological data and suggesting that management efficacy may be substantially affected by natural variation in the values of these parameters.

Our simulations of uncontrolled spread align with previous models (Keeling et al. 2017; Hassall et al. 2024), with widespread establishment in GB after three to seven years depending on the annual incursion rate (Table 2). Keeling et al. (2017)

used fixed probabilities of nest detection (and destruction) and rationally found that the probability of eradication increased with the likelihood of nest detection and that eradication was achievable when nest destructions were complemented by subsequent search efforts covering increasingly large radii around nests (0–32 km). When the efficiency of subsequent search efforts decreased, higher detection probabilities were required to achieve eradication. Conversely, Hassall et al. (2024) developed a model which predicted the spread of *V. velutina nigrithorax* based on environmental suitability and dispersal kernels estimated from historical reports in France. Management was not explicitly modelled but rather inferred based on historical distributions. Similar inferences were also made with regard to life-history characteristics (e.g. propagule production timing). Unlike the Keeling et al. (2017) and the Hassall et al. (2024) models, the current model explicitly models biological processes, including mating dynamics, haplodiploidy, genetic load arising from low genetic diversity at the sex-determining locus (i.e. incidence of diploid males and triploid queens), as well as dispersal dynamics of both male and female hornets. As well as the genetic aspect, the current model also considers management efficacy when predicting spread, density and population-level dynamics. In addition, the number of public reports is adjusted for the realistic distribution of people and apiaries in 30 km radii around nests, rather than fixed probabilities of detection across the entirety of GB. Nests are more or less likely to be reported when close to or more distant from population zones, with proximity to larger human populations increasing the likelihood of reporting. Once nests are located, NBU inspectors have a further probability of detecting surrounding nests within 5 km (Lioy et al. 2019), based on the distance of the reports to the nest.

The proportional success of nest destructions increased logically with the national reporting probability and with the abundance of observers in the landscape around nests (Fig. 4).

Concurrently, areas with low human populations were more vulnerable to uncontrolled spread as nests went unreported, and the inverse was true for highly populated areas. Public awareness programmes have been prudently promoted by the government and the beekeeping sector in GB through press alerts, online training material, and events for stakeholders and the wider public. Indeed, approximately 63,000 reports were filed by the public between 2016 and 2023 in GB, of which 178 were verified as *V. velutina nigrithorax* by the UK Centre of Ecology and Hydrology (UKCEH) and triaged to the NBU. Our results highlight the potential of such campaigns, anecdotally supported by spikes in reporting following public awareness events (N. Semmence, pers. comm.). However, the impacts of such publicity or awareness programmes on the reporting of *V. velutina nigrithorax* remain unclear – for example, in low population areas. In addition, our model considers only the time required to locate and destroy nests by NBU inspectors following the triaging of true positive reports but does not consider the time required for triaging by UKCEH. Whilst greatly aided by the development of online reporting apps and the ability to upload images to reports, this triaging process could become overwhelmed and represent a point of failure. It is therefore desirable to gain an understanding of how awareness campaigns can be better targeted and improve the accuracy of reports.

In the current model, diploid males sire sterile triploid gynes (Harpur et al. 2013; Darrouzet et al. 2015; van der Leung and van der Meulen 2022). However, the success of *V. velutina nigrithorax* in Europe and simulations of uncontrolled spread clearly demonstrate that diploid males cannot substantially limit invasion

alone, even at high frequencies (Darrouzet et al. 2015; Keeling et al. 2017; Jones et al. 2020; INPN 2025). Our results suggest that enough allelic diversity is maintained at the CSD locus to avoid the purported diploid male extinction vortex (Zayed and Packer 2005), where we would expect the proportion of diploid drones to increase over time. Nonetheless, the percentage of nests that produced non-viable triploid gynes (sired by diploid males only) remained between 9% and 25% across all simulations. If new CSD alleles enter the population from Asia, this repressive effect could be relieved, and population growth could be promoted beyond the predicted levels. Continued attention should therefore be given to identifying the global origin of new incursions. We acknowledge that our predictions are based on a fixed set of six hypothetical CSD alleles, based on a single founder queen and four 'founder males' in the continental population (Arca et al. 2015). Identification of the CSD alleles in *V. velutina nigrithorax*, as for the honey bee, *Apis mellifera* (Beye et al. 2003), may allow more accurate predictions of the limiting effects of diploid males in invasive populations of *V. velutina nigrithorax* suffering founder effects.

Acknowledgements

We thank Thomas O'Shea-Wheller for his comments, which improved the quality of the manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

Funding

No funding was reported.

Author contributions

B.J. and R.B. conceived the study; D.A.W. developed, and R.B. advised and contributed to, model design and functionality; and B.J., R.B. and D.A.W. wrote the manuscript. E.P.J., R.B. and B.J. provided GB nest data and summarised key literature for model parametrisation. B.J., D.A.W., E.P.J., R.B. and N.S. edited the manuscript and gave final approval for publication.

Author ORCIDs

Daniel A. Warren https://orcid.org/0000-0002-2073-7857
Richard Budgey https://orcid.org/0000-0002-9938-2584

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

Arca M, Papachristoforou A, Mougel F, Rortais A, Monceau K, Bonnard O, Tardy P, Thiéry D, Silvain JF, 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. Behavioural Processes 106: 122–129. https://doi.org/10.1016/j.beproc.2014.05.002

Arca M, Mougel F, Guillemaud T, Dupas S, Rome Q, Perrard A, Muller F, Fossoud A, Capdevielle-Dulac C, Torres-Leguizamon M, Chen XX (2015) Reconstructing the invasion and the demographic history of the yellow-legged hornet, *Vespa velutina*, in Europe. Biological Invasions 17: 2357–2371. https://doi.org/10.1007/s10530-015-0880-9

Archer ME (1984) Life and fertility tables for the wasp species *Vespula vulgaris* and *Dolichovespula sylvestris* (Hymenoptera: Vespidae) in England. Entomologia Generalis 9(3): 181–188. https://doi.org/10.1127/entom.gen/9/1984/181

Barbet-Massin M, Rome Q, Muller F, Perrard A, Villemant C, Jiguet F (2013) Climate change increases the risk of invasion by the Yellow-legged hornet. Biological Conservation 157: 4–10. https://doi.org/10.1016/j.biocon.2012.09.015

Barbet-Massin M, Rome Q, Villemant C, Courchamp F (2018) Can species distribution models really predict the expansion of invasive species? PLoS One 13(3): e0193085. https://doi.org/10.1371/journal.pone.0193085

Barbet-Massin M, Salles JM, Courchamp F (2020) The economic cost of control of the invasive yellow-legged Asian hornet. NeoBiota 55: 11–25. https://doi.org/10.3897/neobiota.55.38550

Beye M, Hasselmann M, Fondrk MK, Page RE, Omholt SW (2003) The gene csd is the primary signal for sexual development in the honeybee and encodes an SR-type protein. Cell 114(4): 419–429. https://doi.org/10.1016/s0092-8674(03)00606-8

Budge GE, Hodgetts J, Jones EP, Ostojá-Starzewski JC, Hall J, Tomkies V, Semmence N, Brown M, Wakefield M, Stainton K (2017) The invasion, provenance and diversity of *Vespa velutina* Lepeletier (Hymenoptera: Vespidae) in GB. PLoS One 12(9): e0185172. https://doi.org/10.1371/journal.pone.0185172

CABI (2025) *Vespa velutina* (Asian hornet). https://www.cabidigitallibrary.org/doi/10.1079/cabicompendium.109164 [Accessed on 15.05. 2025]

Carnell R (2024) lhs: Latin Hypercube Samples. R package version 1.2.0, https://CRAN.R-project.org/package=lhs

Cini A, Cappa F, Petrocelli I, Pepiciello I, Bortolotti L, Cervo R (2018) Competition between the native and the introduced hornets *Vespa crabro* and *Vespa velutina*: A comparison of potentially relevant life-history traits. Ecological Entomology 43(3): 351–362. https://doi.org/10.1111/een.12507

Cook JM, Crozier RH (1995) Sex determination and population biology in the Hymenoptera. Trends in Ecology & Evolution 10(7): 281–286. https://doi.org/10.1016/0169-5347(95)90011-x

Darrouzet E, Gévar J, Guignard Q, Aron S (2015) Production of early diploid males by European colonies of the invasive hornet *Vespa velutina nigrithorax*. PLoS One 10(9): e0136680. https://doi.org/10.1371/journal.pone.0136680

Dillane E, Hayden R, O'Hanlon A, Butler F, Harrison S (2022) The first recorded occurrence of the Asian hornet (*Vespa velutina*) in Ireland, genetic evidence for a continued single invasion across Europe. Journal of Hymenoptera Research 93: 131–138. https://doi.org/10.3897/jhr.93.91209

Esri Inc (2022) ArcGIS Pro version 3.0.1. https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview

Faria LR, Soares EDG, Carmo ED, Oliveira PMCD (2016) Diploid male dynamics under different numbers of sexual alleles and male dispersal abilities. Theory in Biosciences 135: 111–119. https://doi.org/10.1007/s12064-016-0226-x

Franklin DN, Brown MA, Datta S, Cuthbertson AG, Budge GE, Keeling MJ (2017) Invasion dynamics of Asian hornet, *Vespa velutina* (Hymenoptera: Vespidae): a case study of a commune in south-west France. Applied Entomology and Zoology 52: 221–229. https://doi.org/10.1007/s13355-016-0470-z

Granato A, Negrisolo E, Bonomi J, Zulian L, Cappa F, Bortolotti L, Mutinelli F (2019) Recent confirmation of a single haplotype in the Italian population of *Vespa velutina.* Biological Invasions 21: 2811–2817. https://doi.org/10.1007/s10530-019-02051-4

Harpur BA, Sobhani M, Zayed A (2013) A review of the consequences of complementary sex determination and diploid male production on mating failures in the Hymenoptera. Entomologia Experimentalis et Applicata 146(1): 156–164. https://doi.org/10.1111/j.1570-7458.2012.01306.x

Hassall RM, Purse BV, Barwell L, Booy O, Lioy S, Rorke S, Smith K, Scalera R, Roy HE (2024) Predicting the spatio-temporal dynamics of biological invasions: Have rapid responses in Europe limited the spread of the yellow-legged hornet (*Vespa velutina nigrithorax*)? Journal of Applied Ecology. https://doi.org/10.1111/1365-2664.14829

Haxaire J, Tamisier JP, Bouguet JP (2006) *Vespa velutina* Lepeletier, 1836, une redoutable nouveauté pour la faune de France (Hym., Vespidae). Bulletin de la Société Entomologique de France 111(2): 194–194. https://www.persee.fr/doc/bsef_0037-928x_2006_num_111_2_16309

Heimpel GE, De Boer JG (2008) Sex determination in the Hymenoptera. Annual Review of Entomology 53: 9–230. https://doi.org/10.1146/annurev.ento.53.103106.093441

Herrera C, Ferragut JF, Leza M, Jurado-Rivera JA (2023) Invasion genetics of the yellow-legged hornet *Vespa velutina* in the Westernmost Mediterranean archipelago. Journal of Pest Science 97: 645–656. https://doi.org/10.1007/s10340-023-01680-y

INPN (2025) Inventaire National du Patrimoine Naturel. Yellow-legged hornet. https://inpn.mnhn.fr/espece/cd_nom/433589?lg=en [Accessed on 15.05.2025]

Jones EP, Conyers C, Tomkies V, Semmence N, Fouracre D, Wakefield M, Stainton K (2020) Managing incursions of *Vespa velutina nigrithorax* in the UK: An emerging threat to apiculture. Scientific Reports 10(1): 1–8. https://doi.org/10.1038/s41598-020-76690-2

Jung C (2012) Spatial expansion of an invasive hornet, *Vespa velutina nigrithorax* Buysson (Hymenoptera: Vespidae) in Korea. Korean Journal of Apiculture 27: 87–93.

Keeling MJ, Franklin DN, Datta S, Brown MA, Budge GE (2017) Predicting the spread of the Asian hornet (*Vespa velutina*) following its incursion into GB. Scientific Reports 7(1): 6240. https://doi.org/10.1038/s41598-017-06212-0

Laurino D, Lioy S, Carisio L, Manino A, Porporato M (2019) *Vespa velutina*: An alien driver of honey bee colony losses. Diversity 12(1): 5. https://doi.org/10.3390/d12010005

Leung K, van der Meulen H (2022) Revisiting the hymenopteran diploid male vortex: A review of avoidance mechanisms and incidence. Entomologia Experimentalis et Applicata 170(12): 1010–1031. https://doi.org/10.1111/eea.13234

Leza M, Herrera C, Picó G, Morro T, Colomar V (2021) Six years of controlling the invasive species *Vespa velutina* in a Mediterranean island: The promising results of an eradication plan. Pest Management Science 77(5): 2375–2384. https://doi.org/10.1002/ps.6264

Lioy S, Manino A, Porporato M, Laurino D, Romano A, Capello M, Bertolino S (2019) Establishing surveillance areas for tackling the invasion of *Vespa velutina* in outbreaks and over the border of its expanding range. NeoBiota 46: 51–69. https://doi.org/10.3897/neobiota.46.33099

Martín-Ávila JA, Díaz-Aranda LM, Fernández-Pereira JM, Rebollo S (2025) The European honey buzzard (*Pernis apivorus*) as an ally for the control of the invasive yellow-legged hornet (*Vespa velutina nigrithorax*). Pest Management Science 81(4): 2237–2247. https://doi.org/10.1002/ps.8622

Meiborg AB, Faber NR, Taylor BA, Harpur BA, Gorjanc G (2023) The suppressive potential of a gene drive in populations of invasive social wasps is currently limited. Scientific Reports 13(1640). https://doi.org/10.1038/s41598-023-28867-8

Monceau K, Arca M, Leprêtre L, Mougel F, Bonnard O, Silvain JF, Maher N, Arnold G, Thiéry D (2013) Native prey and invasive predator patterns of foraging activity: The case of the yellow-legged hornet predation at European honeybee hives. PLoS One 8(6): e66492. https://doi.org/10.1371/journal.pone.0066492

Monceau K, Bonnard O, Thiéry D (2014) *Vespa velutina*: A new invasive predator of honeybees in Europe. Journal of Pest Science 87(1): 1–16. https://doi.org/10.1007/s10340-013-0537-3

National Bee Unit (2025a) Historic UK Asian Hornet Incursions. https://www.nationalbeeunit.com/diseases-and-pests/asian-hornet/historic-uk-asian-hornet-incursions [Accessed on 15.05.2025]

National Bee Unit (2025b) Asian Hornet [online]. https://www.nationalbeeunit.com/about-us/beekeeping-news/asian-hornet-2024-rolling-update [Accessed on 15.05.2025]

O'Shea-Wheller TA, Curtis RJ, Kennedy PJ, Groom EK, Poidatz J, Raffle DS, Rojas-Nossa SV, Bartolomé C, Dasilva-Martins D, Maside X, Mato S (2023) Quantifying the impact of an invasive hornet on *Bombus terrestris* colonies. Communications Biology 6(1): 990. https://doi.org/10.1038/s42003-023-05329-5

Pazos T, Álvarez-Figueiró P, Cortés-Vázquez JA, Jácome MA, Servia MJ (2022) Of fears and budgets: Strategies of control in *Vespa velutina* invasion and lessons for best management practices. Environmental Management 70(4): 605–617. https://doi.org/10.1007/s00267-022-01690-z

Pedersen S, Kennedy PJ, O'Shea-Wheller TA, Poidatz J, Christie A, Osborne JL, Tyler CR (2025) Broad ecological threats of an invasive hornet revealed through a deep sequencing approach. The Science of the Total Environment 970(178978). https://doi.org/10.1016/j.scitotenv.2025.178978

Poidatz J, Monceau K, Bonnard O, Thiéry D (2018) Activity rhythm and action range of workers of the invasive hornet predator of honeybees *Vespa velutina*, measured by radio frequency identification tags. Ecology and Evolution 8(15): 7588–7598. https://doi.org/10.1002/ece3.4182

Posit Team 2022. Rstudio: Integrated Development Environment for R. Posit Software, PBC, Boston, MA. http://www.posit.co/

Quaresma A, Henriques D, Godinho J, Maside X, Bortolotti L, Pinto MA (2022) Invasion genetics of the Asian hornet *Vespa velutina nigrithorax* in Southern Europe. Biological Invasions 24(5): 1479–1494. https://doi.org/10.1007/s10530-022-02730-9

R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Requier F, Rome Q, Chiron G, Decante D, Marion S, Menard M, Muller F, Villemant C, Henry M (2019) Predation of the invasive Asian hornet affects foraging activity and survival probability of honey bees in Western Europe. Journal of Pest Science 92: 567–578. https://doi.org/10.1007/s10340-018-1063-0

Robinet C, Suppo C, Darrouzet E (2017) Rapid spread of the invasive yellow-legged hornet in France: The role of human-mediated dispersal and the effects of control measures. Journal of Applied Ecology 54(1): 205–215. https://doi.org/10.1111/1365-2664.12724

Robinet C, Darrouzet E, Suppo C (2019) Spread modelling: A suitable tool to explore the role of human-mediated dispersal in the range expansion of the yellow-legged hornet in Europe. International Journal of Pest Management 65(3): 258–267. https://doi.org/10.1080/09670874.2018.1484529

Rome Q, Muller F, Gargominy O, Villemant C (2009) Bilan 2008 de l'invasion de *Vespa velutina* Lepeletier en France (Hymenoptera: Vespidae). Bulletin de la Société Entomologique de France 114: 297–302. https://doi.org/10.3406/bsef.2009.2741

Rome Q, Muller FJ, Touret-Alby A, Darrouzet E, Perrard A, Villemant C (2015) Caste differentiation and seasonal changes in *Vespa velutina* (Hym.: Vespidae) colonies in its introduced range. Journal of Applied Entomology 139(10): 771–782. https://doi.org/10.1111/jen.12210

Rome Q, Perrard A, Muller F, Fontaine C, Quilès A, Zuccon D, Villemant C (2021). Not just honeybees: predatory habits of *Vespa velutina* (Hymenoptera: Vespidae) in France. *A*nnales de La

Société Entomologique de France (N.S.) 57(1): 1–11. https://doi.org/10.1080/00379271.2020.1867005

Sauvard D, Imbault V, Darrouzet E (2018) Flight capacities of yellow-legged hornet (*Vespa velutina nigrithorax*, Hymenoptera: Vespidae) workers from an invasive population in Europe. PLoS One 13(6): e0198597. https://doi.org/10.1371/journal.pone.0198597

Stainton K, McGreig S, Conyers C, Ponting S, Butler L, Brown P, Jones EP (2023) Molecular Identification of Asian Hornet *Vespa velutina nigrithorax* Prey from Larval Gut Contents: A Promising Method to Study the Diet of an Invasive Pest. Animals (Basel) 13(3): 511. https://doi.org/10.3390/ani13030511

Stevenson M, Sergeant E (2024) epiR: Tools for the Analysis of Epidemiological Data. R package version 2.0.75, https://CRAN.R-project.org/package=epiR

Tan K, Yang MX, Wang ZW, Li H, Zhang ZY, Radloff SE, Hepburn R (2012) Cooperative wasp-killing by mixed-species colonies of honeybees, *Apis cerana* and *Apis mellifera.* Apidologie 43: 195–200. https://doi.org/10.1007/s13592-011-0098-5

Turchi L, Derijard B (2018) Options for the biological and physical control of *Vespa velutina nigrithorax* (Hym.: Vespidae) in Europe: A review. Journal of Applied Entomology 142(6): 553–562. https://doi.org/10.1111/jen.12515

Villemant C, Barbet-Massin M, Perrard A, Muller F, Gargominy O, Jiguet F, Rome Q (2011) Predicting the invasion risk by the alien bee-hawking Yellow-legged hornet *Vespa velutina nigrithorax* across Europe and other continents with niche models. Biological Conservation 144(9): 2142–2150. https://doi.org/10.1016/j.biocon.2011.04.009

Zayed A, Packer L (2005) Complementary sex determination substantially increases extinction proneness of haplodiploid populations. Proceedings of the National Academy of Sciences of the United States of America 102(30): 10742–10746. https://doi.org/10.1073/pnas.0502271102

Supplementary material 1

Description of model structure and functionality, Validation Model, Scenario Modelling and Sensitivity Analysis

Authors: Daniel A. Warren, Richard Budgey, Nigel Semmence, Eleanor P. Jones, Ben Jones

Data type: docx

Link: https://doi.org/10.3897/neobiota.101.148570.suppl1

Supplementary material 2

Outputs of Validation Model, Scenario Models and Sensitivity Analysis

Authors: Daniel A. Warren, Richard Budgey, Nigel Semmence, Eleanor P. Jones, Ben Jones

Data type: docx

Link: https://doi.org/10.3897/neobiota.101.148570.suppl2