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Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our Editorial Policies and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☒	☐	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	Whole-genome and RNA-seq data were generated using Illumina NovaSeq 6000 instruments with vendor-supplied control software. Library quality and fragment sizes were assessed using Qubit 4 Fluorometers, Agilent Bioanalyzer/Tapestation systems and associated manufacturer software (Illumina, Thermo Fisher Scientific, Agilent). No custom software was used for data collection
Data analysis	Genomic reads were mapped with NextGenMap v0.5.0, processed with SAMtools v1.10, and variants were called and filtered using FreeBayes v1.1.0 and VCFtools v0.1.12b within a Snakemake v6.0 workflow. RNA-seq reads were processed with fastp v0.23.2, mapped using HISAT2 v2.2.1, and variants were called with GATK and annotated with ANNOVAR. All statistical analyses and figure generation were carried out in R v4.2.2 using standard packages (e.g. tidyverse, ggplot2, vcfr, patchwork, ggpubr). Custom R scripts for the mathematical modelling and for processing genomic and transcriptomic data are available in the project GitHub repository (Varroa-pedigree-study) and the accompanying R Markdown document, as stated in the Code availability section

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

All data supporting the findings of this study are available within the Article, its Supplementary Information and the accompanying Source Data file. Raw whole-genome sequencing reads for the Varroa pedigree have been deposited in the Sequence Read Archive (SRA) under accession PRJNA794941, and raw RNA-seq reads for mothers and sons under accession PRJNA1216898. Biosample metadata, including sex, developmental stage, pedigree information and sequencing coverage, are provided in Supplementary Table 2 and Supplementary Table 1. Additional variant annotations, Sanger validation data and modeling details are provided in Supplementary Tables and Supplementary Text. No restrictions apply to data access

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	Not applicable; this study did not involve human participants or human-derived data.
Reporting on race, ethnicity, or other socially relevant groupings	Not applicable; this study did not involve human participants or human-derived data.
Population characteristics	Not applicable; this study did not involve human participants or patient populations.
Recruitment	Not applicable; this study did not involve human participants or patient populations.
Ethics oversight	Experimental work on honey bees and Varroa mites was conducted under the institutional guidelines of the Okinawa Institute of Science and Technology (OIST); no human participants were involved.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	The study combines experimental pedigrees and population-genetic modelling to investigate the mode of genetic inheritance in the honey bee parasite Varroa destructor and its consequences for effective population size. We constructed three-generation pedigrees (F0 foundress, F1 adult offspring, F2 offspring) using a semi-natural infestation system in honey bee brood cells, and quantified inheritance patterns using whole-genome resequencing of 223 mites from 30 families alongside RNA-seq from 10 mites (5 mother–son pairs). We then derived analytical expectations for heterozygosity decline under haplodiploidy, diploid arrhenotoky and complete diploidy, and compared the resulting effective population sizes under realistic demographic scenarios.
Research sample	The research sample consisted of Varroa destructor mites collected from managed Apis mellifera colonies in Okinawa, Japan (pedigree experiment) and Hangzhou, China (RNA-seq analysis). For the genomic pedigree, we obtained 223 mites from 30 three-generation families, each including a foundress female, her adult male and female offspring, and their F2 offspring. These families represent typical Varroa infestations in mite-infested honey bee colonies. For the transcriptomic analysis, we sequenced 5 mother–son pairs sampled from naturally infested colonies. Sample sizes were chosen to balance logistical constraints of multi-generation pedigree construction and sequencing depth with the need to robustly infer inheritance patterns across multiple families.
Sampling strategy	For the pedigree experiment, we first collected naturally infested brood cells containing a single foundress female and her offspring, then used an artificial infestation protocol to establish standardized F1 and F2 generations within controlled brood cells. Families with double infestations or unmarked mites were excluded to ensure unambiguous pedigree structure, resulting in 30 usable families out of 78 successful infestations. For the RNA-seq component, we sampled 5 families each contributing one adult female and her son. No formal a priori sample size calculation was performed; sample sizes were based on previous Varroa experimental work and were considered sufficient to detect consistent, qualitative deviations from haplodiploid inheritance across multiple independent families.

Data collection	Mites and honey bee pupa were collected by hand from experimental colonies using established Varroa sampling protocols. Experimental pedigrees were generated by introducing marked F1 females into freshly sealed worker brood cells and allowing them to reproduce under controlled incubator conditions, after which all family members were recovered and individually preserved. Sex, developmental stage and viability were scored visually under a stereomicroscope. DNA and RNA were extracted from single mites following standardized protocols, libraries were prepared using commercial kits, and sequencing was carried out on Illumina platforms at institutional sequencing facilities as described in the Methods.
Timing and spatial scale	Pedigree experiments were conducted at the Okinawa Institute of Science and Technology apiaries in Okinawa, Japan, between July and November 2020. Varroa mites for the RNA-seq analysis were collected from colonies at Zhejiang University, Hangzhou, China, in November 2024. Each experimental family was followed over a single reproductive cycle within an individual brood cell; there was no long-term temporal monitoring beyond this generational window. The spatial scale of inference corresponds to mite populations within managed A. mellifera colonies at these two locations.
Data exclusions	For the pedigree analysis, we prospectively excluded brood cells that contained more than one foundress mite, double-infested experimental cells, and any unmarked mites, to ensure accurate pedigree assignment; this reduced the dataset from 78 successful infestations to 30 unambiguous families. For genomic data, low-quality and poorly covered variant sites were filtered using predefined thresholds on depth, missingness, variant quality, and VAF/QAF metrics as described in the Methods and Supplementary Figures. No families or RNA-seq samples were excluded based on outcomes.
Reproducibility	Experimental findings were based on 30 independent mite families generated using a standardized artificial infestation protocol, all processed with the same DNA/RNA library preparation and sequencing pipelines. The key inheritance patterns (diploid males preserving maternal heterozygosity and transmitting both alleles) were observed consistently across multiple families and crosses. All bioinformatic and statistical analyses, including figure generation, are fully reproducible from the shared R scripts, R Markdown document and GitHub repository described in the Code availability section.
Randomization	Random allocation to experimental groups was not applicable, because all mites belonged to naturally occurring families and experimental brood cells each received a single marked F1 female. Families were selected based on the presence of a single foundress and successful reproduction, not on outcome; potential confounders such as double-infested cells were excluded prospectively according to predefined criteria.
Blinding	Blinding was not relevant to data acquisition or analysis. Sex, developmental stage and family identity were determined based on clear morphological criteria and experimental markings, and genotypes were obtained by high-throughput sequencing followed by automated variant calling. Analytical scripts were applied uniformly to all samples without reference to expected outcomes.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Varroa-infested honey bee colonies were maintained in standard managed apiary in Okinawa, Japan (OIST apiary and Onna village apiary) and Hangzhou, China (Zhejiang University apiary). Colonies were kept under typical local climatic conditions, with supplemental sugar solution and pollen patties provided as needed, as described in the Methods. Experimental brood frames were temporarily removed to a controlled dark incubator (34–34.5 °C, 60–75% relative humidity) during artificial infestation and mite reproduction, after which they were returned or bees were allowed to emerge.
Location	Pedigree families were obtained from A. mellifera colonies at the Onna village apiary and the experimental apiary of the Okinawa Institute of Science and Technology (OIST), Okinawa, Japan. Varroa mites for the RNA-seq analysis were collected from A. mellifera colonies at Zhejiang University, Hangzhou, China. All work was conducted in managed apiaries on institutional or collaborating facilities; no sampling was performed in protected natural areas.
Access & import/export	Access to apiaries was granted by collaborating beekeepers and institutional facilities. All collection and transport of Varroa mites and honey bee brood complied with local and national regulations in Japan and China. No international transport of live mites or bees was required for the experiments; only preserved DNA/RNA samples and sequencing data were shared between institutions in accordance with institutional guidelines.
Disturbance	Disturbance to bee colonies was minimized by sampling only a subset of brood cells per frame and by promptly returning frames to the hives or incubators after manipulation. Sampling did not involve habitat modification or removal of wild organisms outside of managed colonies. Colonies continued to function normally after sampling, and no long-term adverse effects were observed.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☐	☒ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern
☒	☐ Plants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other research organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research, and Sex and Gender in Research

Laboratory animals	Not applicable; the study did not involve vertebrate laboratory animals or established laboratory animal strains. Experimental work was conducted on invertebrate honey bees (Apis mellifera) and their ectoparasitic mites (Varroa destructor) maintained in managed apiaries and incubators.
Wild animals	The study did not involve wild populations sampled from natural habitats. All honey bee colonies were managed colonies at institutional and collaborating apiaries, and Varroa mites were obtained from these colonies as described in the Methods.
Reporting on sex	For Varroa mites, both sexes were included: foundress adult females (F0), adult sons and daughters (F1), and their F2 offspring in various developmental stages. Sex was determined based on external morphology and cuticle colour following established criteria. For honey bees, only worker brood and adult nurse bees were used; sex was not a variable of interest. The study did not test sex-specific hypotheses, so no formal sex-based comparisons were performed beyond the mother–son heterozygosity analysis, which is fully described in the main text.
Field-collected samples	Field-collected samples consisted of brood frames and adult bees from managed A. mellifera colonies in Okinawa, Japan, and Hangzhou, China. Frames were temporarily removed to controlled incubators (34–34.5 °C, 60–75% relative humidity) during artificial infestation experiments and then returned or allowed to complete development. Housing and maintenance conditions for colonies followed standard beekeeping practices, as described in the Methods.
Ethics oversight	Work with honey bees and Varroa mites followed institutional guidelines for invertebrate research at the Okinawa Institute of Science and Technology (OIST) and Zhejiang University. No vertebrate animals or human participants were involved, and formal animal ethics committee approval was not required under local regulations.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Plants

Seed stocks	Not applicable
Novel plant genotypes	Not applicable
Authentication	Not applicable