Trends in
Parasitology

CellPress
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Review

Coevolution stabilizes the honey bee–*Varroa destructor*–virus system on islands

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For 65 years, the ectoparasitic mite *Varroa destructor,* along with the deformed wing virus (DWV) it vectors, has killed millions of *Apis mellifera* honey bee colonies globally. The coevolution of the 'bee–mite–virus' system in Hawaii over 17 years has been closely followed. Resistance to *V. destructor* evolved in the free-living honey bees on Oahu by detecting and removing a high proportion of mite-infested brood cells, as seen in other mite-resistant honey bees. On Big Island, miticides remain widely used, so on both islands, DWV prevalence decreased, but a more virulent recombinant form evolved. Thus, coevolution on Oahu has produced a new stable 'bee–mite–virus' state that has been exploited by beekeepers and provides a global solution to the *V. destructor* problem.

Highlights

A 17-year case study in Hawaii revealed adaptations between the honey bee (*Apis mellifera),* the parasitic mite (*Varroa destructor),* and the deformed wing virus it vectors.

The free-living honey bee population on Oahu developed *Varroa destructor* resistance by improving its ability to detect and remove mite-infested cells. The resistance mechanism on Oahu is the same as, or has strong parallels with, other *Varroa destructor*-resistant populations around the world.

On mite-infested islands, deformed wing virus initially showed dominance of deformed wing virus-A, followed by deformed wing virus-B, with these parent strains now being replaced by virulent B/A recombinants, which may explain the recent high colony losses on the US mainland and elsewhere when miticide resistance appears.

Coevolution between host, vector, and virus has allowed a new balanced state to be achieved, despite each party evolving in a direction that benefits itself.

Varroa destructor remains a major threat to *Apis mellifera* honey bees after 65 years

The coevolution of viruses, their hosts, and vectors is a fundamental process, shaping the 'origin of life' and driving species diversity and large-scale extinctions [1]. Outside of the several well-studied examples, due to their influence on human health, such as the human–mosquito–*Plasmodium* system [2], one of the best-studied systems is that of the economically important honey bee ***Apis mellifera*** (see Glossary), the ectoparasitic mite ***Varroa destructor,*** and **deformed wing virus (DWV)** that it vectors [3–5]. Moreover, this interaction has hardly been uninterrupted or managed in any meaningful way, especially as it pertains to virus infectivity, persistence, and evolution over the last 65 years.

V. destructor is a specialized ectoparasite that is highly adapted to the biology of its honey bee host. It spends long periods of time on the adult bees and reproduces within sealed brood cells, feeding on the developing honey bee pupae. In its native honey bee host (*Apis cerana)*, *V. destructor* reproduction occurs only on the drone (male) pupae since, if mites invade worker brood cells, they are typically detected and removed. Whereas in its new host (*A. mellifera),* mite reproduction occurs in both drone and worker brood cells, as initially this new host was poor at detecting mite-infested cells. It was in the late 1950s when *V. destructor* jumped the species barrier from *A. cerana* to the globally managed honey bee *A. mellifera*. This occurred in Asia, and subsequently, *V. destructor* spread globally [6] killing millions of colonies annually since the mite's feeding behavior provided a new viral transmission route for DWV, which had previously been transmitted from bee to bee [7]. This transformed DWV from a previously largely benign honey bee pathogen into one of the world's most important insect pathogens [4]. When pupae become infected with DWV through mite feeding, they suffer from reduced adult longevity, which can weaken the colony, and when worker brood infestation rates increase above the colony's threshold, the colony collapses [8].

Beekeepers in wealthier countries particularly across the Northern Hemisphere commonly responded to the arrival of mite through endless and costly cycles of miticide use or, otherwise

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through targeted biotechnical methods such as **drone trapping**, required due to the commercial value of *A. mellifera* honey bees, estimated globally to be between US$235–577 billion [9]. While miticides have been successful in controlling *V. destructor*, colony losses due to the mites continue to persist or even increase [10–12]. This is largely due to the rise of resistance to most miticides [10,13,14] following decades of continuous use. *V. destructor*-associated losses have been particularly striking in the USA, where, in 2023/2024, beekeepers experienced a staggering 56% overwintering colony loss, with a further 62% (1.5+ million colonies) lost between summer 2024 and January 2025 due to miticide resistance [10][i]. However, in many countries such as sub-Saharan Africa, Latin America, and the Caribbean, where miticides have not been widely used due to cost or availability, honey bee populations have become naturally resistant to *V. destructor* [15–19], potentially representing a solution to mite control for other honey bee populations globally. However, the ***V. destructor* resistance** mechanism remains largely theoretical [17].

Why the Hawaiian case study is important

Isolated islands have long been used to gain unique insights into evolution and ecological processes, for example, Darwin's finches [20] and the terraforming of Ascension Island [21], since their small size and isolation increase selective pressure and cause accelerated evolution [22]. *A. mellifera* was introduced to the Hawaiian Islands in 1857 from California, where they thrived in the subtropical climate, and both large managed and **free-living populations** quickly became established on all islands [23]. By 1909, there were over 20 000 managed colonies in Hawaii [24], and due to concerns over introduced pathogens and parasites, a ban on the importation of live bees was introduced in 1908 [24]. Despite this, *V. destructor* was first detected in 2007 on Oahu and was detected in 2008 on the Big Island, where it spread rapidly [25] causing the widespread collapse of both the managed and free-living populations on both islands [3] by providing a new DWV transmission route, mirroring the situation worldwide [10,26,27]. Increased mite reproduction results in increased viral loads [3], and coinfections of different variants become more frequent, which in turn can lead to the formation of viral recombinants [28]. Recombination in viruses can result in weakened or even beneficial forms of the virus [29], or conversely, more virulent forms [30,31]. Therefore, understanding the composition of viral populations at the genome level is critical for understanding their threat to bee health. Furthermore, given the increasing interest in and successes with sustainable solutions to mite control involving *V. destructor*-resistant bees, it is critical to understand how free-living and managed bee populations are affected by the 'bee–mite–virus' dynamics under different miticide approaches.

The Hawaiian archipelago is an ideal natural laboratory to study the 'bee–mite–virus' system since *V. destructor* is present only on two islands (Oahu and Big Island) and remains absent from the rest, which act as controls (Figure 1). Furthermore, large differences in the ratio of managed to free-living honey bee colonies exist between Oahu and Big Island. That is, in 2015, on Big Island, around 14 000 colonies were managed [32], dominated by large-scale bee breeding operations, which were maintained in areas where few free-living colonies persist—a pattern that persists today. Whereas on Oahu, smaller-scale and hobbyist beekeeping is more common [32], with around 600 managed colonies in 2015, which are vastly outnumbered by the many thousands of free-living colonies that exist in the extensive forests. This allows the differences between largely managed and unmanaged honey bee populations to be compared over time on different islands. Furthermore, Hawaii's favorable climate allows both honey bees and *V. destructor* to reproduce year-round, which is not possible in temperate climates. This increased reproduction greatly amplifies the selective pressure on the hosts, mites, and the viruses they vector, as well as the number of generations on which selection is acting. Therefore, the Hawaiian system provides an accelerated way to gain insights into 'bee–mite–virus' evolution and offers valuable insights into understanding the emergence of *V. destructor* resistance.

Glossary

***Apis mellifera*:** one of only a few insect species managed by humans and has a global distribution. Each colony consists of a single queen, between 10 000 and 60 000 workers, and a few hundred drones. They reproduce by swarming, which occurs when a newly mated queen leaves the colony with around half of the worker bees. *V. destructor* invades cells containing bee pupae (worker and drone) just before they are sealed and reproduces within the sealed cells, feeding on the developing pupa and transmitting DWV. The virus does not kill the bee but reduces its longevity. An estimated 2500 or 12 000 mites are required to kill a colony under temperate or tropical conditions, respectively.

Deformed wing virus (DWV): a small 30 nm RNA virus whose natural prevalence and load in honey bees are both very low, only very rarely killing a colony. *V. destructor* provided a new DWV transmission route, resulting in it becoming one of the most widespread insect viruses globally.

Drone trapping: a mite control method, which relies on the fact that the favored host for *V. destructor* to reproduce on is the drone (male) pupae. In this method, sections of drone brood containing a large proportion of the colony's mites are periodically removed from colonies, reducing mite numbers with minimal effects on the colony.

Free-living populations: colonies originated from managed colonies at some time in the past and survive in cavities in trees, buildings, or rocks without any human intervention.

Master variants: virus variants significantly different from each other in their genome sequences, although each master variant contains a swarm of subvariants due to their high mutation rates.

Requeen: when the existing queen in a colony is replaced by a new queen, allowing beekeepers or researchers to alter the genetic composition of the colony.

***Varroa destructor*:** a large (1.2 mm × 1.7 mm) external parasitic mite relative to its honey bee host. Only the adult female mites can survive outside the sealed cells that contain developing pupae on which the mites reproduce. During each reproductive cycle, one male and three to four female eggs are laid, but fewer than two female offspring and the male

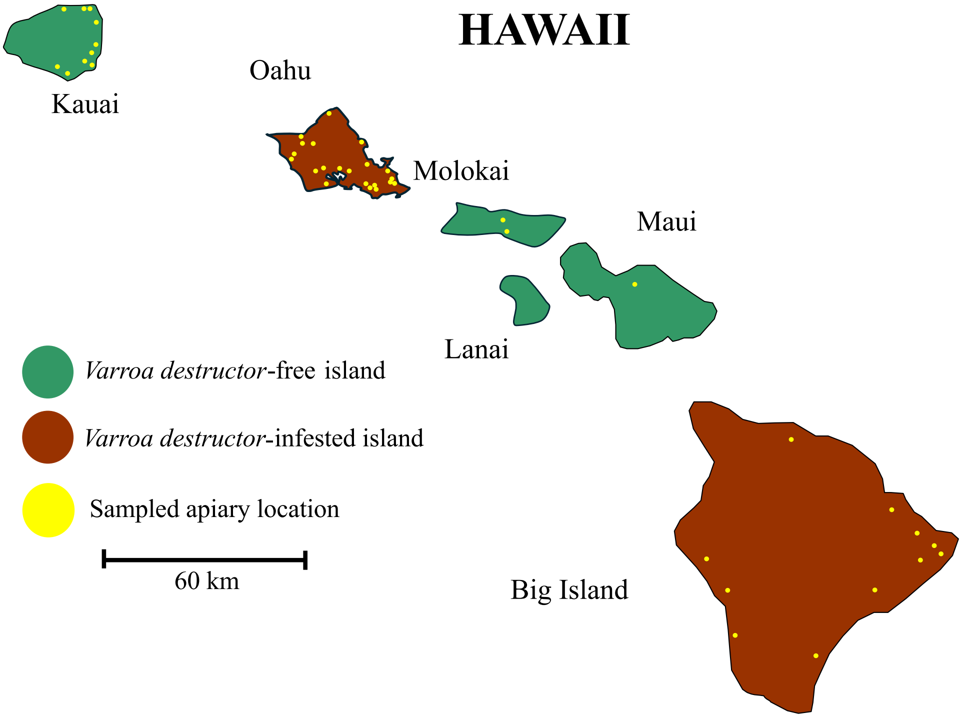

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Figure 1. Map of the main Hawaiian Islands, indicating the islands infested with *V. destructor* and those that are mite-free, along with the approximate locations of apiaries sampled during various studies.

Changing honey bee–mite dynamics in the 17 years following *V. destructor*'s arrival

V. destructor was first detected on Oahu in April 2007, and an immediate survey of 25 managed colonies by the U.S. Department of Agriculture (USDA) showed it was already established across Oahu, infesting 88% of the surveyed colonies. Then, from May to October, the USDA found that 79% of free-living colonies ($n = 48$) surveyed had an average worker infestation level of 6% (range: 1–57%, $n = 30136$ bees). Six months later, the University of Hawaii found that 65% of their 419 surveyed colonies had already died [3]. A survey in 2011 on Big Island, 2 years after the mite's arrival there, also found that 55% of colonies had died, with 34% of beekeepers losing all their colonies [33]. By 2010, almost all beekeepers on Oahu and Big Island were treating their colonies with miticides [34]. This reduced the annual colony losses to 15–20% on Oahu and Big Island[ii] due to the miticides reducing the mite population and, consequently, the number of DWV-infected pupae. On the 'control', mite-free islands of Kauai and Maui, annual losses of only 3% were reported [34], where DWV prevalence and load were low or undetectable. Between 2009 and 2011, beekeepers, pest control officers, and bee researchers all noticed the disappearance of free-living colonies on Oahu and Big Island, initially from urban areas and then from the more mountainous and rural areas [35]. Around 2014–2015, free-living colony numbers started increasing again on both Oahu and Big Island [36]. During this time, several beekeepers on Oahu started collecting free-living swarms and withdrew all miticide treatments, based on their personal observations that free-living colonies were persisting without any treatment. Over the next decade, these beekeepers increased their colonies from tens to hundreds while continuing not to treat (Box 1). Currently, beekeepers that remove swarms on Oahu report that they are very busy (personal communication), supporting the observations that a large (thousands of colonies) free-living population has become re-established on Oahu.

have time to mature and mate before the worker bee emerges.

***V. destructor* resistance:** the ability of a bee colony to survive without needing any form of externally applied mite control.

Box 1. Dynamics of the bee–virus–mite system over 17 years in Hawaii

Before *V. destructor*'s arrival, Oahu maintained a large free-living honey bee population with around 600 managed honey bee colonies [32] that intermixed freely and harbored very low levels of DWV with high variant diversity [3]. Within 1 year of the mite's arrival (see Figure I in Box 1), the majority of managed colonies had collapsed, and beekeepers started treating their colonies (gray hives) (Figure I). During this period, a single virulent master variant of DWV-A dominated [3]. During the next 5 years, the free-living population collapsed[ii], leading to a lack of pollination, which required some farmers to hand-pollinate their melon and pumpkin crops, and in late 2012 caused the complete failure of the pumpkin crop on Big Island[iii] (Figure I). From 2014, the free-living population started to recover, and beekeepers discovered that free-living caught swarms could survive without treatment. During this period, a new master variant (DWV-B) became common and coinfected colonies along with DWV-A [38,46,47] (Figure I). From 2019 to 2024, it was confirmed that the honey bees had developed resistance to *V. destructor* (see Figure I in Box 2). In 2022, 64% of beekeepers on Oahu managing over 1500 colonies had stopped all mite treatment (Table S3 in the supplemental information online). In 2025, 70 and 8% of the managed colonies were not treated for *V. destructor* on Oahu and Big Island, respectively (Table S3). There was an increase from 600 to 1800 managed colonies on Oahu between 2015 and 2025 (Table S3), whereas numbers on Big Island have remained similar over this period. On both islands, 70% of beekeepers reported that their annual colony losses were below 20% (Table S3), far below the 40–65% reported on the US mainland [10]. This is despite the appearance of more virulent DWV-B/A recombinant(s) on both mite-infested islands (Figure 3). Meanwhile, on the mite-free islands of Maui and Kauai, DWV prevalence and colony losses have remained very low.

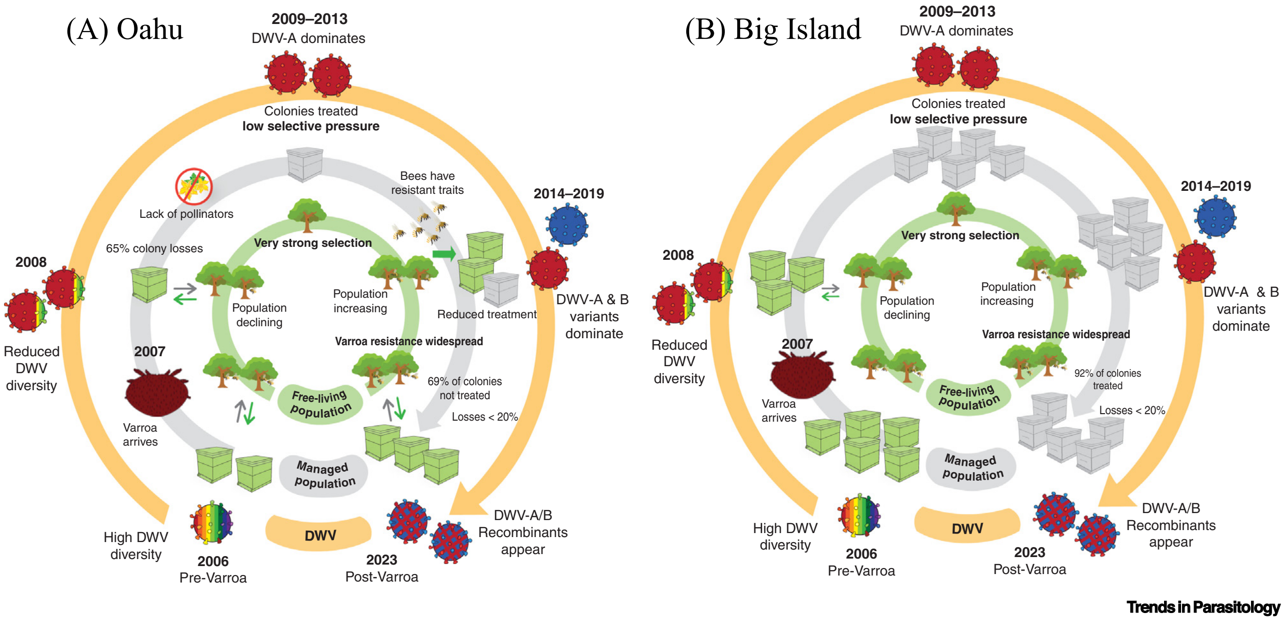

Figure I. (Figure360video).

For a Figure360 author presentation of Figure I, see the figure legend at https://doi.org/10.1016/j.pt.2026.04.001

The diagram summarizes the key changes that have occurred over a 17-year period on the islands of Oahu (A) and Big Island (B), Hawaii. These include the changes observed in the managed and free-living honey bee populations, the *V. destructor* mite, the DWV that *V. destructor* transmits, and the beekeepers' mite-treatment strategies.

The emergence of resistance to *V. destructor* in the Oahu honey bees

V. destructor reproduces within sealed brood cells, and mite resistance is achieved through honey bee workers accurately detecting and removing (cannibalizing) these parasitized worker brood cells [15,40] as occurred in the mite's natural host, *A. cerana*. A proxy for the accuracy of detecting mite-infested cells is to measure the proportion of infested sealed cells that have been recapped, that is, opened and investigated by workers, then resealed [15,16]. To measure the other key trait of 'removal of mite-infested pupae', more laborious artificial mite-introduction studies are required.

In 2019, a small study [35] found a recapping accuracy of 78% (i.e., 78% of mite-infested cells had been recapped) in the worker brood of five colonies (three apiaries) that all originated from the free-living population. This suggested that colonies were becoming resistant to

V. destructor, as the ability to accurately detect mite-infested worker cells is a key trait found in resistant populations [17]. Between 2022 and 2024, an additional 108 colonies from 27 apiaries (14 670 cells) on Oahu were investigated and showed a recapping accuracy of 81% in worker cells (see Figure IA in Box 2, and Box S1 and Figure S1 in the supplemental information online). The targeted uncapping of infested drone cells was not observed on Oahu (Figure S1), mirroring what has been seen in *V. destructor*-resistant colonies in South African [16] and Cuban [19] honey bee populations.

Box 2. Oahu honey bees' key hygienic adaptations to *V. destructor*

The two key hygienic behavioral adaptions found in *V. destructor*-resistant honey bee colonies throughout the world are the increased detection (Figure IA,C) and removal (Figure IB,D) of worker-infested pupal cells [17][i]. The mite-resistant population on the island of Oahu, Hawaii, has evolved the ability to detect and remove mite-infested worker cells at a higher level than most other mite-resistant populations around the world, as evidenced by comparing the Hawaiian data to that of a meta-analysis of 60 previous studies [17]. This rapid adaptation is probably a result of the increased selective pressure and accelerated evolution [21] aided by the subtropical climate that allows for increased reproduction of both *V. destructor* and *A. mellifera*.

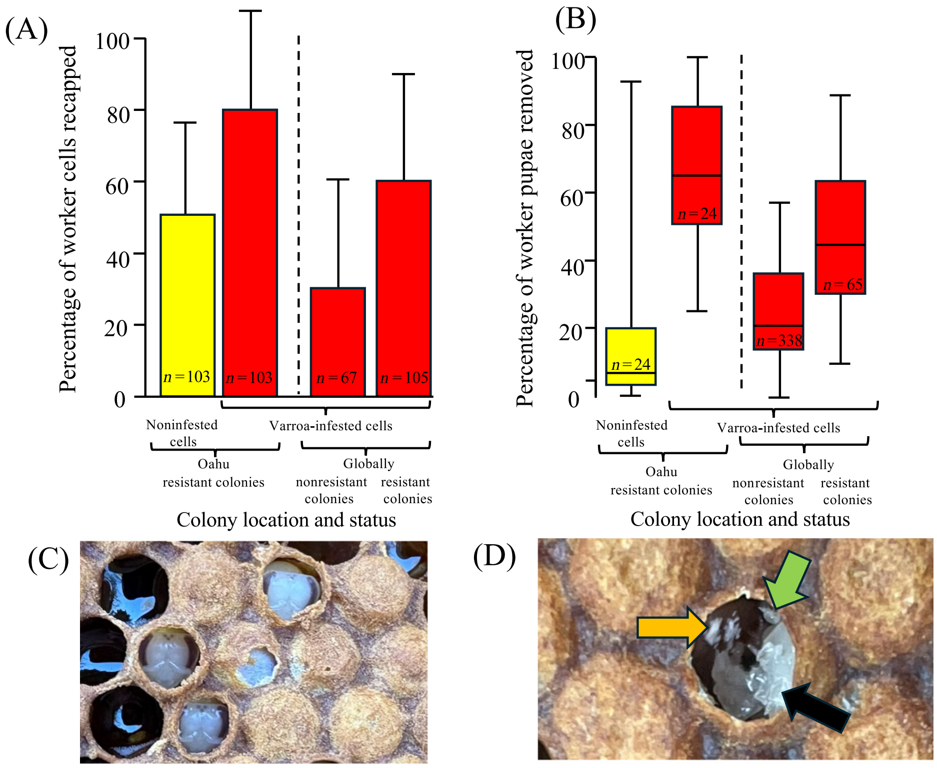

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Figure I. How the two key *V. destructor* resistance behaviors, detection and removal of mite-infested cells, that arose in the Oahu honey bee population compared to other populations. Comparison of the percentage of recapping (A) and pupal removal (B) of noninfested (yellow) and mite-infested (red) cells between colonies in Oahu, Hawaii, and 60 studies conducted around the world [17]. The number of colonies (N) used in each group is given. The photographs by the author show a typical patch of honey bee pupae that have had their cell caps removed (C) and will soon be resealed with wax (recapped), and partial removal of an infested pupa (D), with the arrows indicating the half-cannibalized bee pupa (black), the white mite feces on the side of the cell (orange), and a *V. destructor* protonymph (green). The photographs are provided by the authors.

In 24 long-term untreated colonies on Oahu, all originating from the free-living population, the bees detected and removed 67% of the 369 artificially infested worker-sealed cells compared to 17% of the 371 control (noninfested) cells (Box 2). Of the remaining unremoved artificially infested cells, 95% had been recapped, that is, investigated, in comparison to 62% of the remaining control noninfested cells. The Oahu honey bee population was found to be highly effective at detecting (see Figure IA in Box 2) and removing (see Figure IB in Box 2) infested worker pupae relative to other mite-resistant populations. The high level of detection and removal of *V. destructor*-infested cells was found to reduce levels of mite fertility (Figure 2C), since, although the mother mite escapes from the cannibalized cell, she loses all her offspring, resulting in low mite reproductive values (Figure 2D**)**, as found in the Oahu population (Table S1 in the supplemental information online). Low fertility rates of *V. destructor* have long been associated with mite-resistant honey bee populations [17]. These observations demonstrate how the Oahu honey bee population has rapidly evolved resistance to *V. destructor* (Figure 2) supporting a previously proposed resistance mechanism, that is, through increased ability to detect and remove mite-infested worker brood [17]. Furthermore, this ability to detect and remove *V. destructor*-infested pupae has been shown to be passed from queens to daughter workers in both Hawaii and the UK [41]. That is, when locally mated mite-resistant queens were used to **requeen** nonresistant colonies, they became resistant. In contrast, when a nonresistant queen was placed into a colony with resistant workers, it succumbed to *V. destructor* [41].

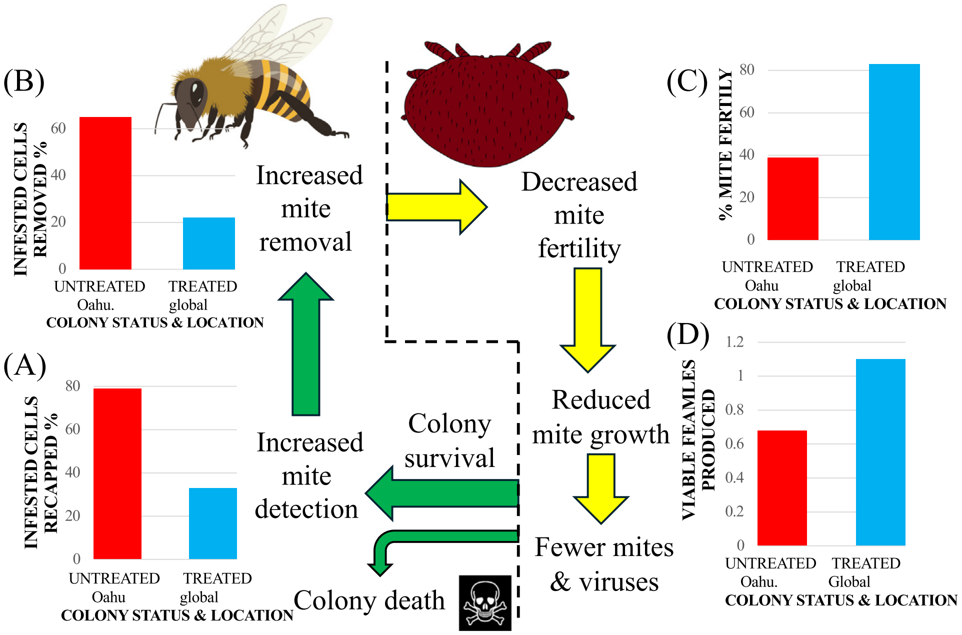

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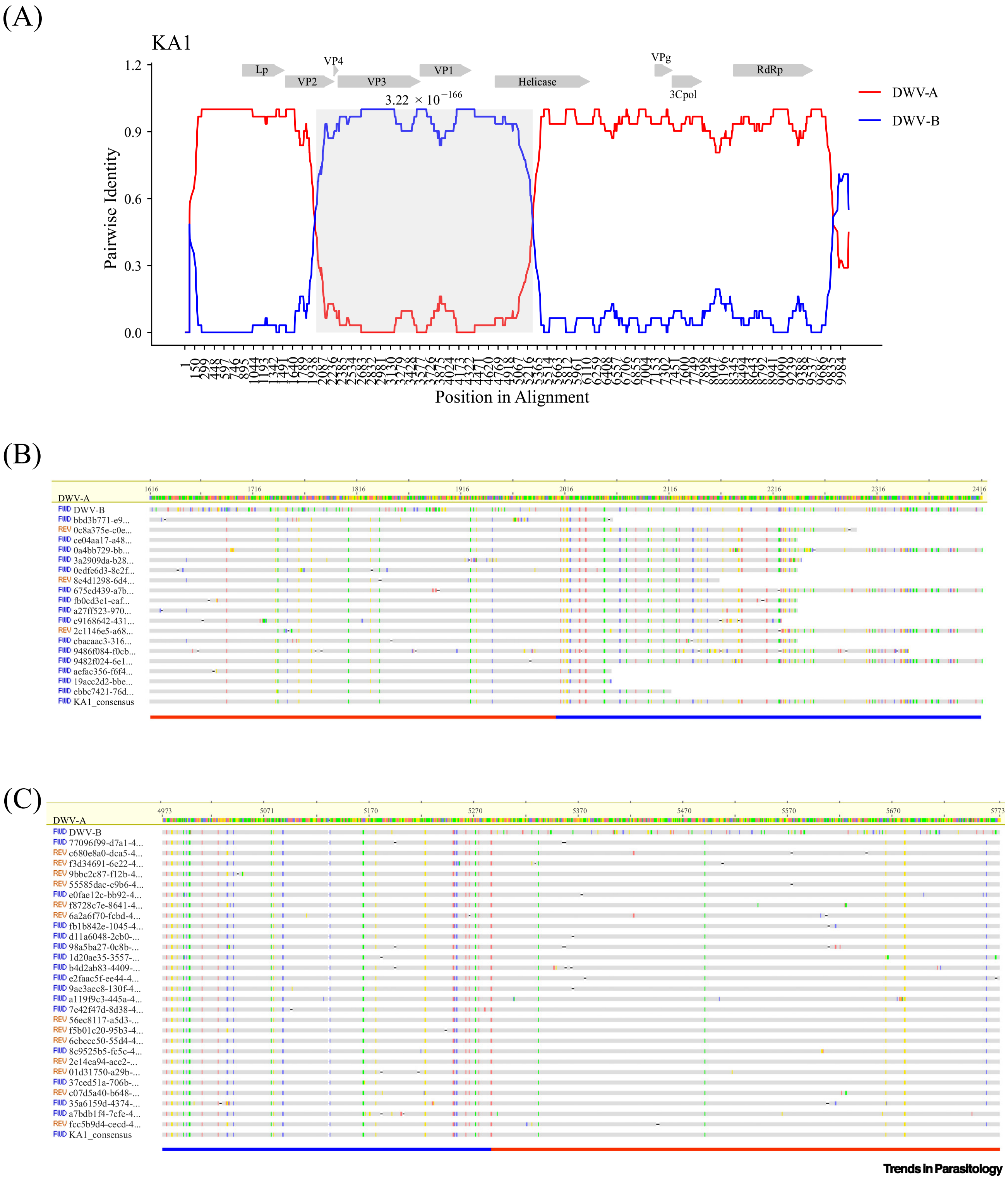
Figure 2. How the various measured traits link together to explain *V. destructor* resistance in the Oahu honey bee population. The data obtained from the resistant Oahu population from untreated colonies (red bars) are compared with the average value from 60 susceptible (treated) populations from around the globe (blue bars) [17]. The left-hand side (green arrows) indicates the levels of key aspects of *A. mellifera* hygienic behavior, while how this affects the mites is shown on the right-hand side (yellow arrows). This shows increased detection of infested cells (A), that is, recapping rates (see Figure IA in Box 1) and removal of mite-infested cells (B) (Figure IB in Box 1) which leads to decreased levels of mite fertility (C) and mite reproduction (D) in the resistant population relative to treated colonies (Table S1). If the mite population and viral load are low enough for the colony to survive, then the cycle repeats, allowing the colony to improve its ability to detect and remove infested cells; otherwise, the colony dies.

Has coevolution of *V. destructor* occurred in Hawaii?

Having originally been a parasite of *A. cerana,* where it reproduced only in drone brood cells, the timing of *V. destructor* reproduction is closely tied to that of drone development. Therefore, reproducing in the brood cells of *A. mellifera* workers, which have a development time 2 days shorter than drones, shortens the window in which mite reproduction can take place. Specifically, there is insufficient time for the third and fourth female offspring to mature, resulting in half of the foundress (mother) mite's reproductive capacity being lost. Thus, since *V. destructor* can produce 18–30 eggs across its lifetime, reducing the number of eggs laid per reproductive cycle and increasing the number of reproductive cycles would provide a significant selective advantage and spread through the mite population quickly, as was seen when resistance to pyrethroids arose [13]. However, in Hawaii, *V. destructor* typically lays 4–5 eggs per reproductive cycle in worker cells, as was found in studies conducted 30–40 years ago [37,42]. Thus, the number of mite offspring has not yet changed in the Hawaiian population (Table S1) relative to previous studies, suggesting that any coevolution to increase its reproductive output has yet to occur. As predicted by the Red Queen hypothesis [43], *V. destructor* must adapt to survive and, interestingly, mites from resistant honey bee populations are approximately 6.8% smaller in body size (dorsal shield area 1.37 mm^2 vs. 1.47 mm^2) than mites from nonresistant populations. This finding was consistent across geographical areas, honey bee subspecies, and beekeeping practices. As body size depends on nutritional availability, the observed pattern may reflect altered developmental environments imposed by resistant hosts, as well as provide a valuable tool in identifying resistant honey bee populations [44].

Evolution of DWV status from full-length variants to recombinants

When *V. destructor* initially became established in Hawaii, it led to DWV-A becoming the dominant virus in infested honey bee colonies, in contrast to colonies on mite-free islands where DWV (multiple variants) was, and continues to be, rarely detected [3,38,39,45]. Several years later, a second, more transmissible [38,46,47] **master variant** (DWV-B) became more common, since it was suggested that it was better adapted to *V. destructor* [48–50], resulting in coinfected colonies along with DWV-A (Box 1 [38,47]), mirroring the situation throughout many areas of the world (e.g., [51–54]). Subsequently, B/A recombinant(s) of DWV arose on both Big Island and Oahu and became more prevalent than either of their parent master variants. Interestingly, whereas in the early years of *V. destructor* establishment, DWV was detected in nearly all colonies, in 2024 the prevalence has decreased to 26/30 colonies tested on Oahu and 26/34 on Big Island. Through analyzing the genomes of DWV circulating in colonies over time, we have been able to more fully understand the changing virus dynamics in the population. In the initial years following *V. destructor* introduction into Hawaii (2009–2012), most colonies were dominated by full-length DWV-A or DWV-B genomes [3,38,47,55] (Box S1, Figures S2 and S3, and Table S2 in the supplemental information online). By 2015–2016, recombinants had become widespread, with mixed infections common in colonies [38], and by 2024, almost all (28/29) samples were dominated by recombinant genomes (e.g., Figure 3, Box S1, and Figures S2 and S3). Samples from both Oahu and Big Island showed similar patterns in the presence and genomic organization of recombinants over time (Figures S2 and S3), despite their different approaches to mite control (Box 1). Interestingly, this recombination structure has arisen independently across the world, for example, France [56], the UK [45], Cuba [57] and the US mainland [58], where, as in this review, it is widespread in mite-infested colonies. Laboratory studies have found DWV recombinants with the genome organization seen here can be more virulent than their parent genomes in pupae and infect bees at higher copy numbers when vectored by *V. destructor* [58]. Furthermore, like severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2), which has become more transmissible over time [59], DWV-B and the B/A recombinant(s) are frequently detected at higher loads than DWV-A when transmitted by *V. destructor*



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[38,58]. Despite this, throughout Latin America, China, and Japan, the DWV-A master variant remains dominant in *V. destructor*-infested colonies, with DWV-B being detected at a very low prevalence [57]. This situation has been observed in both *V. destructor*-resistant (Latin America and Cuba) and *V. destructor*-susceptible (China and Japan) [57] honey bee populations. How and why these two distinct evolutionary DWV pathways have arisen across the world currently remains a mystery.

Finally, there is, as yet, no direct evidence that any of the DWV variants impact the reproductive ability of *V. destructor*, since the developmental times of mite offspring and the reproductive success of the 'DWV-free' mites living on a remote Brazilian island [60] were similar to or lower than those found in mites containing DWV-A, -B, or the B/A recombinant(s) in Hawaii (Table S1), Cuba [19], Brazil, or South Africa [16].

Concluding remarks

The Hawaiian case study has followed the associated changes in the behavior of the honey bees (evolved *V. destructor* resistance), the beekeepers (switched from treating to nontreating), and DWV (recombinants outcompeting the original master variants), all within a single population in Oahu (Box 1). The resistance mechanism that has evolved in the free-living honey bee population on Oahu provides empirical support for the proposed *V. destructor*-resistant mechanism [17] and is the same as, or has strong parallels with, *V. destructor*-resistant populations studied in Norway, Sweden, France [15], the UK [61], Cuba [19], Brazil, and South Africa [16]. Furthermore, the efficient detection and removal of mite-infested worker cells are the same behaviors found in the mite's native host, *A. cerana* [62]. This study has shown that when natural selection is allowed to act, that is, on untreated free-living colonies, coevolution between host, vector, and virus has permitted a new balanced state to be achieved, despite each party evolving in a direction that benefits itself.

Moving forward, revealing the changes that allow colonies to develop resistance to *V. destructor* will provide a deeper understanding of hygienic behavior (see Outstanding questions). However, transferring the findings from this case study to improve honey bee selection programs will remain challenging [63,64] (see Outstanding questions), since the cost involved in allowing large numbers of managed colonies to die before resistance arises—that is, mimicking free-living colonies—is prohibitive. Whereas treating colonies greatly reduces any selection pressure to develop mite resistance. Beekeepers who have moved to treatment-free beekeeping have often collected swarms from long-lived, free-living honey bee populations[iv] as occurred in Oahu. This is partly due to the limited success of *V. destructor*-resistant breeding programs [65], which may be due to not fully understanding the impact drones have on transferring resistant traits (see Outstanding questions). Thus, on Big Island, commercial pressures continue to lock beekeepers into endless treatment cycles.

Interestingly, on Big Island, where miticides are used routinely, similar changes in DWV were seen as in the *V. destructor*-resistant colonies on Oahu (Box 1), that is, dominance of recombinants and reduced DWV prevalence. However, as long as *V. destructor* persists, even in low numbers, it will perpetuate transmission of DWV as well as coevolve toward their host. Hence, when miticide resistance develops, it inevitably leads to increased losses in honey bee populations,

Outstanding questions

Can studying free-living colonies that have adapted to *Varroa destructor* help improve the selection criteria used by bee breeders?

How do *Varroa destructor*-resistant colonies improve their ability to detect and remove infested cells?

What contribution do drones make in passing on resistant traits to the next generation?

How and why are deformed wing virus variants changing across the world?

What are the adaptations of the mites to their evolving hosts?

Figure 3. Evidence for deformed wing virus (DWV) recombination using 'recombination detection program analysis' [66] (A) and inspection of sequencing reads mapping the recombination breakpoints (B,C), showing sample KA1 from Oahu as an example. Regions of similarity to DWV-A are indicated in red, and similarity to DWV-B is shown in blue. Recombination breakpoints are identified through the switches in the dominant variant. Gene positions according to the DWV-A genome (NC_004830.2) are shown above for reference. Alignments are shown in relation to the DWV-A reference genome, with matching bases shown in gray and discrepant bases in color. The DWV-B genome is included in the alignments to identify where sequences shift in homology from one reference to the other.

as occurred in Europe [13] and in the USA [10], so miticides are not a sustainable solution to the *V. destructor* problem. Exploiting the *V. destructor* resistance mechanism that has evolved naturally on Oahu and in several other countries provides a promising alternative to miticides, but more research is needed to understand how to encourage the bees to express these traits more fully and to understand whether drones play a role in transferring mite resistance traits (see Outstanding questions). This would then allow beekeepers in the Northern Hemisphere all the benefits associated with treatment-free beekeeping that is already widely practiced in many Southern Hemisphere countries.

Acknowledgments

We would like to thank S. Nikaido for his assistance, as well as all the beekeepers in Hawaii who provided access to their bees and apiaries. The work was supported by an Apis-M grant awarded to S.J.M. and by Leverhulme Trust Emeritus Professorial Fellowship (EM-2023-042) held by S.J.M. Start-up funding was provided by the University of Minnesota to D.C.S. and by the University of Salford through a University Fellowship start-up funding scheme to L.E.B.

Declaration of interests

The authors declare no competing interests.

Resources

[i] https://Apiaryinspectors.org.

[ii] http://beeinformed.org.

[iii] https://www.youtube.com/watch?v=DWt7hmfJd0k.

[iv] https://www.varroaresistant.uk.

Supplemental Information

Supplemental information associated with this article can be found online at https://doi.org/10.1016/j.pt.2026.04.001

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