

Coevolution while you wait: *Varroa jacobsoni*, a new parasite of western honeybees

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In 1905, the trans-Siberian railroad was completed, allowing through traffic from Moscow to Vladivostok. Doubtless, some of the early passengers from west to east were western honeybees, *Apis mellifera*. Here, the bee was united with its sibling species, *Apis cerana*, from which it had been speciating allopatrically for about 10 000 years. *Apis cerana* is parasitized by *Varroa jacobsoni*, a mite that sucks the blood of developing bee pupae and adults. Some time early this century, mites successfully extended their host range from *A. cerana* to *A. mellifera*. Thus, when European bees were exported back to Russia, they were infested with the mite. Since then, the mite has spread worldwide, so that, today, only Australia, New Zealand and central Africa remain free of it.

Biogeography of *Varroa* populations

Until recently, it was widely believed that *V. jacobsoni* was a fairly homogeneous species. However, recent research using molecular markers indicates that there is detectable genetic variance among populations^{1,2} and that such variance can be correlated with pathogenicity³. These studies reveal that there have been at least two independent introductions of *V. jacobsoni* into the Americas. The first probably occurred in 1971, when infested *A. mellifera* queens and brood combs were taken to Paraguay from Japan. *Apis mellifera* was first introduced to Japan in 1877, and the host shift from *A. cerana* to *A. mellifera* might have occurred around 1957, possibly from bees introduced from Indonesia⁴. This infestation was transported to Brazil in 1972 (Ref. 2). Interestingly, these Japanese mites have never caused mortality of bee colonies in South America. This has often been thought to be because of resistance exhibited by the extant populations of 'africanized' bees there. Although this is true to some extent^{5,6}, mites of Japanese origin are also less pathogenic on European bees in Brazil⁷. The second introduction appears to be of east Russian origin, via Europe. Mites were established in

The mite *Varroa jacobsoni* is a brood parasite of the Asian hive bee, *Apis cerana*. The recent switch in host from *A. cerana* to the western honeybee, *Apis mellifera*, offers an exceptional opportunity for studying preadaptation and host-parasite relations. The fact that this host shift appears to have happened on at least two separate occasions, with differing outcomes, must be unique. At another level, the rapacious spread of this mite throughout the world is testimony to the ineffectiveness of international quarantine laws.

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A. mellifera populations in eastern Russia as early as 1952 (Ref. 8). It is unknown how Russian mites got to America, but they first appeared in Wisconsin in 1987 (Ref. 9).

Evolutionary history

Like all animals that build nests, bees are hosts to a wide variety of mites¹⁰. Many mites are cosmopolitan species that are only occasionally found in association with bee nests, but mites of at least 30 lineages have specialized in living with bees. Most mite species associated with bee nests are saprophagous or cleptophagous (Box 1). Only very few have evolved to become parasitic and, with one exception (*Acarapis*),

these groups appear to have arisen from predatory lineages. Twelve genera of the family Laelapidae are predators of stingless bees (Meliponinae), and it is from this general group that the brood parasites (Varroidae) of honeybees (Apinae) appear to have evolved¹⁰.

The fact that brood parasitism has only evolved in the honeybees and not in the closely related stingless bees is difficult to understand. Nevertheless, with the exception of *A. mellifera*, all honeybee species appear to have parasitic brood mites¹⁰. Interestingly, although only *A. mellifera* has escaped natural parasitism, this species is highly susceptible to at least two mites (Table 1).

Life cycle

On *A. mellifera* worker brood, the life cycle (Fig. 1) of *Varroa* begins with a mature mated female entering a brood cell of the host just before the cell is capped. After the cell is capped, this 'mother' mite hides in the larval food at the bottom of the cell for about five hours, by which time the host will have adopted an elongated posture along the length of the cell and commenced to spin a cocoon and feed on the brood food. This releases the mite from the brood food, whereupon it begins feeding on the host's haemolymph¹¹. About 60 h after the cell is capped, the mother mite will lay her first egg on the wall of the cell near the top, where it is less likely to be damaged when the host moults¹². Because *Varroa* is haplodiploid, unfertilized eggs result in males and fertilized eggs result in females. The mother refrains from fertilizing her first egg, which therefore results in a male. Up to five more fertilized (female) eggs will be laid at approximately 30-h intervals. The mother maintains a communal feeding site for her brood as the nymphs are unable to penetrate the skin of the host¹¹.

The sexual proclivities of *Varroa* mites are idiosyncratic to say the least¹³. *Varroa* eggs hatch within 36 h (Ref. 12).

Box 1. Glossary

- Cleptophagous:** eats pollen and other nutrients stored by bees.
Kairomone: analogous to a hormone, a compound secreted by an individual of one species that modifies the behaviour of individuals in another species.
Phoretic: living on a host without causing harm.
Saprophagous: eats hive detritus, especially fungi growing thereon.

Nymphs develop extraordinarily rapidly, and the male is ready to mate within 190 h of being laid. The mother mite prepares a rendezvous point for her offspring, consisting of a mound of her faeces placed on the cell wall, and it is here that the male copulates with his sisters¹¹. Rematings are frequent with the first sister, until the second matures, whereupon the male concentrates his attentions on her.

Adult mated female mites emerge from the cell along with the host. It is important that the mite does not kill the host so that the bee can emerge from the cell, thus liberating the parasites. The mother mite can invade a second cell, and has been observed to go through up to eight cycles of reproduction¹⁴, although 1.5–3 cycles is more typical^{14,15}. A single mother infesting *A. mellifera* will produce, on average, about 1.1–2.5 mated female offspring in drone cells^{13,16} and 0.83–1.3 in worker cells^{16–18}.

Host-parasite relationships

...with A. cerana

The association between *V. jacobsoni* and *A. cerana* appears to have been a long one, and the mite rarely causes harm. On its natural host, mite reproduction is almost exclusively restricted to male (drone) brood¹⁹. Male brood is frequently absent from colonies and is restricted in numbers even when it is present. Thus, during those periods when males are absent, the mites must exist phoretically (Box 1) on adult workers, and are unable to reproduce because of the lack of male brood. Further, if multiple mites invade a drone cell, emergence rates of the host are reduced to 28%. Any mites that do parasitize worker cells are likely to be detected and eliminated, and workers groom phoretic adult mites from each other²⁰. Hence, mite populations are held at a low level in *A. cerana*.

...with A. mellifera

Conversely, effects on *A. mellifera* colonies are usually catastrophic. Although mites have a strong (on average eightfold) preference for parasitizing drone brood¹⁶, they successfully reproduce in worker cells, especially when drone brood is absent or heavily parasitized^{21,22}. Reproduction on worker brood leads to an exponential increase in mite numbers^{12,14,22,23}. Mite reproduction on worker brood is debilitating to the emerging worker, and the mite's feeding

helps spread viral infections among bees. Consequently, heavy mite infestations kill the colony.

Key variables in the population dynamics of *Varroa*

Development time

Fries *et al.*²² and Martin and Kemp¹⁴ have developed important simulations of *Varroa* population dynamics, including the variables listed in Table 2. Sensitivity analysis involves repeatedly running a simulation while altering each variable in turn in order to determine those that are most important to the model's outputs. Such analyses have shown that the number of fertile offspring produced per cell and the number of reproductive cycles achieved by each mite have the largest impact on mite populations. An important factor in determining how many fertile offspring will be produced appears to be the development time of the host. Development time is defined here as the period from when the brood cell is sealed to the moment when the adult bee emerges. Most *A. mellifera* worker bees will emerge about 280 h after their cell is capped²⁴,

Table 1. Mites associated with various species of honeybee (*Apis*)

Original host(s)	Mite species	Geographical range of host	Refs
<i>A. cerana</i>	<i>Varroa jacobsoni</i> ^a <i>Varroa underwoodi</i>	Asia west of the Wallace line, Nepal and Borneo	34,35
<i>A. nuluensis</i>	<i>Varroa jacobsoni</i> ^a <i>Varroa underwoodi</i>	Borneo	36
<i>A. nigrocincta</i>	<i>Varroa underwoodi</i>	Sulawesi	35
<i>A. koschevnikovi</i>	<i>Varroa rindereri</i> <i>Varroa jacobsoni</i>	Borneo	37
<i>A. mellifera</i>	None reported	Europe and Africa	
<i>A. florea</i>	<i>Euvaroa sinhai</i>	Middle East, Himalayas, SE Asia and Java	38
<i>A. andreniformis</i>	<i>Euvarroa wongsiri</i>	SE Asia, Borneo and the Philippines	38
<i>A. dorsata</i>	<i>Tropilaelaps clareae</i> ^a <i>Tropilaelaps koenigerum</i>	Southern Asia generally, including the Philippines	39
<i>A. laboriosa</i>	<i>Tropilaelaps clareae</i> ^a <i>Tropilaelaps koenigerum</i>	Nepal	39

^aThese species can successfully reproduce on *A. mellifera*.

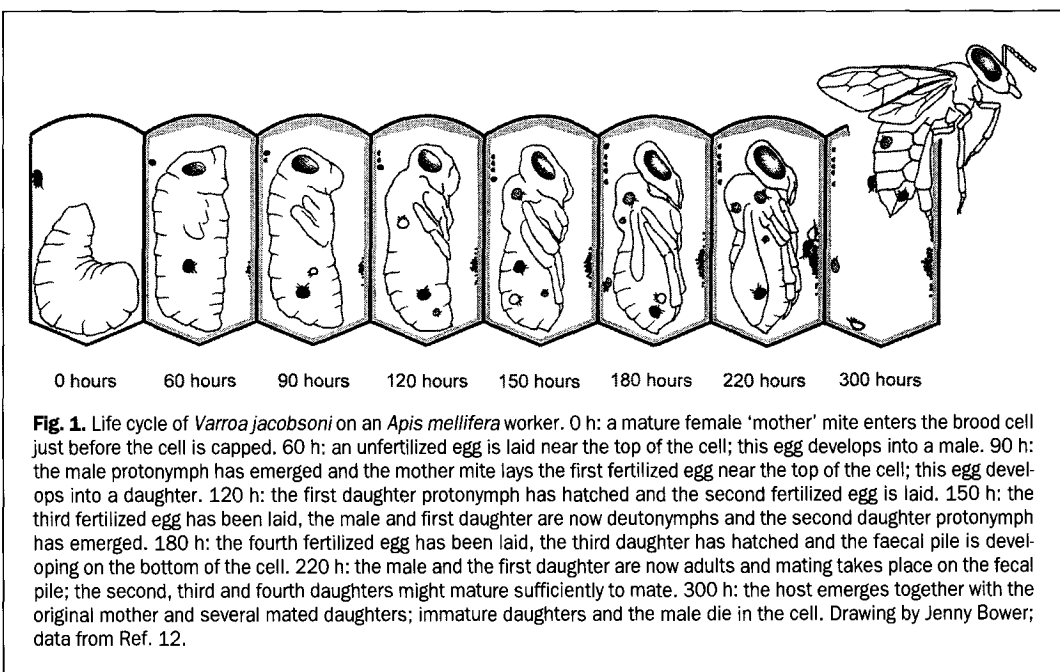


Table 2. Critical variables and typical values for the development of the mite *Varroa jacobsoni* in an *Apis mellifera* (honeybee) colony in the northern hemisphere^a

Parameter	Typical values	Refs
Worker development period	492 hours	12
Drone development period	576 hours	16
Worker postcapping period	282 hours	12
Drone postcapping period	360 hours	16
Area of worker and drone brood	Varies over season ^b	22
Mite phoretic period	5.9 days	
Mite preference for drone cells over worker cells	12.1 times	
Attractive period of worker brood for mother mite	20 hours before capping	
Attractive period of drone brood for mother mite	50 hours before capping	
Mite fertility on worker brood ^c	1.01	27
Mite fertility on drone brood	2.91	27
Number of reproductive cycles of mite	1.5 to <2	15
Number of female offspring produced in a worker cell by reproducing mothers	1.45	12
Number of female offspring produced in a drone cell by reproducing mothers	3.90	16
Density-dependent infestation level for worker cells ^d	3	
Density-dependent infestation level for drone cells ^e	6	
Factor by which worker removal of infested brood decreases the number of offspring produced in worker and drone cells	0.95	
Winter mortality of mite population during nonbrood rearing period	0.002 per day	27
Mortality of phoretic phase mites during brood rearing	0.006 per day	27

^aValues taken from the population dynamics model of Fries *et al.*²² except where noted.

^bWorker brood = 300–1000 cm² of brood; drone brood = 0–200 cm².

^cProportion of mites that produce potentially fertile offspring.

^dAverage number of mites per cell at which no offspring are produced in a worker cell.

^eAverage number of mites per cell at which no offspring are produced in a drone cell.

whereas the first female adult mite appears about 223 h after cell capping and the second after 258 h (Ref. 12). Therefore, up to two, possibly three, daughter mites can be produced and mated before the bee emerges. Obviously, bee genotypes with shorter development times will potentially reduce the rate at which mite populations increase. For this reason, the length of the postcapping period has been recognized by bee breeders as a potentially important character to select for resistance to *Varroa*^{25,26}. Indeed, it has been suggested that some naturally occurring strains of *A. mellifera* have a sufficiently short postcapping time that development of *Varroa* populations is retarded^{24–26}. However, some recent reports have played down the relative importance of the postcapping period in *Varroa* population dynamics (e.g. Ref. 27).

Failure to oviposit on *A. mellifera*

A second key factor in population dynamics is the proportion of mites that fail to reproduce in worker cells. As already mentioned, *V. jacobsoni* is poorly adapted to its new host, *A. mellifera*. Commonly, mother mites fail to oviposit on pupae of *A. mellifera*²⁸. This might be because the signals that initiate egg development in the mite are poorly expressed in *A. mellifera*. Furthermore, the high mortality of males on *A. mellifera* means that a significant proportion of female mites emerge from cells unmated. Although these mites enter new host cells in the normal way, they fail to oviposit²⁸.

Anderson²⁹ has shown that some New Guinea populations of *V. jacobsoni* fail to oviposit on *A. mellifera* at all. Mites (at least some of which can be safely assumed to be mated) enter brood cells in the normal way, but then wait in vain for the putative signal from the host that initiates egg development. What this signal is remains unclear. An early report³⁰ suggested that juvenile hormone (JH III) levels in the developing bee might elicit oviposition, but this now seems unlikely³¹. What is known is that failure to oviposit can occur because some *Varroa* genotypes fail to recognize

the signal. Very recently, this was decisively demonstrated by Anderson and Fuchs³, who divided a shipment of Australian bees between New Guinea and Germany. German *Varroa* happily reproduced on the Australian bees, but in New Guinea the mites failed to oviposit. The difference is not environmental. Until recently, Javanese *Varroa* also failed to oviposit on *A. mellifera*²⁹. Since 1993, however, a genetically distinct strain of *V. jacobsoni* has emerged in Java that can successfully reproduce on *A. mellifera* in the tropics. This has occurred either because of an independent host shift or because a virulent strain was introduced from elsewhere in Asia³².

It is interesting to note that the type specimen of *V. jacobsoni* was described from *A. cerana* colonies in Java. Given that the original Javanese mites were unable to reproduce on

*A. mellifera*²⁹, we have the intriguing possibility that the mite that has spread throughout the world is not in fact *V. jacobsoni* but some other closely related species from further north (D. Anderson, pers. commun.). Sequencing work would resolve this taxonomic puzzle.

Where from here?

Predictions about the future impacts of *Varroa* are bound to be wrong, so I will refrain from making any except to say that it is unlikely that Australia will remain free of the mite. Populations of *Varroa*-infested *A. cerana* are now present in Australian territories in the Torres Strait, and in 1998 a single (uninfested) *A. cerana* colony was located in Darwin. The origin of this colony is unknown. Of course, the *A. cerana* population in New Guinea is host to a strain of mite that is harmless to *A. mellifera*^{3,29}. This situation could change if selection brings about a new (fourth?) host shift that results in a strain that can infest *A. mellifera*, or if *A. mellifera*-virulent strains colonize New Guinea from Java.

Perhaps more interesting than New Guinea is the situation in the Americas. Here, two strains of *Varroa* coexist – one highly destructive, one potentially benign. The relative fitness of these two strains within one colony is unknown. One might predict that the less virulent Japanese strain would be less competitive than the more virulent Russian one. However, this is not necessarily the case. If the Japanese strain does prove to be more, or equally, competitive than the Russian strain, intriguing possibilities for biological control by deliberately releasing Japanese mites into commercial colonies should be investigated. At a less practical level, because there are reliable nuclear and mitochondrial markers² for both strains, it should be possible to track the progress of these competing populations.

Bee breeders will continue to focus on selecting strains of bees that have a short development time and are less attractive to the parasite. In an ironic twist, scientists from the US Department of Agriculture are surveying *A. mellifera*

populations in eastern Russia for resistance to *Varroa*⁸. Certainly, these bees have been exposed to *Varroa* for the longest period, and, if natural selection can produce tolerance to *Varroa*, then it is in Russia that this resistance is most likely to be found. Early indications are that bees imported from Russia show considerable promise⁸. A second promising approach to breeding for resistance is the selection of 'hygienic' strains of bee, which detect and remove infested pupae before the mites can reproduce³³.

Other important avenues for research will involve elucidating the precise nature of the kairomones (Box 1) that cause *Varroa* to enter a brood cell and those that stimulate oviposition. If these compounds can be identified, then technologies for residue-free chemical abatement of *Varroa* could become a reality.

Interactions between honeybees and their parasitic mites offer a superb system for studying host-parasite relationships after a recent host shift. The fact that these mites are of considerable economic importance means that researchers should be relatively well funded, and we can expect that the *Varroa* story will continue to unfold.

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