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Biology and control of *Varroa destructor*

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ABSTRACT

The ectoparasitic honey bee mite *Varroa destructor* was originally confined to the Eastern honey bee *Apis cerana*. After a shift to the new host *Apis mellifera* during the first half of the last century, the parasite dispersed world wide and is currently considered the major threat for apiculture. The damage caused by Varroosis is thought to be a crucial driver for the periodical colony losses in Europe and the USA and regular *Varroa* treatments are essential in these countries. Therefore, *Varroa* research not only deals with a fascinating host–parasite relationship but also has a responsibility to find sustainable solutions for the beekeeping.

This review provides a survey of the current knowledge in the main fields of *Varroa* research including the biology of the mite, damage to the host, host tolerance, tolerance breeding and *Varroa* treatment. We first present a general view on the functional morphology and on the biology of the *Varroa* mite with special emphasis on host–parasite interactions during reproduction of the female mite. The pathology section describes host damage at the individual and colony level including the problem of transmission of secondary infections by the mite. Knowledge of both the biology and the pathology of *Varroa* mites is essential for understanding possible tolerance mechanisms in the honey bee host. We comment on the few examples of natural tolerance in *A. mellifera* and evaluate recent approaches to the selection of *Varroa* tolerant honey bees. Finally, an extensive listing and critical evaluation of chemical and biological methods of *Varroa* treatments is given.

This compilation of present-day knowledge on *Varroa* honey bee interactions emphasizes that we are still far from a solution for *Varroa* infestation and that, therefore, further research on mite biology, tolerance breeding, and *Varroa* treatment is urgently needed.

1. Introduction

The hemophagous honey bee mite *Varroa destructor* is still the greatest threat for apiculture. No other pathogen has had a comparable impact on both beekeeping and honey bee research during the long history of apiculture. There are several reasons for this unique status of *Varroa* mites:

(1) *V. destructor* is a new parasite of the honey bee *A. mellifera*. Therefore, a balanced host–parasite relationship is lacking and beekeepers do not have long-term experience in dealing with this pest.
(2) *V. destructor* has spread almost worldwide within a short time period and it may now be difficult to find a "*Varroa* free" honey bee colony anywhere, other than in Australia.
(3) Without periodic treatment, most of the honey bee colonies in temperate climates would collapse within a 2–3 year period.
(4) Regular treatments increase the costs for beekeeping and the risk of chemical residues in bee products.
(5) The *Varroa* mite is considered a crucial factor in the decreasing numbers of beekeepers and honey bee colonies in Europe; together with the worldwide decline of natural pollinators, the *Varroa* mite may exacerbate future problems for pollination (De la Rua et al., 2009).

Therefore, *Varroa* research is a challenge for all scientists working in the fields of apiculture, insect pathology and acarology. We will present a general view on the biology of the *Varroa* mite with special emphasis on recent results on host–parasite interactions, breeding honey bees for tolerance, and treatment for *Varroa* infestation.

2. Taxonomy, morphology and geographical distribution

The mite which is responsible for the clinical symptoms of "Varroosis" in *A. mellifera* belongs to the species *V. destructor*, which was assumed to be *Varroa jacobsoni* until the year 2000 (Anderson

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Table 1
Species and haplotypes of the genus *Varroa* parasitizing on honey bees. Only *Varroa destructor* with two haplotypes on *Apis mellifera* is of economic importance.

Parasite	Host	Haplotypes	Pathogenicity
Varroa destructor	*Apis mellifera*	Japan/Thailand	+
		Korea	++
		China	–
		Korea	–
	Apis cerana	Japan/Thailand	–
		Nepal	–
		Vietnam	–
Varroa jacobsoni	*Apis cerana*	Ambon	–
		Bali	–
		Borneo	–
		Flores	–
		Java	–
		Lombok	–
		Sumatra	–
		Sumbawa	–
		Malaysia	–

and Trueman, 2000). Therefore, all *Varroa* articles from the last century refer to *V. jacobsoni* although in nearly all cases *V. destructor* was the research subject.

The Genus *Varroa* is currently represented by at least four species of obligate ectoparasitic mites (Table 1):

- *Varroa jacobsoni* Oudemans was first described as a natural ectoparasitic mite of the Eastern honey bee *A. cerana* in Java (Oudemans, 1904) and has a wide distribution on this bee throughout Asia (Koeniger et al., 1981) and *Apis nigrocincta* in Indonesia (Anderson and Trueman, 2000; Hadisoesilo and Otis, 1998).
- *Varroa underwoodi* was first described from *A. cerana* in Nepal (Delfinado-Baker and Aggarwal, 1987).
- *Varroa rindereri* was described from *Apis koschevnikovi* in Borneo (De Guzman and Delfinado-Baker, 1996).
- *V. destructor* was described both from *A. cerana* (original host) and *A. mellifera* (new host), formerly erroneously also classified as *V. jacobsoni* (Anderson, 2000; Anderson and Trueman, 2000).

2.1. V. jacobsoni and V. destructor: redefinition and worldwide spread

Although *Varroa* mites from different populations are physically alike, their virulence toward *A. mellifera* is not uniform. The greatest variation is associated with *V. jacobsoni* of Javanese origin, from which the species was first described (Oudemans, 1904). These mites completely lack the ability to reproduce on *A. mellifera* (Anderson, 1994; Anderson and Sukarsih, 1996) and their mitochondrial DNA (mtDNA) cytochrome oxidase I (CO-I) gene sequences differ from those of phenotypically similar mites that reproduce on *A. mellifera* in Europe (Anderson and Fuchs, 1998). Other reports confirm the variation among *V. jacobsoni* populations (De Guzman et al., 1998; De Guzman and Rinderer, 1999; Kraus and Hunt, 1995) and, therefore, it was suggested that *V. jacobsoni* may be more than one species (Table 1). This hypothesis was later confirmed by Anderson and Trueman (2000):

(1) *V. jacobsoni* is a species complex with two distinct sibling species and was redefined by body size and mtDNA gene sequences (GenBank database; *V. jacobsoni*: AF106902–AF106910; *V. destructor*: AF106897–AF106901). The mean body length and body width is 1063.0 μm (±26.4 μm) and 1506.8 μm (±36.0 μm), respectively. The mtDNA CO-I gene sequences differ by 6.7% from those of *V. destructor* (Anderson and Fuchs, 1998). At least 9 haplotypes are described (Anderson and Trueman, 2000; Warrit et al., 2006), all parasitizing *A. cerana*. *V. jacobsoni* is only a vagrant guest on *A. mellifera*.

(2) *V. destructor*, the new species, is represented by mites of the Japan/Thailand-Vietnam clade. Mites of Korean haplotype parasitize *A. mellifera* worldwide, and are significantly larger and reproductively isolated from the *V. jacobsoni* haplotypes (Anderson and Trueman, 2000). At least six other haplotypes are described, of which only the Japanese/Thailand haplotype also infests and reproduces on *A. mellifera*. However, this haplotype has a more restricted distribution than the Korean haplotype and is considered less virulent (De Guzman and Rinderer, 1999). The Korean type has worldwide spread on *A. melllifera*, while the Japanese/Thailand type has only been reported from *A. mellifera* colonies in Japan, Thailand and North- and South-America (Anderson and Trueman, 2000; De Guzman et al., 1998; Garrido et al., 2003; Muñoz et al., 2008). By the use of microsatellites, Solignac et al. (2003, 2005) found almost no polymorphism within the two haplotypes and considered them a quasi clonal population structure.

Therefore, the only mite of economic importance is *V. destructor*, which successfully shifted from the original host, *A. cerana* to the Western honey bee, *A. mellifera*. It is not surprising that the new host lacks features which obviously established a stable host–parasite relationship in *A. cerana* during a long period of coevolution (Rath, 1999). The details of the host shift are unclear. Most likely this shift occurred when *A. mellifera* colonies were transported to Eastern Russia or the Far East in the first half of the past century which led to a sympatric distribution of both honey bee species (Oldroyd, 1999) and might have allowed the parasite to infest the new host. *Varroa* mites were found in the eastern coastal region of the USSR (1952), in Pakistan (1955), Japan (1958), China (1959), Bulgaria (1967), South-America (Paraguay, 1971), Germany (1977: Ruttner and Ritter, 1980) and the first record for the United States originates from 1987 (De Guzman and Rinderer, 1999). Today, *V. destructor* is almost cosmopolitan, but has not yet been found in Australia (AQIS, Australian Government: http://www.daff.gov.au/aqis/quarantine/pests-diseases/honeybees).

2.2. Morphology

In relation to the biology of *V. destructor*, the genital system and the sensory organs of the parasite are of particular interest. The following overview will, therefore, focus on these two aspects of mite morphology.

Varroa mites show a distinct sexual dimorphism (Ifantidis, 1983) with many morphological adaptations to their host (Fig. 1). A common feature of both sexes is the division of the body into two well-defined parts, the idiosoma and the gnathosoma. The idiosoma comprises the larger part and one dorsal shield and different ventral shields. The female mites have a flattened, ellipsoidal idiosoma with greater width than length. The legs of the female are short and strong, and show specialized structures, the apoteles, for adherence to the host (De Ruijter and Kaas, 1983). The dorsal and ventral shields are highly sclerotised and show a reddish-brown coloration. Thin and flexible membranes between the shields enable the mite to dilate during feeding and egg formation. The male body is pear shaped and shows only weak sclerotisation, which is mainly present in the legs and the dorsal shield. Males are clearly smaller than females in all developmental stages. The legs of the males are longer in relation to the body size than the legs of females.

The gnathosoma is situated anteroventrally, forming the mouthparts which consist of two sensory pedipalps and two chelicerae. The chelicerae are formed by three segments, the basal,

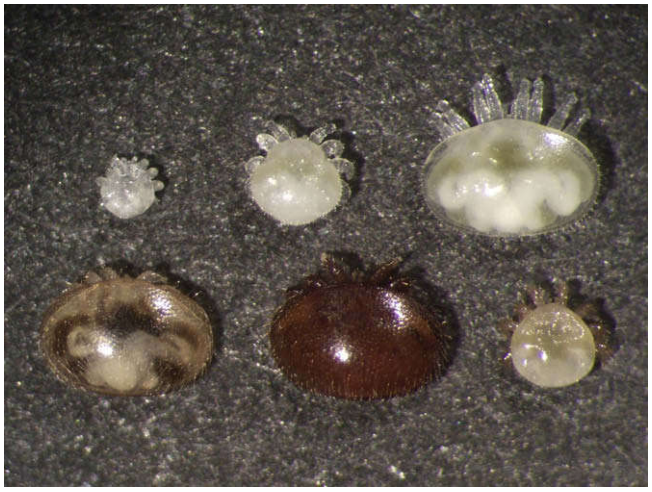

Fig. 1. The normal composition of a "*Varroa* family" within a honey bee worker brood cell, approximately 11 days after the capping of the brood cell. Upper row from left to right: Protonymph, deutonymph, deutochrysalis. Lower row from left to right: freshly moulted young female, mother mite, adult male.

the middle and the distal digit. The last digit is movable in females and has two small teeth. In males the movable digit is transformed into a spermatodactyl, a cannula-like structure that allows the transfer of sperm into the female genital tract.

The female genitalia are divided into two systems: the first one is formed by an ovary, a uterus and a vagina, which leads to the genital orifice through which the eggs are released. The genital opening is situated between the second pair of legs. The second part of the genital system permits the reception and maturing of sperm. It is formed by a pair of pores, the solenostomes, which are located on each side between coxae III and IV. The solenostomes open up into tubuli followed by the rami. The rami coalesce in the center of the female body and pass into the sperm duct. The sperm duct leads to the spermatheca, a large sac-like organ (Alberti and Hänel, 1986), which serves as a reservoir for the spermatozoa until the fertilization of eggs. The camera spermatica forms the connection between the ovary, the spermatheca and the uterus. The ovary with the two lyrate organs is located ventral to the spermatheca (De Ruijter and Kaas, 1983). Later, the oocytes develop within the ovary, while the lyrate organ has a nutritional function (Alberti and Zeck-Kapp, 1986).

The male genital system is formed by a single testis in the rear of the body. From the testis, two vasa deferentia emerge and coalesce to the unpaired ejaculatory duct which opens at the edge of the sternal plate between the second pair of legs. The sperms belong to the ribbon type (Alberti, 1980a, 1980b), and pass through eight stages of maturation, six in the body of the male and two after mating in the inseminated female.

The sensory organs of *Varroa* females are reviewed in detail in Dillier et al. (2006). The whole body, including legs and mouthparts, is covered with different types of hairs; at least some have mechano- and chemoreceptive functions (Milani and Nannelli, 1988). The front legs are rarely used for movement but are frequently raised in the air like the antennae of insects (Rickli et al., 1992). On the tarsi of the front legs is a sensory pit organ (Ramm and Böckeler, 1989) that consists of nine internal sensilla with nine longer hair sensilla surrounding the organ, similar to the Haller's organ in ticks. Some of the sensilla are wall pore sensilla (Ramm and Böckeler, 1989) and bear similarity to the olfactory sensilla of other arthropods, presumably for the perception of volatiles. Other sensilla are non-pore sensilla and serve as hygro- and thermo-receptors, whereas the morphology of a third type indicates a gustatory function. The sensilla surrounding the pit are divided in two groups. The first group shows characteristics of contact chemo-receptors indicating a gustatory role; the second group has structures similar to sensilla, which in arthropods serve as chemo-receptors with an additional thermoperceptive function. Chemoreceptive sensilla were also described on he palptarsus (Liu and Peng, 1990) with large setae on the palptarsus of the same type as the gustatory sensilla in the tarsal pit organ, and smaller setae which may have an olfactory function. The olfactory sensilla allow the reception of a broad range of chemicals. In electrophysiological approaches, for instance, salicylaldehyde, methylsalicylate, and benzaldehyde – a known volatile in royal jelly – elicited an electrophysiological response in the sensilla (Endris and Baker, 1993).

3. Mite biology and behavior

The host finding and reproductive behavior of *V. destructor* is essential for understanding the population dynamics of the parasite, but it is also of particular significance for the beekeeping practice. Certain cues for the orientation of the mites could be used for development of biological control methods such as traps, repellents or mating disruption by certain pheromones. The control of reproduction of a parasite is, in general, a crucial point for the stability of a host–parasite relationship (Walter and Procter, 1999), which, obviously, is also the case in the honey bee-*Varroa* arms race (Fries et al., 1994). Therefore, knowledge of factors that trigger the mite's reproduction might help for selective breeding of tolerant honey bees.

3.1. Life cycle

V. destructor is closely linked to its honey bee host and lacks a free living stage. There are two distinct phases in the life cycle of *V. destructor* females: A phoretic phase on adult bees and a reproductive phase within the sealed drone and worker brood cells (Figs. 2–4). Males and nymphal stages of the mite are short lived and can only be found within the sealed brood cells. On the adult bees the *Varroa* females are transported to brood cells for their reproduction or spread by foraging and swarming bees (Kuenen and Calderone, 1997). On the adult bees the *Varroa* female usually is hidden under the sternites of the bee (Fernández et al., 1993). The mites suck substantial amounts of hemolymph from both the adult bees and from the preimaginal host stages within the sealed brood cells

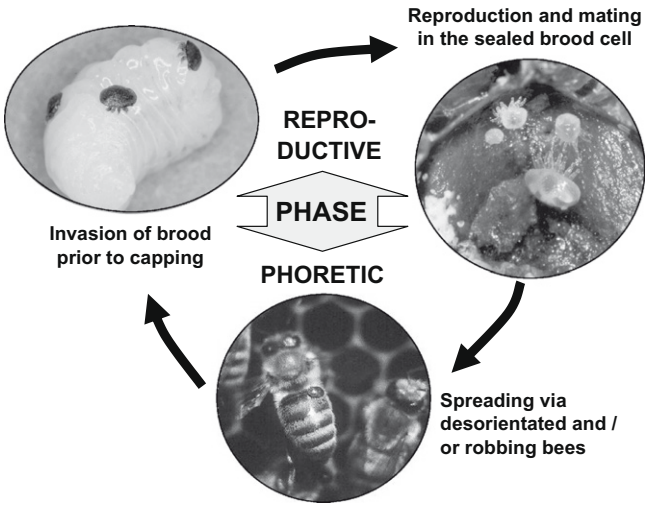

Fig. 2. Simplified life cycle of the *Varroa* mite. *Varroa* females switch between a phoretic phase on adult bees and a reproductive phase within the sealed honey bee brood cells. The nymphal stages and the males are short lived without a phoretic phase outside the brood cells.

Fig. 3. A phoretic female *Varroa* mite on the thorax of a hive bee.

(De D'Aubeterre et al., 1999; Donzé and Guerin, 1994; Garedew et al., 2004; Tewarson and Engels, 1982).

3.2. Orientation and host finding

Except for distribution by swarms or foragers the *Varroa* mites spend their whole life within the dark honey bee nest, preferably within sealed brood cells (Boot et al., 1993). *Varroa* mites are able to perceive light and vibration (Kirchner, 1993). However, there are no indications that these senses are used for orientation or host finding. This may also be true for sensitivity to temperature. Depending on the test system *Varroa* mites prefer temperatures between 26 and 33 °C (Le Conte and Arnold, 1987, 1988; Pätzold and Ritter, 1989; Rosenkranz, 1988), which are significantly lower than the normal temperature in the brood nest of approximately 34.5–35 °C (Becher and Moritz, 2009; Rosenkranz and Engels, 1994). *Varroa* mites are able to discriminate temperature differences of about 1 °C (Le Conte and Arnold, 1987). It was assumed that *Varroa* females preferably invade colder brood cells at the periphery of the brood nest; however, there is no solid evidence for this hypothesis and the preference for low temperature may, at least in part, be due to the artificial test conditions in a laboratory temperature gradient (Dillier et al., 2006).

Without doubt, chemical orientation plays the crucial role during all parts of the *Varroa* life cycle. This becomes obvious in the preference behavior of female mites for certain host stages. As a parasite without a free living phase, the *Varroa* mite sticks either to the adult bees or stays within a brood cell. For the reproductive success of the *Varroa* females, two host stages are of crucial importance: the suitable adult bee which transports the mite to non-sealed brood cells and the 5th instar larvae in brood cells shortly before cell capping.

In the case of adult bees *Varroa* females are obviously able to recognize the age and/or function of the adult bee. Shortly after leaving the brood cell on a young bee, the mites preferentially infest nurse bees for transport to the brood cells (Kraus, 1993; Kuenen and Calderone, 1997). Freshly hatched infested bees are less attractive than older ones and the middle age nurse bees are the most infested group of adult bees in breeding colonies (Kraus et al., 1986; Steiner, 1993). This may be an adaptive strategy for the *Varroa* females to increase their reproductive success. It is assumed that age and/or task specific patterns of cuticular hydrocarbons of the adult bee are used for the selection of the optimal host. Age dependent patterns have been described for drones (Wakonigg et al., 2000) and workers (Chiroudi et al., 1997). However, confirmation that mites use the hydrocarbon pattern of the bee's cuticle for host selection is lacking.

Additional details concerning the recognition of a suitable larval host are known: A long established phenomenon is the 8–10-fold higher infestation rates of drone brood compared to worker brood (Boot et al., 1995b; Calderone and Kuenen, 2001; Fuchs 1990). Several reasons for this unequal distribution have been discussed. Within the honey bee colony, worker larvae are infested 15–20 h prior to cell capping, and drone brood 40–50 h (Boot et al., 1992; Ifantidis et al., 1988), which may be one of the reasons for the higher invasion rate into drone brood cells. Another fact that contributes to the higher infestation of drone larvae is a more frequent and intensive tending of the drone larvae with the consequence that mites on nurse bees have a significantly more opportunity to reach a 5th instar drone brood cell than a worker cell (Calderone and Kuenen 2003; Fuchs 1990).

The attraction of *Varroa* females to several fractions of the extract from the larval cuticle has been confirmed in different bioassays. Le Conte et al. (1989) first described a kairomonal effect of three methyl- and ethyl esters in an olfactometer, which was confirmed by further experiments (Le Conte et al., 1994; Trouiller et al., 1992). These esters of straight-chain fatty acids also act as brood pheromones and elicit the capping behavior in hive bees (Le Conte et al., 1990). The secretion of the esters by the honey bee larvae shows a clear ontogenetic pattern with a distinct maximum at the 5th instar during the time of cell capping (Trouiller et al. 1991). Drone larvae produce slightly higher quantities over a longer time period, which also supports the preferred infestation of drone brood (Calderone and Lin, 2001; Le Conte et al., 1989). However, the pheromonal effect of these substances is more apparent than the kairomonal effect. After application of the esters to

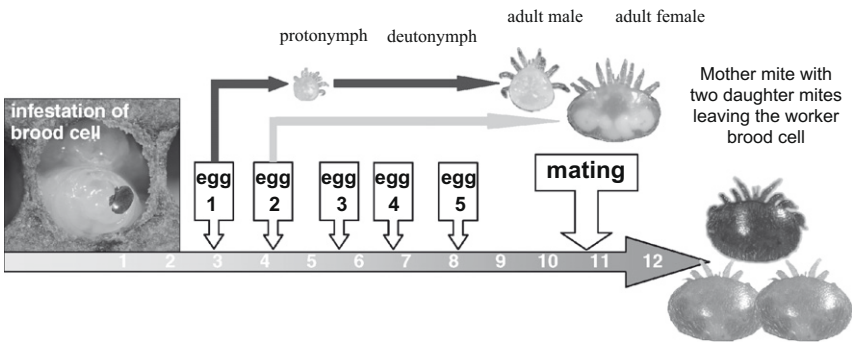

Fig. 4. The reproductive cycle of *Varroa destructor* within the sealed honey bee worker brood cell, with the normal sequence of the sexes of mite offspring. A female mite enters the brood cell shortly before capping; approximately 3 days later the first male egg is laid followed by up to four female eggs. Depending on the post-capping period, one or two mature daughter mites will leave the brood cell together with the mother mite and the hatching bee. The numbers on the arrow correspond to the days after cell capping.

dummies, Zetlmeisl and Rosenkranz (1994) confirmed the pheromonal but not the kairomonal effect. By the use of a servosphere, which measures the specific movements of the mites during the application of volatile substances, Rickli et al. (1994) found only weak reactions of mites toward methyl palmitate, but a strong response toward palmitic acid. Using another approach, even simple odd-numbered hydrocarbons from C-19 to C-29, the major part of the non-polar fraction of the cuticle extract, induced strong arrestment behavior of the mites when applied on a running surface (Rickli et al., 1994). Salvy et al. (2001) revealed differences in the cuticular hydrocarbon profile between parasitized and non-parasitized hosts but could not answer the question of whether these differences are the reason for the infestation or the effect of the parasitation. Aumeier et al. (2002) confirmed that the hydrocarbon pattern of 4th and 5th instar larvae differ significantly and could, therefore, also be used for the chemotactic recognition of the suitable host stage.

Not only the larva itself but also semiochemicals from the cocoon and larval food have some attractiveness to *Varroa* females. Aliphatic alcohols and aldehydes with chain lengths from C17 to C22, extracted from the larval cocoon, elicited strong arrestment behavior in the mites (Calderone and Lin, 2001; Donzé et al., 1998). Nazzi et al. (2001) could prove the attractiveness of larval food using a different bioassay, where larvae and/or treated dummies are offered in a choice test in a closed arena (Rosenkranz, 1993). The attractive components were analyzed as several carboxylic acids with low molecular weight. One of these compounds, 2-hydroxyhexanoic acid, even had a significant attractive effect on mites when applied to brood cells in the colony (Nazzi et al. 2004).

Obviously, there are also natural compounds within the honey bee brood nest which show a repellent effect on *Varroa* females. Queen larvae and extracts of queen larvae were significantly less attractive than worker and drone larvae, and the royal jelly of the queen larvae even had a repellent effect (Calderone and Lin, 2001; Calderone et al., 2002; Trouiller et al., 1994). Nazzi et al. (2009) confirmed these results for octanoic acid, which is present in higher quantities in royal jelly than in the food of worker or drone larvae. This may at least in part explain the extraordinary low infestation rate of queen cells (Harizanis, 1991).

However, the invasion of *Varroa* females is also influenced by some additional non-chemical factors. A strong effect has been demonstrated for the size, height and age of the brood cell itself. Shortened brood cells, i.e. brood cells with a shorter distance between the larva and the cell rim, are more frequently infested than artificially elongated brood cells. This effect was confirmed by the use of different methods with manipulated brood cells inside the honey bee colony (Boot et al., 1995a; De Ruijter and Calis, 1988; Goetz and Koeniger, 1993; Kuenen and Calderone, 2000). Also the size of the cell and the relative larval size to cell size affect the invasion behavior of the mites. Brood cells of European honey bees are, in general more highly infested than slightly smaller brood cells of Africanized bees within the same colony (Message and Gonçalves, 1995; Piccirillo and De Jong, 2003). However, drone brood cells containing smaller worker larvae are less infected than normal worker brood cells, probably an effect of too much space between the larva and cell wall (Calderone and Kuenen, 2001). Older brood cells containing cocoons from several brood cycles are also more highly infested than newly built comb (Piccirillo and De Jong, 2004). In this case, the somewhat smaller size of the old cells is presumably compensated by the stronger smell of the cocoons.

We can summarize, that the host-finding behavior of *Varroa* females is triggered by a variety of factors including physical parameters, but the suitable host stage is finally recognized by chemical volatile signals of the host larva and the adult bee. The biological activity of many chemical blends has been demonstrated in laboratory bioassays including compounds of several fractions from the extracts of larval cuticle and larval food. However, we still have not identified the real "host odor" of the 5th instar larva of the honey bee: not a single experiment succeeded in luring the *Varroa* female from the adult bees to a dummy containing a certain blend, neither in the laboratory (Kraus, 1994) nor within the colony (reviewed in Dillier et al., 2006). In all experimental setups, adult bees were always more attractive than any larval stage (LeDoux et al., 2000; Zetlmeisl and Rosenkranz, 1994). This contradicts the natural situation in the honey bee colony, where generally significantly more mites are within sealed brood cells than on adult bees (Boot et al., 1993; Martin et al., 1998). During the summer, up to 90% of the mite population can be within the brood (Rosenkranz and Renz, 2003).

We must conclude that as long as *Varroa* research fails to elicit the shift of *Varroa* females from bees to brood under controlled conditions, the development of a *Varroa* trap seems unrealistic.

3.3. Reproduction

After entering a brood cell with a 5th instar larva the *Varroa* female passes between the larva and the cell wall to the bottom of the cell and becomes stuck within the larval food. This behavior may be an adaptation of the mite to avoid detection and removal by hygienic bees. Respiration takes place by the peritreme, the common respiratory organ of Gamasid mites (Richard et al., 1990). Approximately 5 h after cell capping the larvae has consumed the rest of the larval food (Ifantidis et al., 1988) and the mite sucks hemolymph from the larva. Within a few hours oogenesis starts, followed by vitellogenesis (Garrido et al., 2000; Steiner et al., 1994, 1995) and approximately 70 h after the cell capping the first egg is laid (Ifantidis, 1983; Steiner et al., 1994).

This first egg is normally unfertilized and due to the haplo-diploid sex determination system it develops into a haploid male, while subsequent female eggs are fertilized and laid in 30 h intervals (Ifantidis, 1990; Martin, 1994; Rehm and Ritter, 1989). Up to five eggs in worker brood and up to six eggs in drone brood are considered as the normal "reproductive program" (Garrido and Rosenkranz, 2003; Martin, 1994, 1995a). The normal sequence of a reproductive cycle is shown in Fig. 4.

The mite larva develops within the egg during the first hours after oviposition (Nannelli, 1985). From hatching out of the egg until the adult molt the mite offspring pass through proto- and deutonymph stages; the developmental time is about 5.8 and 6.6 days for female and male mites, respectively (Donzé and Guerin, 1994; Ifantidis, 1990; Martin, 1994; Rehm and Ritter, 1989). Both nymphal stages are divided into a mobile and an immobile pharate phase just before the molt (Donzé and Guerin, 1994; Ifantidis, 1983; Laurent and Santas, 1987). The immobile stages are called proto- and deutochrysalis (Fig. 1). *Varroa* mites display a clear sexual dimorphism (Ifantidis, 1983). Males are smaller than females throughout the whole ontogenetic development and have longer legs in relation to the body size. The female mites change during their development from an oblong to a transversely elliptical body shape; the deutochrysalis already exhibiting the final body shape. In the deutochrysalis stage the coloration starts on the periphery of the opisthosoma and shifts to a reddish-brown color after the molt of the female. In contrast, the male's definite body shape is triangular with a light yellow color (Fig. 1).

The mother mite creates a hole in the cuticle of the pupa for the nymphs to feed through. This single "feeding zone" is generally located on the 5th segment on the bee pupa and near to the so called "fecal accumulation site" (Donzé and Guerin, 1994; Kanbar and Engels, 2003). This behavior is part of "parental care" and necessary because the soft chelicerae of the nymphal stages can not perforate the pupal cuticle and the male's chelicerae are modified for sperm transfer. After feeding, the mites return to the fecal accumulation site (Donzé and Guerin, 1994).

Varroa mites become sexually mature immediately after the last molt. Males reach maturity before the females and stay at the fecal accumulation site, waiting for the first adult female which molts to adulthood some 20 h later. As reproduction can only occur inside the brood cell, males start mating as soon as the female arrives (Donzé et al., 1996).

Before copulation starts the male cleans his chelicerae. At the beginning of the mating, the male touches the female with his first pair of legs and ascend her dorsum. He then examines the frontal margin of the female's dorsum and slips to the ventral side. Young females facilitate this action by lifting their bodies. In the venter-to-venter position the male searches for the gonopores (which are separated from the genital opening where the eggs are delivered) of the female which are located transversely between the third and fourth pair of legs (Alberti and Hänel, 1986; De Ruijter and Kaas, 1983). Then he takes the spermatophore out of his genital opening and transfers it into the gonopore of the female by means of the chelicerae. Within 2 days after insemination, the roundish prospermatozoa migrate into the spermatheca and change to a fusiform shape.

Multiple mating is common until the next daughter female is mature and arrives on the fecal accumulation site. To fill the spermatheca with up to 35 spermatozoa several matings are needed (Donzé and Guerin, 1994; Donzé et al., 1996). The mating behavior is initiated by female sex pheromones (Ziegelmann et al., 2008). Due to these volatile pheromones, young freshly molted females are significantly more attractive than older females or deutochrysalis (Fahle and Rosenkranz, 2005), which ensures that the male copulates with the youngest female until the next deutochrysalis molts to the adult stage.

3.3.1. Infertility and low reproductive rates of Varroa females

It is difficult to measure the real reproductive rate (=number of viable adult offspring per mother mite), which among other things depends on mite fertility (reproduction, yes or no) and fecundity (=number of offspring per reproductive cycle) under natural conditions. Martin (1994, 1995b) calculated the reproduction rate of 1.3–1.45 in single infested worker brood and, due to the longer capping period, 2.2–2.6 in drone brood. An example for the maturation of two female daughter mites is given in Fig. 4. During her life time a *Varroa* female can perform up to 7 reproductive cycles under laboratory conditions (De Ruijter, 1987); under field conditions an average number between two and three reproductive cycles can be expected (Fries and Rosenkranz, 1996; Martin and Kemp, 1997).

In the original host *A. cerana* the reproduction of *Varroa* mites (*V. jacobsoni* and *V. destructor*) is limited to drone brood for yet unknown reasons (Anderson, 2000; Boot et al., 1996; Garrido, 2004; Rath, 1999). This phenomenon is considered a crucial point for the balanced host–parasite relationship in *A. cerana* (Rath, 1999). The two haplotypes of *V. destructor* that are capable of reproducing on *A. mellifera* (Muñoz et al., 2008) can reproduce in both, drone and worker brood. However, a certain percentage of *Varroa* females which have entered a drone or worker brood cell do not lay any egg at all. This percentage of non-reproducing mites is slightly variable according to the species or subspecies of the host and climatic conditions and might, therefore, contribute to differences in the host tolerance of European bees (Fries et al., 1994; Martin, 1998; Rosenkranz, 1999). In European honey bee subspecies about 5–20 % of the mites remain infertile after invading worker or drone brood cells (Al Aattal et al., 2006; Garrido et al., 2003; Martin, 1994, 1995a; Martin et al., 1997; Rosenkranz, 1999; Rosenkranz and Engels, 1994a). A long-term example of higher infertility rates in *A. mellifera* is confined to the Africanized honey bees of Brazil: Over a period of more than 15 years an average rate of infertile mites of about 50% in worker brood was confirmed; mite fertility in drone brood, however, did not show any particularities (reviewed in Rosenkranz, 1999). Transfer of *Varroa* mites among different honey bee subspecies at a Brazilian study site confirmed that low mite fertility was more a host than a parasite trait (Rosenkranz, 1999), independent of the possible presence of different mite haplotypes with possible different reproductive abilities.

It was assumed that a lower fertility of *Varroa* females in worker brood represents an adaptation of the host to limit the reproductive rate of the parasite and that the huge feral population of Africanized honey bees in tropical America supports such adaptations (Camazine, 1986; De Jong, 1996; Rosenkranz and Engels, 1994a). However, Africanized honey bees in other parts of South and Central America did not show this feature (Marcangeli et al., 1992; Medina and Martin, 1999; Medina et al., 2002). Recent reports indicate that even in Africanized bees of Brazil the rate of fertile mites in worker brood has increased to levels similar to European bees (Carneiro et al., 2007; Correa-Marques et al., 2003; Garrido et al., 2003). Nevertheless, Africanized honey bees in Brazil are still tolerant toward Varroosis and *Varroa* treatments are not performed (De Jong, pers. comm.). This example may illustrate that (i) there is still some flexibility in the host–parasite adaptations in feral honey bee populations and (ii) "*Varroa* tolerance" does not depend on a single factor.

Unfortunately, the reasons for the infertility of *Varroa* females, in general, are unknown. As unfertilized females are not able to reproduce (Martin et al., 1997) it was assumed that these infertile mites represent young *Varroa* females which failed to copulate during their maturation (Harris and Harbo, 1999). Fuchs (1994) supposed that infertile females had lost their reproductive ability. Two observations contradict these hypotheses: In the phoretic mite populations on adult bees nearly all mites have filled spermatheca (Garrido, 2004) and "infertile" brood mites, which were transferred artificially to other newly sealed brood cells, were still able to reproduce (Weller, 2008). This suggests that temporary infertility of *Varroa* females is induced by host factors.

It is important to consider that not all fertile *Varroa* females, i.e. females which lay at least one egg, are really reproducing successfully. The production of one adult viable daughter requires at least the maturation of one male and one female offspring including mating. Therefore, female mites producing only one egg, no males or with delayed start of oviposition may not contribute to the growth of the *Varroa* population. For example, in 11–21% of the brood cells the male is lacking (Donzé et al., 1996; Martin et al., 1997). The mortality of mite offspring seems to be a main factor for differences in the reproductive rate and varies according to climate, season and honey bee subspecies (Eguaras et al., 1995; Ifantidis et al., 1999; Mondragón et al., 2005, 2006). A strange case of mite mortality is reported from the pseudo clone *A. mellifera capensis* in South Africa: The mortality of *Varroa* offspring in the brood cells of the parasitic *A. mellifera capensis* is somewhat higher compared to that in *A. mellifera scutellata*, due to a "trapping effect" in the upper part of the larger *capensis* brood cells (Martin and Kryger, 2002).

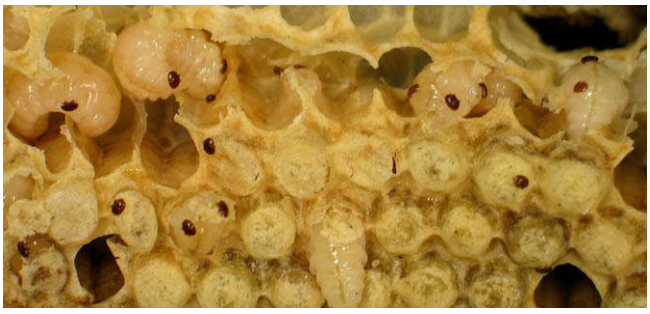

Fig. 5. Recently capped drone brood cells with 5th instar larvae multiply infested by *Varroa* mites.

Additionally, the reproductive rate depends on the infestation of a single brood cell; in multiply invaded drone and worker brood cells (Fig. 5) the reproductive rate per female mite is significantly reduced (Fuchs and Langenbach, 1989; Martin, 1995b; Martin and Medina, 2004; Mondragón et al., 2006).

3.3.2. Triggering of Varroa reproduction

The reproduction of *Varroa* mites is closely synchronized with the brood development of the host. Even the sequence of male and female eggs of the *Varroa* mite depends on signals from the corresponding stage of the host larvae and pupae, respectively (Garrido and Rosenkranz, 2003). The reproductive success of a single *Varroa* female can be defined by the number of adult, mated and viable daughter mites produced during a reproductive cycle within the honey bee brood cell. Reproductive success depends on the number of female offspring which successfully mate before hatching of the brood (see also in Section 3.3.1). Therefore, the duration of brood development is a limiting factor for the development of the mite. This creates a strong selective pressure on reproducing mites for rapid oogenesis and preimaginal development. The phoretic mites are already well prepared for reproduction by the presence of a large terminal oocyte which will develop into the first egg (Steiner et al., 1994), a characteristic for most mesostigmatid mites (Vitzthum, 1931). Certain proteins of the host hemolymph are stored directly in the ovary of the mite (Steiner et al., 1994; Tewarson and Engels, 1982).

During the phoretic phase the oocytes are arrested in a previtellogenic stage (Garrido et al., 2000). Immediately after the invasion of the brood cell the oogenesis is activated by volatiles of the host larva (Garrido and Rosenkranz, 2004; Milani and Chiesa, 1990; Trouiller and Milani, 1999). An earlier hypothesis that the juvenile hormone of the host acts as a trigger for mite oogenesis was disproved (Rosenkranz et al., 1993a). With a new bioassay, Garrido and Rosenkranz (2004) showed that only the polar fraction of cuticular extracts from freshly capped larvae was able to initiate mite oogenesis. This is the first proof of a kairomonal primer effect in insects.

There are also inhibitors of mite reproduction within a brood cell. Several authors described fewer reproducing mites and less offspring in multiply infested cells compared to singly infested cells (Donzé et al., 1996; Martin, 1995b; Nazzi and Milani, 1996). In artificial brood cells treated with a hexane extract from multiply infested brood cells the mean number of *Varroa* offspring was significantly reduced (Nazzi and Milani, 1996). Nazzi et al. (2004) identified the active substance from infested brood cells as (Z)-8-heptadecene. In a laboratory test they showed that this particular isomer significantly affects the fecundity of the *Varroa* female. When (Z)-8-heptadecene was applied to freshly capped brood cells in the colony it reduced the number of *Varroa* offspring and the number of viable adult *Varroa* daughters (Milani et al., 2004). The authors assumed that (Z)-8-heptadecene is produced under the stress condition of multiple infestations, however, proof is lacking that this carbohydrate is produced by infested larvae.

The relevance of the phoretic phase for the reproductive cycle of *Varroa* mites is not clear. Under laboratory conditions, *Varroa* females can successfully be transferred from brood cell to brood cell without a phoretic phase (De Ruijter, 1987); under field conditions, older mites seem to invade brood cells more rapidly than nulliparous *Varroa* females (Fries and Rosenkranz, 1996). It seems that especially under unfavorable conditions, the phoretic phase may have negative effects on the reproductive capacity of *Varroa* mites: After a long phoretic phase of 5 weeks or more, or after a starvation period of 7–18 h the number of infertile mites was two–three-fold higher than in the control (Rosenkranz and Bartalszky, 1996; Rosenkranz and Stürmer, 1992).

3.4. Population dynamics

After the first infestation of a new honey bee colony, *Varroa* mites are able to build up huge populations within a few years (Büchler, 1994; Fries et al., 2003). The population growth is highly variable and depends on all of the traits of the host and the parasite that may influence the reproductive rate and the mortality of the mite (Calis et al., 1999b; Fries et al., 1994). Features of the parasite that influence population growth are the reproductive capacity during the mite's lifetime and the lifespan, features of the host are brood availability, presence of drone brood, swarming, and level of defense behavior, among others (see also in Section 5.2.3). Some of the host features that influence mite population growth are additionally triggered by ambient factors such as climate and nectar flow (Currie and Tahmasbi, 2008). The exact impacts of the individual parameters on the population dynamics are not known. Additionally, most of these parameters are mutually influenced and part of complex multifactorial interactions. Some authors tried to extract the most important factors by the use of multifactorial analyses (Arechavaleta-Velasco and Guzman-Novoa, 2001; Harris et al., 2003; Lodesani et al., 2002). They confirmed significant correlations between the amount of brood and/or the fertility of the mites and population growth; however, prediction to what extent a starting mite population in the spring will increase until autumn is still not possible.

A further problem is that there are significant differences between feral colonies and colonies hived at apiaries. In regions with a high density of honey bee colonies the population dynamics are influenced by a permanent exchange of mites when foragers or drones enter foreign colonies or by robbing (Goodwin et al., 2006; Greatti et al., 1992). Through this so called "reinfestation", some colonies will loose mites, and others will receive mites. It is interesting to note that the robbing bees will "receive" the mites from the victim colonies, which often are already weakened through a high *Varroa* infestation, and that the effective "robbing distance" is more than 1 km (Renz and Rosenkranz, 2001). This behavior means that during periods with low nectar flow and, therefore, high robbing activities, strong colonies may significantly increase their mite population.

Several reports confirm that under temperate conditions untreated colonies may collapse due to Varroosis 3–4 years after the initial infestation (Büchler, 1994; Korpela et al., 1993). There are, obviously, significant differences between the population dynamics in temperate and subtropical/tropical climates with a clear tendency for lower mite population growth under tropical conditions (De Jong et al., 1984; Eguaras et al., 1994; Garcia-Fernandez et al., 1995; Moretto et al., 1991; Rosenkranz et al., 2006). This lower population growth is striking because under tropical conditions honey bee brood is available throughout the year and therefore, mite reproduction is not interrupted as it is during the winter under temperate climatic conditions. This demonstrates a possible trade-off between brood availability, parasitization rate and mite mortality: under temperate conditions, damage at the colony level mainly appears during fall and winter, when the host population declines, the relative parasitization increases and consequently the long-living winter bees are damaged (Amdam et al., 2004). If we accept that the short-term decline of the host population rather than the growth of the parasite population, is the real colony level threat, the disadvantage of higher brood availability may be compensated for. A crucial and unresolved question is the mortality of *Varroa* mites in "summer" and "winter" colonies (Fries and Perez-Escala, 2001). For instance, the extreme turnover of bees in a strong honey bee colony during the summer could also increase the "turnover" of mites parasitizing on adult bees.

4. Pathology

4.1. Damage at the individual level

The individual honey bee is damaged in a variety of ways, with the developing larvae and pupae clearly representing the most sensitive host stages. First, the loss of hemolymph during the ontogenetic development within the brood cell significantly decreases the weight of the hatching bee. The weight loss depends on the number of mother mites and the amount of mite reproduction, but even a single infestation results in an average loss of body weight of 7% for the hatching bee (De Jong et al., 1982; Schatton-Gadelmayer and Engels, 1988). This has also been proven for parasitized drones, which loose 11–19% of their body weight depending of infestation rate (Duay et al., 2003), which led to decreased flight performance (Duay et al., 2002). Worker bees which were parasitized during their development, start earlier with foraging and have a significantly reduced life span (Amdam et al., 2004; De Jong et al., 1982; Schneider and Drescher, 1987). The parasitized foragers display a decreased capability of non-associated learning, prolonged absences from the colony and a lower rate of return to the colony (Kralj and Fuchs, 2006; Kralj et al., 2007), which may be due to a reduced ability to navigate (Ruano et al., 1991).

4.1.1. Varroa mites and honey bee viruses

V. destructor is a vector for various honey bee viruses. So far, about 18 different viruses have been isolated from honey bees (Chen and Siede, 2007) and many of them can be vectored by *Varroa* mites. This has been proven for Kashmir bee virus (KBV), Sacbrood virus (SBV), Acute bee paralysis virus (ABPV), Israeli acute paralysis virus (IAPV), and Deformed wing virus (DWV) (Boecking and Genersch, 2008). Before the occurrence of *Varroa* mites, bee viruses have been considered a minor problem to honey bee health (Allen et al., 1986; Bailey and Ball, 1991; Bowen-Walker et al., 1999; Yue and Genersch, 2005). Obviously, the direct injection of virus particles into the hemocoel of honey bee pupae and activation of latent virus infections through the additional injection of foreign salivary proteins of the mite provoke typical disease symptoms. Best known is the DWV infection causing the typical symptoms of crippled wings and shortened abdomen in heavily infested honey bee colonies (Boecking and Genersch, 2008; De Miranda and Genersch, 2010; Fig. 6). Some of the viruses are transmitted horizontally and vertically (Boecking and Genersch, 2008) supporting covert infections in managed honey bee populations. Additionally, *Varroa* mites may induce immunosuppression in parasitized pupae and, thus, activate these covert virus infections (Yang and Cox-Foster, 2007).

It is assumed that the final breakdown of a honey bee colony with the typical "damage symptoms", such as scattered brood nest, crippled bees (Figs. 6 and 7), eventual loss of coordinated social behavior like hygienic behavior and queen attendance, as well as rapid loss of bee population, is an effect of virus infections rather then the effect of direct parasitation through the *Varroa* mites. For instance, a 4-year monitoring of about 1250 honey bee colonies in Germany revealed a significant correlation of colony winter losses with (i) *Varroa* infestation and (ii) with the prevalence of DWV (German Bee Monitoring Project, 2008). However, the correlation between virus detection, *Varroa*-infestation level and colony mortality is not as clear as expected and demonstrates the need of a standardized quantitative virus analysis under field conditions with a definition of damage thresholds.

More detailed information of the current knowledge of *Varroa*-virus–honey bee interactions are presented in three reviews of this issue (De Miranda and Genersch, 2010; De Miranda et al., 2010; vanEngelsdorp and Meixner, 2010).

4.1.2. Synergistic effects

Recent colony losses in Europe and the United States have raised the question of synergistic effects as cause for bee damage or colony losses. These synergistic factors may include several honey bee pathogens – especially novel parasites such as *V. destructor* and *Nosema ceranae* (Anderson and East, 2008; Cox-Foster et al., 2007; Higes et al., 2008; Ribiere et al., 2008), environmental factors including pesticides, GM crops (Desneux et al., 2007; Faucon and Chauzat, 2008; Frazier et al., 2008; Nguyen et al., 2009), climate

Fig. 6. A young bee with crippled wings and shortened abdomen, presumably due to *Varroa* and Deformed Wing Virus (DWV) infections during the ontogenetic development.

Fig. 7. A brood cell containing a pupa damaged through *Varroa* infestation was opened by hygienic bees; the *Varroa* female is escaping from the opened brood cell.

change (Le Conte and Navajas, 2008), and peculiarities of the beekeeping management. The most famous example for a possible interaction of several problems is the so called Colony Collapse Disorder (CCD: Oldroyd, 2007). The exact cause of the sudden high colony mortality in the US in the year 2006 has still not been ascertained. However, bee scientists and beekeepers are increasingly aware that honey bee colonies are continuously exposed to basic threats such as *Varroa*, associated viruses, new *Nosema* species, and a changing environment. This is clearly different to the situation before the spread of *V. destructor*.

Unfortunately, synergistic effects are extremely difficult to analyze experimentally. Therefore, only a few reports are available including the effect of "*Varroa* + X" (American foulbrood: Brødsgaard et al., 2000; tracheal mite: Downey and Winston, 2001). However, the quantification of such effects seems to be a requirement for future research on colony losses.

4.2. Damage at the colony level

The reproductive capacity and, therefore, the fitness of a *Varroa* infested honey bee colony as a "superorganism", is reduced in two ways, even if the infestation is moderate: Drones which have been parasitized during their development have a significantly lower chance to mate (Duay et al., 2002) and infested colonies produce less swarms (Fries et al., 2003; Villa et al., 2008).

From the beekeeping point of view there exist certain thresholds for economic damage and for irreversible colony damage. At low infestation rates clinical symptoms are not visible, and the infestation often remains undetected. Moderate infestation rates may reduce the growth of the honey bee population and, therefore, the honey yield, but clinical symptoms may still not be evident. However, the steps to irreversible colony damage are small, especially if during fall the mite population still increases while the host population is decreasing (Fries et al., 2003). The final breakdown of a honey bee colony is associated with the typical "parasitic mite syndrome" such as scattered brood, crawling or even crippled bees, supersedure of queens and unexplainable reduction of the bee population (Shimanuki et al., 1994). The damage threshold is not correlated with a fixed number of mites per colony. It is rather highly variable and depends on the bee and brood population, the season and the presence of bee viruses. Under German conditions, an infestation rate of the winter bees of more than 7% may lead to colony collapse (Liebig, 2001); Delaplane and Hood (1999) suggested a significantly higher economic threshold for the Southern USA of 3000–4000 mites per colony (compare also Currie and Gatien, 2006). Interestingly, Fries et al. (2003), Rosenkranz et al. (2006) found independently that untreated colonies which exceed an infestation rate of about 30% in the adult bees during the summer do not have a chance to survive the following winter.

5. Tolerance toward Varroosis

5.1. Natural selection

The most striking example of a balanced host–parasite relationship is that of the original host *A. cerana* and *V. destructor/V. jacobsoni*. In this host species, three extraordinary host factors are described which obviously are sufficient to control the growth of the *Varroa* population and prevent any visible damage to the infested colonies:

- No reproduction in worker brood at all (Boot et al., 1999; Garrido, 2004; Koeniger et al., 1981; Rath, 1999; Rosenkranz et al., 1993a). Therefore, the reproduction of the mites is limited to drone brood.
- Effective grooming and hygienic behavior (Boecking, 1992; Peng et al., 1987a,b; Rath, 1999; Rosenkranz et al., 1993b).
- The "entombing" of drone brood. Multiply infested drone pupae which are to weak to open their hard cocoon cap themselves (Boecking et al., 1999) will be "willfully neglected" (Rath, 1992) and die within the brood cell. About one quarter of the reproducing mite population could be killed by entombing (Rath, 1999).

However, the *A. cerana* – *Varroa* situation is only of limited value in understanding the relationship between *V. destructor* and *A. mellifera*. Two of the tolerance factors, non-reproduction in worker brood and entombing of drone larvae, are unique and do not occur in *A. mellifera*. The active defense mechanisms known from *A. cerana* do exist in *A. mellifera* (and are widely used for selective breeding) but, obviously, to a somewhat lower extent (Fries et al., 1996). A final evaluation of tolerance factors is hampered by the lack of comparative experiments on both host species at the same study site.

Examples of natural selection have also been reported in the new host, *A. mellifera*, and several attempts have been made to use natural selection for solving the *Varroa* problem. The best documented reports come from tropical countries with African or Africanized honey bee populations (Boecking and Ritter, 1993; De Jong, 1996; De Jong et al., 1984; Echazarreta and Paxton, 1997; Eguaras et al., 1995; Guzmán-Novoa et al., 1999; Martin and Kryger, 2002; Moretto et al. 1991, 1995; Ruttner et al., 1984). Of special interest is the situation in Brazil where many and long-term observations on the Africanization of the feral honey bee population (De Jong, 1996) and proof of their *Varroa* tolerance exist (Carneiro et al., 2007; Correa-Marques et al., 2003; reviewed in Rosenkranz, 1999).

The occurrence of natural tolerance to Varroosis seems to be linked to the huge feral honey bee populations in the tropics. Under temperate conditions, these feral populations seem to be significantly smaller than in tropical countries (Moritz et al., 2007) so that natural selection probably is counteracted by the huge numbers of drones and swarms from managed colonies. Additionally, tropical conditions influence the population dynamics of the honey bees (see Section 3.4) and favor the spread of African derived honey bee subspecies, which are considered to have preadaptations for *Varroa* resistance. Probably, the "costs" of *Varroa*-specific defense behavior are lower under tropical conditions than in more temperate climates (Vandame et al., 2002). Consequently, the first proven example of a long-term tolerance of European bees was reported from the tropical North Brazilian island Fernando de Noronha. An isolated population of European honey bees (*A. m. ligustica*) survived without *Varroa* treatment for more than 25 years (De Jong and Soares, 1997). Unfortunately, a first proof of queens from this island in Germany did not confirm the *Varroa* tolerance under temperate climatic conditions (Correa-Marques et al., 2002).

However, also from more temperate regions there are some promising examples of an obvious natural selection. It is a common phenomenon that, if feral honey bee populations exist, they first decline significantly after the arrival of *Varroa* mites, but recover some years later (Villa et al., 2008). Recently, long-term survival of unmanaged honey bee populations was reported from France (Le Conte et al., 2007) and the United States (Seeley, 2007). A further strain of the so called "Russian" or "Primorski" bees from Far East Russia has been introduced to the United States and used as the starting point for a large breeding program (De Guzman et al. 2007; Rinderer et al., 2000, 2001, 2003; see Section 5.3). The bees originate from a region with a sympatric distribution of *A. cerana* and *A. mellifera* and are considered to have established *Varroa* tolerance during a long period of coexistence.

A selection experiment was performed on the island Gotland in the Baltic Sea. The so called "Bond-Project" started in 1999 with

150 infested colonies that were kept without *Varroa* treatment for up to 10 years. After a dramatic decline within the first 3 years, a small honey bee population became established which has survived without any treatment (Fries et al., 2003, 2006). Colonies headed by queens of this population revealed a clearly reduced growth of the *Varroa* population compared to European control colonies and confirmed host selection rather than selection of less virulent mites (Fries and Bommarco, 2007; Rosenkranz and Fries, 2005). However, these colonies also had, on average, a somewhat lower brood production, a slightly higher prevalence of brood diseases (which may also reduce the reproductive success of "brood mites"), the tendency of overwintering with a relatively small number of bees (which may reduce the absolute number of mites present in the spring) and a less gentle behavior (Rosenkranz and Fries, 2005; Weller, 2008). Natural selection, therefore, may lead to unexpected results concerning the performance of the colony and beekeepers have to realize that their wish list (strong colonies with gentle bees producing high honey yields) may no longer be fulfilled by bees resulting from such selection.

A basic and important question is whether the observed stable host–parasite relationships are more an effect of the host or the parasite. Without doubt, selection acts on both and according to the established hypothesis of the development of host–parasite relationships depends mainly on the means of transmission. Generally, pathogens that rely mainly on horizontal transmission are likely to develop more virulent host–parasite relationships, while vertical transmission should favor more benign relationships (Fries and Camazine, 2001). However, most honey bee populations in temperate climates are managed and periodically treated by beekeepers and, therefore, the natural rules for coevolution may not be valid.

Several authors supposed that a lower virulence i.e. a reduced reproductive capacity of specific *Varroa* populations is the crucial factor for tolerance to Varroosis (Anderson, 2000; Anderson and Fuchs, 1998; Boot et al., 1999; Seeley, 2007). However, some of these reports refer to the problem of different parasite species (*V. jacobsoni, V. destructor*), which was not clarified before the year 2000. The only *Varroa* haplotypes on *A. mellifera* were the Korean and Japan haplotypes with the latter considered to be less virulent due to reduced reproductive capacity (Anderson, 2000; Anderson and Trueman, 2000; Medina and Martin, 1999; Vandame et al., 2000). The predicted dominance of the Japan haplotype in South-America (Anderson and Trueman, 2000; De Guzman and Rinderer, 1999) was not confirmed by a later analysis of Brazilian mites which exclusively were of the Korean type (Garrido et al., 2003). Obviously, the Korean haplotype with a hypothesized clonal structure (Solignac et al., 2005) has expanded worldwide (Muñoz et al., 2008).

We can summarize that natural selection towards *Varroa* tolerance in the honey bee is possible and in some cases a partial tolerance has already been confirmed. Unfortunately, none of the described cases show a clear correlation of tolerance to a specific host factor. Therefore, it remains unclear whether the study of these tolerant populations will be helpful for the determination of tolerance factors. Nevertheless, managed honey bee colonies may benefit from the introgression of tolerant feral populations through the distribution of germplasm with novel genetic recombinations (Villa et al., 2008).

5.2. Tolerance factors

5.2.1. Environmental conditions

As an obligate parasite of honey bees the "environmental condition" for *V. destructor* mites is provided by the host and reflects to a large extent the conditions within the honey bee hive. However, the microclimatic conditions within the colony are affected by outside factors like temperature, humidity or the availability of pollen and nectar. This may, presumably indirectly, influence the proportion of non-reproducing mites (Eguaras et al., 1994; Garcia-Fernandez et al., 1995; Kraus and Velthuis, 1997; Moretto et al., 1997). Increasing the mites' phoretic phase during winter times or dry seasons decreases the reproductive success (Rosenkranz and Bartalszky, 1996). On the other hand, infestation rates of adult Africanized honey bees rose from 4% to 11%, when they were moved from warmer to colder climates in Brazil (Moretto et al., 1991). In contrast, Rosenkranz and Engels (1994) stated that infertility of mites in Africanized and European colonies did not depend on brood nest or ambient temperatures. However, a general dependence of the population dynamics of *V. destructor* on climate has been assumed several times (De Jong, 1996; De Jong et al., 1984; Moretto et al., 1991). It is likely that environmental factors act indirectly via the host on the parasite, for instance by modulation of honey bee brood amount, the relation of drone to worker brood or the extent of the hygienic behavior of the bees.

5.2.2. Active behavioral defences

In the context of social interactions honey bees exhibit a wide range of behavioral skills. Two of them, the "grooming behavior" and the "removal of parasitized brood cells" (hygienic behavior) might impair the survival and reproductive success of *V. destructor* (reviewed in Boecking and Spivak, 1999; Evans and Spivak, 2010). Moreover, *A. cerana* exhibits the unique behavior of entombing parasitized drone brood, which prevents the hatching of these brood cells and, therefore, kills the invaded mites (reviewed in Rath, 1999).

5.2.2.1. Grooming behavior. Honey bee workers groom themselves (auto-grooming) and other nestmates (allo-grooming). Peng et al. (1987a) reported from the original host *A. cerana* a rapid and effective cleaning behavior: 98% of the mites introduced into *A. cerana* observation hives were removed from the bees' bodies, subsequently killed and evicted from the hive within a few minutes. Thus, grooming behavior was a main factor recommended for breeding programs to reduce the susceptibility of *A. mellifera* colonies to *V. destructor* infestation (Arechavaleta-Velasco and Guzman-Novoa, 2001; Delfinado-Baker et al., 1992; Mondragón et al., 2005; Moretto et al., 1995). However, the significance of grooming behavior for host tolerance is assessed with caution because Peng et al. (1987a) used mites from other honey bee species which may have stimulated the grooming activity by their alien scent (Rosenkranz, 1993) and reproducing the experiments of Peng et al. (1987a) at the same study site with intraspecific mites revealed a significantly lower grooming effect (Fries et al., 1996). Also in *A. mellifera* there seem to exist race-specific differences in the extent of grooming behavior (Moretto, 2002). In general, grooming behavior seems to be highly variable (Büchler, 1994; Currie and Tahmasbi, 2008) which may be an advantage for selective breeding. On the other hand, the results strongly depend on the method used to quantify this trait. For instance, Aumeier (2001) determined in a bioassay lower race-specific differences in grooming activities between Africanized and European bees, respectively, as has been reported by Moretto et al. (1995). Furthermore, there are still conflicting reports on the heritability of the grooming behavior trait in European honey bee stocks (Boecking et al., 2000; Harbo and Harris, 1999; Harbo and Hoopingarner, 1997; Moretto et al., 1993).

It is unknown how the *Varroa* specific grooming behavior is elicited. Allo-grooming may be elicited by a "grooming dance" (Boecking and Spivak, 1999), but a specific scent of the mites could also be detected by the bees. It is interesting that *Varroa* mites have a similar cuticular hydrocarbon profile as their host bee (Nation

et al., 1992) and that this hydrocarbon pattern is variable and, is used for chemical mimicry especially when the mite stays within the brood cell (Martin et al., 2001b).

A general problem represents the comparative quantification of grooming behavior. The often used factor "number of damaged mites on the hive bottom" seems to be of limited value as this presumed damage of the dorsal shield belongs to the normal peculiarities of the body shape of the mite (Davis, 2009). Furthermore, a certain part of the mutilated mites might have been damaged after their natural death within sealed brood cells (Rosenkranz et al., 1997).

5.2.2.2. Hygienic behavior. The hygienic behavior is described as the uncapping and removal of dead, diseased or parasitized brood (Fig. 6). Rothenbuhler (1964) assumed a two-loci model for uncapping and removal for brood diseases. This model was re-evaluated by Moritz (1988) who suggested a more complex three- or more-loci model for the removal behavior. *Varroa*-specific hygienic reactions seem to be even more complex and include repeated uncapping and resealing of infested brood cells (Aumeier et al., 2000; Boot et al., 1999; Rosenkranz et al., 1993b). This may be due to the participation of several genetically distinct worker bees which are specialized in different hygienic tasks. The removal of *Varroa* infested brood does not necessarily include the death of the mites; most mites seem to escape from the opened brood cells during the removal process (Boecking and Spivak, 1999; Fig. 6). However, the removal of mites from the brood leads to an interruption of the reproductive cycle of the parasite, a prolonged phoretic phase or even the death of the mites. In *A. cerana* stocks experimentally inoculated with mites, worker bees removed 97% of *Varroa* mites from open brood cells within a few minutes (Peng et al., 1987a,b). *A. mellifera* removes mite-infested pupae to a lower but still considerable extent (Aumeier et al., 2000; Boecking and Ritter, 1993; Boecking and Spivak, 1999; Boecking et al., 2000; Guzmán-Novoa et al., 1999).

Consequently, the removal of mite-infested brood represents the main factor for the selective breeding of mite tolerant European honey bees (Harris, 2007; Ibrahim and Spivak, 2006; Spivak and Reuter, 1998). Several methods have been described to quantify the hygienic behavior of a honey bee colony, of which the frozen brood test and the pin test are now widely used (Boecking and Spivak, 1999; Gramacho et al., 1999; Spivak, 1996a,b). In both tests, a certain number of brood cells are killed either by freezing or by piercing; after a defined period the percentage of removed dead brood cells is recorded and used as a measure for hygienic behavior. However, there exist several restrictions for successful selection of a *Varroa*-specific hygienic behavior:

- It is not clear whether the mechanisms for the detection of dead brood are the same as for the detection of mite-infested cells and whether there is sufficient correlation between "killed brood" and "removal of *Varroa* infested brood cells" (Boecking et al., 2000). Obviously, *Varroa* infested cells are not only perceived by mite-specific volatile signals of the polar fraction (Martin et al., 2001a) and/or by certain methylalkanes (Martin et al., 2002), but also by unspecific "stress" reactions of the pupa itself (Aumeier and Rosenkranz, 2001; Boecking and Spivak, 1999; Boot et al., 1999; Gramacho et al., 1997, 1999; Rosenkranz et al., 1993b).
- The hygienic behavior is strongly influenced by environmental and in-hive factors (Boecking and Spivak, 1999; Harris, 2008; Spivak 1996a,b).
- The genetic variance and heritability of this trait has yet to be determined (see Boecking and Spivak, 1999; Boecking et al., 2000).

5.2.3. Population dynamics of the host

It is likely that the population dynamics of the host colony significantly influence the dynamics of the *Varroa* population. The amount of brood throughout the season, the temporal pattern of brood availability, the percentage of drone brood, swarming, absconding and brood free periods during winter or dry seasons have an impact on the reproduction of the *Varroa* population. Unfortunately, we do not yet understand and cannot quantify the parameters of these multifactorial relationships. Some models are available but their use is limited if the variation of the underlying parameters is very small (DeGrandi-Hoffman and Curry, 2004; Fries et al., 1994; Martin, 1998). Two examples may illustrate this problem:

- Swarming seems to be a promising strategy for the host (i) to divide the population of the parasite (Wilde et al., 2005), and (ii) to reduce mite reproduction through a broodless phase of several weeks. However, an experiment on an isolated island showed that at the end of the year, the swarm and the mother colony had similar and high infestation rates. This unexpected result may occur because the swarm is prolific and offers ideal breeding conditions for the mites, whereas the broodless period of the mother colony and possible damage from high infestation rates, reduces mite population growth (Fries et al., 2003).
- A shorter post-capping period of the brood cell should reduce the numbers of adult mature daughter mites. However, a shorter developmental time of the brood permits probably one brood cycle more per season which may compensate for the positive effect (Martin, 1998). A shorter post-capping period probably also selects for faster mite development.

An additional complication is that, at a certain threshold, an increasing mite population reduces the host population growth, which again may reduce the reproductive possibilities of the *Varroa* mites. If one considers such effects, the impact of bee viruses as secondary infections must also be included in such models (Martin, 2001a).

5.2.4. Control of mite reproduction

The control of mite reproduction is considered the most effective tool for the host to prevent the growth of a *Varroa* population within the colony (Fries et al., 1994). Various approaches of the honey bee host can limit the reproductive success of *Varroa* mites:

- A low attractivity of the brood may reduce the invasion rate of *Varroa* females. Experiments in Mexico revealed that brood of European honey bees were twice as attractive as brood of Africanized honey bees (Guzmán-Novoa et al., 1996, 1999). The nature of different brood attractivity is unknown. Aumeier et al. (2002) did not find any race-specific differences in the attractivity of individual bee larvae in a bioassay. They concluded that differential *Varroa*-infestation rates are not related to individual larval attraction but rather the effect of other race-specific factors at the colony level.
- The mite fertility and fecundity has been shown to vary according to environmental and host specific factors (see Section 3.3.1). For the rate of infertile brood mites, which has been shown to differ significantly between tolerant Africanized honey bees and susceptible European honey bees (Rosenkranz, 1999), the race-specific variation disappeared for unknown reasons (Correa-Marques et al., 2003; Garrido et al., 2003). Today, there are no proven examples of a population or subspecies of *A. mellifera* with a significantly reduced fertility of *Varroa* mites. This also applies to the fecundity and mortality of *Varroa* females within brood cells. These factors show a variability which could explain at least in part differences between susceptible and

tolerant honey bee colonies (Eguaras et al., 1995; Martin et al., 1997; Mondragón et al., 2005). However, objective comparisons among published data are nearly impossible as the techniques for quantification are not standardized.

- The availability of bee brood, and especially drone brood which provides better reproductive conditions for the mite, is a crucial factor for the reproductive success of the *Varroa* females. Therefore, the duration of the brood rearing period as well as the amount of drone brood significantly influences the population dynamics of the mite (Calis et al., 1999b; Fries and Bommarco, 2007).
- The duration of the post-capping stage limits the time available for the development of the *Varroa* offspring. Simulations indicate that a shortening of the post-capping period by about 10% could reduce the mite population growth by about 30% (Büchler and Drescher, 1990). Africanized honey bees as well as some African subspecies have a significant shorter post-capping period than European honey bee races (Moritz and Mautz, 1990; Rosenkranz, 1999; Rosenkranz and Engels, 1994a). However, Martin (1998) does not expect a considerable effect of a shortening of the developmental time of the bee brood as the number of brood cycles per season may increase; and Bienefeld and Zautke (2007) even expect negative effects due to a reduced vitality of the hatching worker bees.
- The smaller cell size of some honey bee subspecies likely influences the invasion rate as well as *Varroa* reproduction (Message and Gonçalves, 1995; Piccirillo and De Jong, 2003). However, these results were acquired from experimental colonies where both brood types were offered at the same time. So far, there is no proof that under natural conditions smaller cells are a crucial tolerance factor (see also in Sections 3.2 and 6.3)

One can summarize that the triggering of *Varroa* reproduction represents a powerful approach to establishing a stable host–parasite relationship (Fries et al., 1994). However, clear examples of a long-term correlation between host tolerance in *A. mellifera* and reduced *Varroa* reproduction are not available. A main problem is that methods which are currently available are not sufficient to quantify exactly the details of *Varroa* reproduction.

5.3. Tolerance breeding

The selective breeding of *Varroa* tolerant bees is considered to be the only long-term solution of the *Varroa* problem. Therefore, many different attempts have been made by researchers as well as by breeding organisations of the beekeeper communities. In many cases, independent proof of "resistant lines" is lacking and it is often difficult to make recommendations concerning the use of commercially merchandised queens.

One long-term attempt for the selection of tolerant honey bee strains was the introduction of the "Russian (Primorski) bees" about 10 years ago and the subsequent selection with a multifactorial approach of 18 tolerant strains (De Guzman et al. 2007, 2008; Rinderer et al., 2000, 2001, 2003). Various reports during the past 5 years confirmed at least a partial tolerance of these breeding lines, expressed by a significantly lower increase of the *Varroa* population compared to the local *A. m. ligustica* bees (Tarpy et al., 2007a; Ward et al., 2008). Additionally, a resistance of the "Russian bees" towards tracheal mite infestation was reported (Villa and Rinderer, 2008). The tolerance to *Varroa* mites was attributed to several factors, among them the lower attractivity of brood cells, reduced mite reproduction and extended phoretic periods were considered most important (De Guzman et al., 2007, 2008). So far, the selective breeding program over a 10-year period did not result in inbreeding problems (Bourgeois and Rinderer, 2009). However, the results of a 2 year cooperative project of the German working group with "Primorski bees" from the United States did not live up to the initial expectations. A somewhat reduced growth of the *Varroa* population in the "Primorski bees" could be confirmed, however, the brood amount and honey yield were also significantly reduced (Working group of German Bee Institutes, 2003). Therefore, "Primorski queens" were not recommended for beekeepers in Germany. A similar lower production of the "Russian" bees was obtained by Tarpy et al. (2007b) in a field trial with 250 beekeepers.

Another approach in the United States is based on the selection of specific characteristics of bees rather than on general changes in the mite populations. Local colonies in different climatic regions were surveyed and the ones with presumed potential for *Varroa* resistance were used for further artificial cross inseminations (Harbo and Hoopingarner, 1997). Tests of these selected stocks revealed a sufficient heritability for certain characters (Harbo and Harris, 1999a) and a systematic approach was developed to include several characters (for instance initial and final mite populations, reproductive rates, number of reproductive cycles). In a 10-year survey, Harris et al. (2003) confirmed that some reproductive parameters of the mites explain most of the variation of the *Varroa* population dynamics; however, he also pointed out that the weather conditions may significantly alter the reproductive parameters. Meanwhile, there are two characters which are used in different tolerant honey bee strains separately or in combination: The hygienic bees (HYG) and the "suppressed mite reproduction" bees (SMR). Hygienic behavior has been discussed as a suitable selection character for more than 10 years (Boecking and Spivak, 1999; Spivak, 1996b). Hygienic colonies have been proven to maintain lower mite loads, especially at moderate mite infestation rates and the trait was even measurable in the F1-generation (Spivak and Reuter, 2001). Harris and Harbo (2000) succeeded in increasing the rate of infested brood cells without viable *Varroa* progeny and found such colonies more resistant than unselected ones; this trait was also stable within the F1-generation (Harbo and Harris, 2001). Obviously, there are some links between HYG and SMR traits. The SMR bees removed reproductive mites more often than non-reproductive ones; hence the remaining mites in brood cells gave the "illusion" of high non-reproduction rates (Harbo and Harris, 2005). Harris (2007) assumed a particular sensitivity of SMR bees for infested brood. However, Ibrahim and Spivak (2006) compared SMR and HYG bees and found a higher removal rate of infested mite pupae in SMR colonies and an additional lower reproductive rate when the infested brood combs were transferred to the incubator. Therefore, the brood of SMR colonies itself, obviously, suppress the *Varroa* reproduction. In further experiments colonies selectively bred for both HYG and SMR features were compared with colonies solely bred for HYG and unselected control colonies (Ibrahim et al., 2007). The colonies selected for both characters had significantly fewer mites on bees and in brood cells. Surprisingly, the mite reproduction parameters did not differ among the experimental groups. So, the question of which character contributes to what extent to the observed *Varroa* tolerance still remains elusive.

A long-term project has also been started in Germany. In cooperation with beekeepers, the concept includes selection on the basis of hygienic behavior, examination of the difference between the mite population at the beginning and the end of the season, and mating stations with non-treated colonies for drone production (Büchler et al., 2008). The latter should include natural selection in a way that less susceptible colonies produce more drones. However, in the long run more drones may lead to a trade-off by increasing the mortality of successfully reproducing colonies, because a high number of drone brood boost the *Varroa* population within the colony (Kraus et al., 2007).

One has to state that the tolerant breeding lines presented here do not provide long-term and safe tolerance. Beekeepers that use commercially purchased tolerant queens need to continue monitoring the levels of *Varroa* infestations and use treatments if necessary (Tarpy et al., 2007a). Therefore, additional approaches are necessary to increase the efficacy of selective breeding. Multi-level selection including the selection of suitable patrilines has been suggested to improve the success of honey bee breeding programs (Perez-Sato et al., 2009).

A new approach is the search for tolerance factors at the individual level by comparing individuals from susceptible and tolerant stocks. With the aid of the published honey bee genome, major loci from a QTL map can be identified (see EU-Project "BEESHOP": http://www2.biologie.uni-halle.de/zool/mol_ecol/beeshop/index.html). Using microarray techniques the differential gene expression of individual pupae can be analyzed. According to Navajas et al. (2008) bees tolerant to *Varroa* were characterized by differences in the expression of genes regulating neuronal development, neuronal sensitivity and olfaction, which may be related to differential grooming and hygienic behavior.

6. Control

The first "official" detection of *Varroa* mites in a country is usually followed by intensive activities of the responsible bee scientists, extension services and veterinary authorities in order to control the spread of the mite and prevent collapse of honey bee colonies. During the first phase, damage and losses of colonies are common due to the lack of knowledge in control methods. A selection of beekeepers often occurs during the first 10 years, based on whether they are willing or able to include *Varroa* treatment into their management practice. Beekeepers that do not do this will loose their colonies. After several years the beekeeping situation normally stabilizes. However, periodic high losses of 30% or more of the hived honey bee population, mostly during overwintering, are still common and seem to be inevitable (German Bee Monitoring Project, 2008). Regardless of other threats to honey bees and the fact that before the "*Varroa* era" heavy colony losses were also reported (Gnädinger, 1984), *Varroa* mites seem to be the crucial driver for these periodic losses. It is assumed that *Varroa* is also involved in the recent substantial losses of honey bee colonies across the United States and several European countries (CCD: Faucon and Chauzat, 2008; Oldroyd, 2007; vanEngelsdorp et al., 2008a). This link is supported by Nguyen et al. (2009) who explored recent colony losses and found acaricides to be either prohibited or ineffective against *V. destructor*. He concluded that the common treatment methods used by the beekeepers often are inadequate for mite control.

Without any doubt, most of the colonies of *A. mellifera* in temperate climates will be damaged or even collapse within a few years if no control or inappropriate control methods are used (Boecking and Genersch, 2008; Rademacher and Harz, 2006). Nowadays, beekeepers utilize a wide range of different chemical substances, application techniques and methods to keep mite populations under control. An overview of the chemical, biotechnical, and biological methods which are currently used or developed to combat the *Varroa* mite is presented in Table 2.

6.1. "Hard" acaricides

Over the last 15 years, the most noted synthetic acaricides against *V. destructor* are the organophosphate coumaphos (Checkmite®, Asuntol®, Perizin®), the pyrethroids tau-fluvalinate (Apistan®, Klartan®, Mavrik®) and Flumethrin (Bayvarol®), as well as the formamidine amitraz (Milani and Barbattini, 1988; Milani and Lob, 1998; Ritter, 1988). Tau-fluvalinate acts at the voltage-gated sodium channels while coumaphos, an acetylcholinesterase inhibitor, interferes with nerve signaling and function. Most of these pesticides are easy to apply, economically convenient, and do not require refined knowledge of the mites' biology. Furthermore, as lipophilic substances they are mainly absorbed by the bees' wax (Bogdanov et al., 1998; Wallner, 1999, 2000), thus not directly jeopardizing the honey. However, they are persistent and accumulate after repeated treatments. Therefore, these miticides also possess some disadvantages:

- They may harm bees when bees are simultaneously exposed to multiple compounds stored in wax (Chauzat et al., 2009; Johnson et al., 2009; Wallner, 2005).
- They can sustainably pollute the honey and other bee products (Lodesani et al., 2008; Martel et al., 2007; Nasr and Wallner, 2003; Schroeder et al., 2004; reviewed in Wallner, 1999). For Asuntol, residues in honey were found, that exceeded the EU Maximum Limit of Residue (MLR). Contamination of bee's wax even persists through commercial recycling.
- Because several types of wax residues also may have some effect on mites in the sealed cells (Fries et al., 1998), they are likely to create acaricide resistance, thus causing unrecognized failure of control in the field and serious damage to beekeeping.

Already 15 years ago, *V. destructor* became resistant to fluvalinate (Milani, 1994) through metabolic and/or target site desensitivity (Sammataro et al., 2005). Obviously, there is cross resistance to other pyrethroids like acrinathrin and flumethrin. Also for organophosphates like coumaphos and for the formamidine amitraz, resistance of certain mite populations was recorded (Elzen et al., 1999a,b; Lodesani et al., 1995; reviewed in Milani, 1999; Trouiller, 1998). Resistant mite populations may increase and spread with predictable consequences (Elzen et al., 2000; Milani and Della Vedova, 1996, 2002; Sammataro et al., 2005). The development of acaricides on the basis of new active ingredients is not very likely (Dekeyser and Downer, 1994) and still not in sight. "Rotation" in the use of different acaricides within a "resistance management plan" (0., 2000, 2001) may only be a short-term-solution, due to the mainly non-professional structure of the beekeeperś community. Therefore, it is necessary to include alternative methods within the often chemical biased *Varroa* control strategies (Lodesani, 2004; Milani, 2001b).

6.2. "Soft" acaricides – organic acids and essential oils

Organic acids and essential oils, namely formic acid, oxalic acid, lactic acid and thymol, represent the frame of natural compounds used for the control of Varroosis. An enormous number of studies have been conducted regarding the details of application under different climatic and beekeeping conditions, i.e. concentration, time and number of treatments, method of application (powdering, feeding, evaporating, fumigating, trickling or spraying) and others (Calderone, 1999; Calderone and Nasr, 1999; Charrière and Imdorf, 2002; Della Vedova and Milani, 1999; Fries, 1989; Kraus et al., 1994; Milani, 2001a; Nanetti et al., 2003; Rademacher and Harz, 2006; Skinner et al., 2001; vanEngelsdorp et al., 2008b).

The general advantages of these natural compounds are:

- Sufficient efficacy against *V. destructor,* with formic acid as the only acaricide which is able to kill mites within the sealed brood cells (Fries, 1991).
- Low risk of residues and accumulation in bee products. Most of these substances are water soluble and/or volatile and, furthermore, natural ingredients of honey. Therefore, contaminations which jeopardize the quality of honey or bees' wax are unlikely (Bogdanov, 2006; Bogdanov et al., 1998, 2002; Floris et al., 2004).
- Low probability of eliciting resistance after repeated treatments.

Table 2
A compilation of the chemical, biotechnical, and biological treatment currently in use or part of recent research activities. For the different active ingredients and biotechnical control methods, respectively, the registered products, the mode of actions, a general valuation and the most valuable references are given.

Type of treatment	Active ingredient/mode of application		Valuation	Reference
Chemical treatment				
'Hard' synthetic chemicals	Checkmite®, Asuntol®, Perizin® (active component organophosphate coumaphos) are anticholinesterases Apistan®, Klartan®, Mavrik® (pyrethroid tau-fluvalinate), Bayvarol® (Flumethrin) with effect on ion permeability Amitraz®, Apivar®, Miticur® (formamidine) Apitol® (Cymiazole) Folbex-VA Neu® (Brompropylat) and others	Substances are fed or applied via fumigation, trickling or permanent contact in impregnated plastic strips; they are acting systemically or via contact	Substances mostly lipophilic (except Cymiazole) and persistant with high risk to create residues in bee products (especially non-polar substances which are applied in strips), thus boosting resistant mites	Fernández and Coineau (2006), Floris et al. (2001), reviewed in Wallner (1999), and Milani (1995), also see chapter 6.1
'Soft' chemicals (organic acids, essential oils)	Formic acid (>60%)	Applied in several short and/or one long-term treatments in several diffusers; miticidal when vaporized; mode of action unclear, eventually interfering with basic metabolic and respiratory processes	Only acaricide which is effective against phoretic AND reproductive mites; hydrophilic, therefore no accumulation in bees wax; trace amounts naturally occur in honey; contamination of bee products only if inappropriately applied, minimal danger of resistances; requires multiple applications; efficacy influenced by ambient temperature, hive size, placement and colony strength; high concentrations harm brood; precautions for the user recommended; recent gel formulations might probably facilitate application	Bolli et al. (1993), Fries (1989), Hoppe and Ritter (1989), Hoppe et al. (1989), Hoppe et al. (1989), Imdorf et al. (1996), Lindberg et al. (2000), Satta et al. (2005), see also chapter 6.2
	Oxalic acid, aqueous solution (e.g. 3–3, 5%, Oxuvar®)	Applied by trickling, spraying, fumigating or as pure cristals (e.g. sublimated with heat) without or with sugar; acaricidal action partly attributed to strong solution acidity, exact mode of action unclear; probably distributed via direct contact	Efficacy >90% when colonies broodless, less than 60% when brood right; efficacy independent from temperature; negative effects on brood and bees if multiply applied in short intervals	Aliano and Ellis (2008), Bacandritsos et al. (2007), Charrière et al. (1998), Gregorc and Planinc (2001, 2004), Gregorc and Poklukar (2003), Higes et al. (1999), Kraus and Berg (1994), Martin-Hernandez et al. (2007), Milani (2001a), Nanetti et al. (2003), Rademacher (2006), Rademacher and Harz (2006), Rademacher and Imdorf (2004)
	Lactic acid, aqueous solution (e.g. 15%)	Twice spraying on the bees of all combs	High efficacy for treatment of swarms (<95% mites killed), in broodless colonies around 80%, drops to 20–40% with brood; labor-intensive application	
	Apiguard®, Thymovar®, Magic3®, Frakno® or pure cristals (Thymol); Api Life Var (Thymol and other essential oils); Kombi-Am (marjoram oil and formic acid)	Applied as fumigant, powder, sprayed emulsions or in saturated absorbent blocks placed over the brood combs; possibly inhibits feeding, growth, orientation or reproduction of Varroa via its long-term repellent effects	Clear varroacidal properties (up to 90% reduction of mite infestation) only for evaporated thymol; varying results, possibly caused by temperature-dependent effects; can exhibit bee toxicity; lipophilic, thus producing residues in wax, but not stable and in most cases below the "taste threshold" in honey	Colin (1990), Emsen and Dodologlu (2009), Floris et al. (2004), Imdorf et al. (1999), Kraus (1994), Lindberg et al. (2000), also see chapter 6.2
	Other oils (e.g. wintergreen oil = methyl salicylate, camphor)	Mode of action unknown	Effect scarce or only in combination with other factors e.g. heat; high variability in toxicity to bees and mites; further research on improved modes of application required	
Herbal agents and their modifications of known or unclear ingredient	Sucrose octanoate esters (sucrocide) suffocates or desiccates the target insect		Ability of short-term increase of mite mortality but not effectively reducing mite populations	Barrington and Venis (2005), Sammataro et al. (2008)
	Terpens (e.g. Neem, Pichtin) with different insecticidal/acaricidal action		Neem and some others: low efficacy after several spraying treatments, repellent to bees, toxic for brood	Fassbinder et al. (2002), Melathopoulos et al. (2000)
	Rotenone (derris root extract from Lonchocarpus nicou) interfere with the electron transport chain in mitochondria		Highly variable mite mortality, lethal effects on bees and brood, residues in wax, toxicological risks to vertebrates	Satta et al. (2008)
	Extracts or smoke of e.g. male fern (Dryopteris spec.), nasturtium (Tropaeolum spec.), tobacco (Nicotiana spec.), walnut (Juglans spec.), mode of action mainly unknown		Contradictory results; some extracts (tobacco) or smoke (walnut) may cause significant mite mortality or lowered population density; sometimes mites are not killed and may recover	Cakmak et al. (2006), De Ruijter (1982), Eischen and Wilson (1998), Shaddel-Telli et al. (2008)

(*continued on next page*)

Table 2 (*continued*)

Type of treatment	Active ingredient/mode of application	Valuation	Reference
Propolis	Polar extracts (4%) at 40°C affected mites' metabolic activity	Narcotic and lethal effects, resulting in 100% mortality of phoretic and up to 68% in reproductive mites; only in combination with high temperature	Garedew et al. (2003)
Biological/biotechnical methods			
Trapping of mites in worker or drone brood	Uses natural host-finding behavior of mites; trapped mites are killed by heat (e.g. 'MiteZapper'), formic acid application or removal of the entire frame	Up to 95% efficacy in otherwise broodless colonies; up to 50% mites removable with solely drone brood extraction; no detrimental effect on colony development; 'resistance' of mites unlikely	Beetsma et al. (1999), Calis et al. (1999a), Charrière et al. (2003); Engels et al. (1994), Huang (2001), Rosenkranz (1987), see also chapters 3.2 and 6.3
Use of bee-derived kairomones	Confusion of host-finding behavior by evaporation of synthetic volatiles on strips (e.g. PheroVar®)	Field tests missing; inconsistent results of laboratory assays particularly e.g. fatty acid esters	Joder and Sammataro (2003); Pernal et al. (2005), see also chapter 3.2
Use of bee-derived repellents (allomones)	Interfere with the process of cell invasion	Deterrent activity of royal jelly; efficacy in the field still unclear	Drijfhout et al. (2005), Nazzi et al. (2009)
Breeding/use of tolerant bees	Several approaches, see chapter 5		
Use of wire netting bottom boards	Mites which slip accidentially or after behavioral defences of bees, are removed from the hive	Probably no or only small-scale effect on mite population, but as 'natural mite downfall' a valuable tool for beekeepers to monitor treatment-thresholds	Calatayud and Verdu (1995), Ellis et al. (2001), Harbo and Harris (2004), Pettis and Shimanuki (1999), Rinderer et al. (2003), see also chapter 6
Use of specialized bottom boards	Polyethylene tubes on the bottom board "happykeeper" causes increased mite downfall	In field tests no effect confirmed	http://www.beekeeping.org/happykeeper/index_us.htm; Liebig, pers. comm.
'Energy waves'	e.g. 'Bio-Energetic Bee-Vitalizer' activates grooming-skills of not tolerant bees	Anecdotal reports from hobbyists, effect not scientifically affirmed	http://www.n-g.at/Catalogd.pdf
Powdered sugar	After dusting mites loose the grip on their hosts	After direct dusting, up to 99% of the mites can be removed from the bees in laboratory assay; in the field trial low efficacy even if dusted every 2 weeks for 11 months with 120 g powdered sugar per application	Aliano and Ellis (2005), Ellis et al. (2009b), Fakhimzadeh (2001), Randy (2008)
Water	Swarms are completely plunged for 5 min	Under controlled conditions ineffective	Berg, pers. comm.
Heat	Application of heat to isolated brood combs or whole colonies	Effective (especially on brood mites in treated brood combs) but costly on a time and material basis	Brødsgaard and Hansen (1994), Hoppe and Ritter (1987), Rosenkranz (1987), http://www.patent-de.com/20000302/DE19834345A1.html
Ultrasound	Acoustic waves interfere with mites' orientation/communication	No effect on bees or mites under controlled conditions	Berg, pers. comm.; http://www.patent-de.com/pdf/DE10161677B4.pdf
Plastic combs with artificial cell form	Plastic combs with tapered cell sides; interference with the invasion behavior into brood cells	No field tests	http://www.beesfordevelopment.org/info/info/disease/a-varroa-treatment-withou.shtml
Reduced cell size	Might influence the inside-cell-behavior of the mites or just pinch them	Promising reports from hobbyists, but under controlled conditions no effect of inner cell width on reproduction or mite population growth	Ellis et al. (2009a), Liebig and Aumeier (2007), Martin and Kryger (2002), Message and Gonçalves (1995), Taylor et al. (2008), see also chapters 5.2. and 6.3
Rotation of brood combs	Interruption of mites' reproduction	Reports of sweeping effects (if an additional acaricidal treatment is applied at the end of the bee season) could not be affirmed scientifically	Aumeier et al. (2006)

Biological/antagonists Benign haplotype of Varroa	Varroa mites' reproduction is influenced by competition for resources in multiply infested cells. Establishing a benign population of Varroa could therefore induce reproductive suppression in the virulent type.	Up to now only a theoretical approach by use of a model; methodical problems not solved (inoculation of colonies); Reproductive isolation between the benign and virulent haplotypes might be necessary	Mondragón et al. (2006), Vetharaniam and Barlow (2006/0, see also chapter 3.3.1
Predators or parasitoids	e.g. pseudoscorpions might consume mites	Pseudoscorpion–bee-relationship unclear; only sporadic observations directly in-hives; conditions and success of breeding and inoculation of predators unclear	Donovan and Paul (2005, 2006), Gonzales et al. (2007), Van der Geest et al. (2000), see also chapter 6.3
Unspecific entomo-pathogenic fungi	Application of conidia (asexual spores; e.g. Bioblast®, Mycar®) on bees/in-hives by spraying, trickling or suspending impregnated strips yields to lethal fungal infestation	Up to date solely unspecific fungi in tests; contradictory reports regarding impact on mites and bees/brood	Holt et al. (2009), James (2009), Kanga et al. (2003, 2006), Meikle et al. (2008), Shaw et al. (2002), see also chapter 6.3
Viruses, bacteria (BT), protozoa, nematodes, rickettsiae	Pathogens cause lethal infections on mites	Some strains of Bacillaceae and Micrococcaceae increased mortality in in vitro tests; until now no Varroa-specific strains known	Aronson et al. (1986), Ball and Allen (1988), Glinski and Jarosz (1990), Tsagou et al. (2004), Van der Geest et al. (2000)

However, there are also some disadvantages of these natural compounds. Lactic acid and oxalic acid have to be applied under broodless conditions (Emsen and Dodologlu, 2009; Higes et al., 1999) and, therefore, are not suitable in regions without a brood stop during winter. The efficacy of some compounds depends of the evaporation pressure within the colony. Therefore, the climatic and within-hive conditions and the mode of application have to be carefully tuned for the optimal effect. This is crucial as the "therapeutic index", the range between efficacy on the parasite and toxicity for the host, is not very large. This has to be taken into account for the development of treatment concepts which include these compounds (Bolli et al., 1993; Higes et al., 1999; Martin-Hernandez et al., 2007; Mattila et al., 2000). In general this means that the effects from organic acids and essential oils often are more variable, compared to registered acaricides.

6.3. Biotechnical and biological methods

Biological methods which include peculiarities of the biology of host and parasite are the real, sustainable approaches for *Varroa* treatment. So far, real biological and effective treatment methods do not exist. However, use of the chemoecological features of the mites seems to have some potential for future use (Yoder and Sammataro, 2003).

The "trapping comb method" as a biotechnical approach has already been used successfully. The principle is to remove mites within the sealed honey bee brood from the colony which may be rather effective (Engels et al., 1984; Maul et al., 1988) due to the uneven distribution between "brood mites" and "bee mites" (Boot et al., 1993; Rosenkranz and Renz, 2003). Most applications concentrate solely on the removal of drone brood, which can be eliminated without any negative effect on colony size or honey production (Calderone, 2005). The removal of 3–4 completely capped drone combs at the beginning of the season reduces the final mite population about 50–70% (Charrière et al., 2003). The "trapping comb technique" with worker brood requires temporary confinement of the queen to selected combs, subsequent removal of these combs, selective killing of the mites (with formic acid or heat; Calis et al., 1998, 1999a), and returning the combs to the colonies. This is a labor-intensive procedure and only recommended in regions without late honey flows, however, it can cure heavily infested colonies without any chemical treatment (Fries and Hansen, 1993).

Other non-chemical tools include work intensive applications like heat treatments (Hoppe and Ritter, 1987; Rosenkranz, 1987), methods without sufficiently confirmed efficacy (small cells, wire netting bottom boards, powdered sugar or extra fine dust), and "exotic" approaches with only anecdotal "proofs" (acoustic waves, electromagnetic fields, "energized" water, activated metal disks). For more details and references see Table 2.

An example for an initially promising method which did not meet expectations is the use of comb foundations with smaller cells (see also in Sections 3.2 and 5.2.4). Under field conditions, a significant effect of small cells on the *Varroa* population dynamics could not been verified, in the United States Germany or in New Zealand (Berry et al., in press; Ellis et al., 2009a; Liebig and Aumeier, 2007; Taylor et al., 2008).

Even if the predicted efficacy of the open-screened bottom boards is not confirmed (Harbo and Harris, 2004; Rinderer et al., 2003), it is a valuable tool to estimate the size of mite populations (Branco et al., 2006) and/or to monitor the efficacy of treatments (Calderone and Lin, 2003). Compared to other diagnostic methods like acaricidal treatment, alcohol or detergent washes of adult bee and brood samples (Gregorc and Smodis Skerl, 2007; Rinderer et al., 2004) the measurement of the natural mite mortality is easy, cheap and fast. Depending on season and on the amount of brood, a

natural downfall of 0.5–10 mites on the bottom board is regarded to be the threshold for a basic necessity of treatment (Arbeitsgemeinschaft der Institute für Bienenforschung e.V., 2007; Gregorc and Smodis Skerl, 2007; Liebig, 2001; Martin, 2001b). This corresponds to an absolute mite population of 2000–3000 mites which is considered as an economic threshold (Delaplane and Hood, 1999). In general, feasible diagnostic tools are an essential component of integrated pest management (IPM; Faucon et al., 2007).

Another promising approach for *Varroa* management is the use of antagonistic, parasitic or pathogenic organisms. This mode of "natural pest control" could be applied without concern about the contamination of bee products. Those antagonists could even spread autonomously between colonies creating long-term effects (Van der Geest et al., 2000). However, the data base is still weak with contradictory results.

The most substantial efforts have been undertaken with entomo-pathogenic fungi, which are important natural regulators of pestiferous eriophyoid and tetranychid mites (Chandler et al., 2000). Shaw et al. (2002) reported the impressive lethal effects of conidia (asexual spores) of the genera *Metarhizium*, *Beauveria* or *Verticillium* on *V. destructor* in laboratory assays. Additional reports support the hope of the beekeeper that at least during broodless periods an effective control without side effects is possible (Garcia-Fernandez et al., 2008; Kanga et al., 2003; Meikle et al., 2008). Other researchers, however, did not observe a significant mite-specific impact of different strains of these nonspecific entomo-pathogenic fungi (Holt et al., in press; James, 2009). Therefore, to date no biological commercial product for *Varroa* treatment is available. Further research is required to identify and clarify the taxonomic status of *Varroa*-specific fungi (Chandler et al., 2001).

6.4. Treatment concepts

To prevent the occurrence of the "parasitic mite syndrome" in *Varroa*-infested colonies, combined treatments are required which are adapted to the local climatic and beekeeping conditions. A state-of-the-art concept should consider the following aspects:

- Periodic treatment depending on mite population growth and the risk of "reinfestation" from other non-treated bee hives (Fries and Camazine, 2001; Goodwin et al., 2006; Greatti et al., 1992; Sakofski et al., 1990).
- No chemical treatment during the nectar flow.
- If possible, acaricides with natural compounds and biotechnical methods should be preferred.
- In temperate climates, treatments have to be performed prior to the production of overwintering bees. Only healthy winter bees which were not parasitized during their ontogenetic development are long lived with the chance to survive until next spring (Amdam et al., 2004; Martin, 2001b).
- Use of a suitable diagnostic tool to define the optimal time for treatment, to control the efficacy of treatments, and to recognize an unexpected reinfestation of mites.
- Different treatments with different modes of action should be combined to avoid resistance of the mites and increase the overall efficacy.

Meanwhile, several examples of effective strategies for "Integrated *Varroa* Management" are published (Arbeitsgemeinschaft der Institute für Bienenforschung e.V., 2007; European Group for Integrated Varroa Control, 1999; Rice et al., 2004; Sammataro et al., 2004).

7. Summary and outlook

Varroa mites have been considered a problem for beekeeping for about 40 years; 10 years later the mite reached Western Europe and South-America and another 10 years later, the United States. So, we now look back on more than 30 years of intensive research on various aspects of the biology, pathology and management of this parasite. To summarize the efforts we can state that we have significantly increased our knowledge on mite distribution, pathogenesis, host–parasite interactions and effective use of certain treatments. In most countries the *Varroa* situation is stable; the beekeepers have learned to "live with the mite" and most of them do not know beekeeping without Varroosis. Most extension services of state experts and beekeeping organizations have successfully focused on integrated *Varroa* management considering the local beekeeping conditions.

However, we must also state that we have not achieved the original aim to get rid of the parasite or at least to solve the problems related to Varroosis. There is neither a *Varroa* treatment available which fulfills all the criteria "safe, effective and easy to apply" nor a honey bee which is sustainably tolerant to Varroosis under temperate climatic conditions. Rather, we now face new problems with secondary diseases and damage in honey bee colonies caused by synergistic effects of Varroosis plus other pathogens or environmental factors (EU-project COLOSS; Oldroyd, 2007). In addition, there are still no data showing that *Varroa* in general becomes less virulent or that honey bee colonies selected for mite tolerance survive without mite control. These aspects will maintain the pressure on honey bee colonies and beekeepers especially in the non-tropical countries with the significant risks for pollination services.

This also means that further *Varroa* research is urgently needed and that the respective scientists and the research funding organisations have a responsibility to promote applied scientific approaches. Based on our experiences so far in *Varroa* research, the following aspects should be considered for future projects:

(1) Future scientific activities should focus on the most important research fields. These include: (i) the development and optimization of safe and effective treatment concepts including new approaches on biological treatments, (ii) a better understanding of the *Varroa* pathogenesis including secondary infections and synergistic effects, (iii) the detailed study of host factors which abate the growth of the mite population, and (iv) the use of such knowledge for selective breeding of tolerant stocks.
(2) The potential benefit of the results for the beekeeping practice must be estimated realistically. It is naïve to believe that the main problems of Varroosis like effective treatment or host tolerance can be solved within a few years.
(3) Long-term solutions require long-term projects and more international cooperation (i) to prevent redundant approaches, and (ii) to promote multidisciplinary efforts by including scientists from neighboring research fields in honey bee pathology.

Conflicts of interest

There are no conflicts of interest to be declared.

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References

Al Aattal, Y., Rosenkranz, P., Zebitz, C.P.W., 2006. Reproduction of *Varroa destructor* in sealed worker brood cells of *Apis mellifera* carnica and *A. m. syriaca* in Jordan. Mitt. Dtsch. Ges. Allg. Angew. Entom. 15, 315–319.

Alberti, G., 1980a. Zur Feinstruktur der Spermien und Spermiocytogenese der Milben (Acari). I. Anactinotrichida. Zool. Jb. Anat. 104, 77–138.

Alberti, G., 1980b. Zur Feinstruktur der Spermien und Spermiocytogenese der Milben (Acari). II. Actinotrichida. Zool. Jb. Anat. 104, 144–203.

Alberti, G., Hänel, H., 1986. Fine structure of the genital system in the bee parasite, *Varroa jacobsoni* (Gamasida: Dermanyssina) with remarks on spermiogenesis, spermatozoa and capacitation. Exp. Appl. Acarol. 2, 63–104.

Alberti, G., Zeck-Kapp, G., 1986. The nutrimentary egg development in the mite, *Varroa jacobsoni* (Acari, Arachnida), an ectoparasite of honey bee. Acta Zool. (Stock) 67, 11–25.

Aliano, N.P., Ellis, M.D., 2005. A strategy for using powdered sugar to reduce *Varroa* populations in honey bee colonies. J. Apicult. Res. 44 (2), 54–57.

Aliano, N.P., Ellis, M.D., 2008. Bee-to-bee contact drives oxalic acid distribution in honey bee colonies. Apidologie 39 (5), 481–487.

Allen, M.F., Ball, B.V., White, R.F., Antoniw, J.F., 1986. The detection of acute paralysis virus in *Varroa jacobsoni* by the use of a simple indirect ELISA. J. Apicult. Res. 25, 100–105.

Amdam, G.V., Hartfelder, K., Norberg, K., Hagen, A., Omholt, S.W., 2004. Altered physiology in worker honey bees (Hymenoptera: Apidae) infested with the mite *Varroa destructor* (Acari: Varroidae): a factor in colony loss during overwintering? J. Econ. Entomol. 97 (3), 741–747.

Anderson, D.L., 1994. Non-reproduction of *Varroa jacobsoni* in *Apis mellifera* colonies in Papua New Guinea and Indonesia. Apidologie 25, 412–421.

Anderson, D., 2000. Variation in the parasitic bee mite *Varroa jacobsoni* Oud. Apidologie 31, 281–292.

Anderson, D.L., East, I.J., 2008. The latest buzz about colony collapse disorder. Science 319 (5864), 724–725.

Anderson, D.L., Fuchs, S., 1998. Two genetically distinct populations of *Varroa jacobsoni* with contrasting reproductive abilities on *Apis mellifera*. J. Apicult. Res. 37, 69–78.

Anderson, D.L., Sukarsih, 1996. Changed *Varroa jacobsoni* reproduction in *Apis mellifera* colonies in Java. Apidologie 27, 461–466.

Anderson, D.L., Trueman, J.W.H., 2000. *Varroa jacobsoni* (Acari: Varroidae) is more than one species. Exp. Appl. Acarol. 24, 165–189.

Arbeitsgemeinschaft der Institute für Bienenforschung e.V., 2007. *Varroa* unter Kontrolle. <http://www.adiz-online.de/online/102422/*Varroa*.pdf>.

Arechavaleta-Velasco, M.E., Guzman-Novoa, E., 2001. Relative effect of four characteristics that restrain the population growth of the mite *Varroa destructor* in honey bee (*Apis mellifera*) colonies. Apidologie 32 (2), 157–174.

Aronson, A.I., Beckman, W., Dunn, P., 1986. *Bacillus thuringiensis* and related insect pathogens. Microbiol. Rev. 50, 1–24.

Aumeier, P., 2001. Bioassay for grooming effectiveness towards *Varroa destructor* mites in Africanized and Carniolan honey bees. Apidologie 32, 81–90.

Aumeier P., Kirchner W.H., Liebig G., 2006. Topsy-turvy brood combs – Impact on population dynamics of honey bees (*Apis mellifera* L.) and *Varroa destructor*. In: EurBee, Proceedings of the Second European Conference of Pidology 2006, p. 46.

Aumeier, P., Rosenkranz, P., 2001. Scent or movement of *Varroa destructor* mites does not elicit hygienic behaviour by Africanized and Carniolan honey bees. Apidologie 32, 253–263.

Aumeier, P., Rosenkranz, P., Francke, W., 2002. Cuticular volatiles, attractivity of worker larvae and invasion of brood cells by *Varroa* mites. A comparison of Africanized and European honey bees. Chemoecology 12, 65–75.

Aumeier, P., Rosenkranz, P., Gonçalves, L.S., 2000. A comparison of the hygienic response of Africanized and European (*Apis mellifera carnica*) honey bees to *Varroa*-infested brood in tropical Brazil. Genet. Mol. Biol. 23 (4), 787–791.

Bacandritsos, N., Papanastasiou, I., Saitanis, C., Nanetti, A., Roinioti, E., 2007. Efficacy of repeated trickle applications of oxalic acid in syrup for Varroosis control in *Apis mellifera*: influence of meteorological conditions and presence of brood. Vet. Parasitol. 148, 174–178.

Bailey, L., Ball, B.V., 1991. Honey Bee Pathology. Academic Press, London.

Ball, B.V., Allen, M.F., 1988. The prevalence of pathogens in honey bee (*Apis mellifera*) colonies infested with the parasitic mite *Varroa jacobsoni*. Ann. Appl. Biol. 113, 237–244.

Barrington, A., Venis, T., 2005. A new delivery method for Sucrocide, the safe *Varroa* mite treatment. Am. Bee J. 145 (7), 583–586.

Becher, M.A., Moritz, R.F.A., 2009. A new device for continuous temperature measurement in brood cells of honeybees (*Apis mellifera*). Apidologie 40. doi:10.1051/apido/2009031.

Beetsma, J., Boot, W.J., Calis, J.N.M., 1999. Invasion behaviour of *Varroa jacobsoni* (Oud.): from bees into brood cells. Apidologie 30, 125–140.

Berry, J.A., Owens, W.B., Delaplane, K.S., in press. Small-cell comb foundation does not impede Varroa mite population growth in honey bee colonies. Apidologie, in press.

Bienefeld, K., Zautke, F., 2007. Suitability of the trait postcapping stage of brood for selecting *Varroa*-resistant honey bees. Züchtungskunde 79 (3), 209–218.

Boecking, O., 1992. Defences of bees against *Varroa jacobsoni* defence mechanisms in *Apis cerana* and *Apis mellifera*. Deut. Imker J. 11, 426–430.

Boecking, O., Bienefeld, K., Drescher, W., 2000. Heritability of the *Varroa*-specific hygienic behaviour in honey bees (Hymenoptera: Apidae). J. Anim. Breedg. Genet. 117 (6), 417–424.

Boecking, O., Genersch, E., 2008. Varroosis – the ongoing crisis in bee keeping. J. Consum. Protect. Food Safety 3 (2), 221–228.

Boecking, O., Ritter, W., 1993. Grooming and removal behavior of *Apis mellifera* intermissa in tunesia against *Varroa jacobsoni*. J. Apicult. Res. 32 (3–4), 127–134.

Boecking, O., Rosenkranz, P., Sasaki, M., 1999. The pore in the hard conical *Apis cerana* drone capping results from a spinning process. Apidologie 30, 513–519.

Boecking, O., Spivak, M., 1999. Behavioral defenses of honey bees against *Varroa jacobsoni* Oud. Apidologie 30 (2–3), 141–158.

Bogdanov, S., 2006. Contaminants of bee products. Apidologie 37 (1), 1–18.

Bogdanov, S., Charriere, J.D., Imdorf, A., Kilchenmann, V., Fluri, P., 2002. Determination of residues in honey after treatments with formic and oxalic acid under field conditions. Apidologie 33 (4), 399–409.

Bogdanov, S., Imdorf, A., Kilchenmann, V., 1998. Residues in wax and honey after Apilife VAR (R) treatment. Apidologie 29 (6), 513–524.

Bolli, H.K., Bogdanov, S., Imdorf, A., Fluri, P., 1993. Action of formic acid on *Varroa jacobsoni* Oud and the honeybee (*Apis mellifera* L.). Apidologie 24 (1), 51–57.

Boot, W.J., Calis, J.N.M., Beetsma, J., 1992. Differential periods of *Varroa* mite invasion into worker and drone cells of honey bees. Exp. Appl. Acarol. 16, 295–301.

Boot, W.J., Calis, J.N.M., Beetsma, J., 1993. Invasion of *Varroa jacobsoni* into honey bee brood cells: a matter of chance or choice? J. Apicult. Res. 32, 167–174.

Boot, W.J., Calis, J.N.M., Beetsma, J., Hai, D.M., Lan, N.K., Van Tran, T., Trung, L.Q., Minh, N.H., 1999. Natural selection of *Varroa jacobsoni* explains the different reproductive strategies in colonies of *Apis cerana* and *Apis mellifera*. Exp. Appl. Acarol. 23 (2), 133–144.

Boot, W.J., Driessen, R.G., Calis, J.N.M., Beetsma, J., 1995a. Further observations on the correlation between attractiveness of honey bee brood cells to *Varroa jacobsoni* and the distance from larva to cell rim. Entomol. Exp. Appl. 76, 223–232.

Boot, W.J., Schoenmaker, J., Calis, J.N.M., Beetsma, J., 1995b. Invasion of *Varroa jacobsoni* into drone brood cells of the honey bee, *Apis mellifera*. Apidologie 26, 109–118.

Boot, W.J., Tan, N.Q., Dien, P.C., Huan, L.V., Dung, N.V., Long, L.T., Beetsma, J., 1996. Reproductive success of *Varroa jacobsoni* in brood of its original host, *Apis cerana*, in comparison to that of its new host, *Apis mellifera*. Bull. Entomol. Res. 87, 119–126.

Bourgeois, A.L., Rinderer, T.E., 2009. Genetic characterization of Russian honey bee stock selected for improved resistance to *Varroa destructor*. J. Econ. Entomol. 102 (3), 1233–1238.

Bowen-Walker, P.L., Martin, S.J., Gunn, A., 1999. The transmission of deformed wing virus between honeybees (*Apis mellifera*) by the ectoparasitic mite *Varroa jacobsoni* Oud. J. Invertebr. Pathol. 73, 101–106.

Branco, M.R., Kidd, N.A.C., Pickard, R.S., 2006. A comparative evaluation of sampling methods for *Varroa destructor* (Acari: Varroidae) population estimation. Apidologie 37 (4), 452–461.

Brødsgaard, C.J., Hansen, H., 1994. An example of interacted biotechnical and soft chemical control of *Varroa* in a Danish apiary. In: Matheson, A. (Ed.), New Perspectives on *Varroa*. International Bee Research Association, pp. 101–105.

Brødsgaard, C.J., Ritter, W., Hansen, H., 2000. Interactions among *Varroa jacobsoni* mites, acute paralysis virus, and *Paenibacillus larvae larvae* and their influence on mortality of larval honeybees in vitro. Apidologie 31, 543–554.

Büchler, R., 1994. *Varroa* tolerance in honey bees – occurrence, characters and breeding. Bee World 49, 6–18.

Büchler, R., Drescher, W., 1990. Variance and heritability of the capped developmental stage in European *Apis mellifera* L. and its correlation with increased *Varroa jacobsoni* infestation. J. Apicult. Res. 29 (3), 172–176.

Büchler, R., Garrido, C., Bienefeld, K., Erhardt, K., 2008. Selection for *Varroa* tolerance: concept and results of a long-term selection project. Apidologie 39, 598.

Cakmak, I., Aydin, L., Wells, H., 2006. Walnut leaf smoke versus mint leaves in conjunction with pollen traps for control of *Varroa destructor*. Bull. Vet. Inst. Pulawy 50 (4), 477–479.

Calatayud, F., Verdu, M.J., 1995. Number of adult female mites *Varroa jacobsoni* Oud. on hive debris from honeybee colonies artificially infested to monitor mite population increase (Mesostigmata: Varroidae). Exp. Appl. Acarol. 19, 181–188.

Calderone, N.W., 1999. Evaluation of formic acid and a thymol-based blend of natural products for the fall control of *Varroa jacobsoni* (Acari: Varroidae) in colonies of *Apis mellifera* (Hymenoptera: Apidae). J. Econ. Entomol. 92, 253–260.

Calderone, N.W., 2005. Evaluation of drone brood removal for management of *Varroa destructor* (Acari: Varroidae) in colonies of *Apis mellifera* (Hymenoptera: Apidae) in the northeastern United States. J. Econ. Entomol. 98 (3), 645–650.

Calderone, N.W., Kuenen, L.P.S., 2001. Effects of western honey bee (Hymenoptera: Apidae) colony, cell, type, and larval sex on host acquisition by female *Varroa destructor* (Acari: Varroidae). J. Econ. Entomol. 94, 1022–1030.

Calderone, N.W., Kuenen, L.P.S., 2003. Differential tending of worker and drone larvae of the honey bee, *Apis mellifera*, during the 60 hours prior to cell capping. Apidologie 34, 543–552.

Calderone, N.W., Lin, S., 2001. Arrestment activity of extracts of honey bee worker and drone larvae, cocoons and brood food on female *Varroa destructor*. Physiol. Entomol. 26, 341–350.

Calderone, N.W., Lin, S., 2003. Rapid determination of the numbers of *Varroa destructor*, a parasitic mite of the honey bee, *Apis mellifera*, on sticky-board collection devices. Apidologie 34 (1), 11–17.

Calderone, N.W., Lin, S., Kuenen, L.P.S., 2002. Differential infestation of honey bee, *Apis mellifera*, worker and queen brood by the parasitic mite *Varroa destructor*. Apidologie 33, 389–398.

Calderone, N.W., Nasr, M.E., 1999. Evaluation of formic acid formulation for the fall control of *Varroa jacobsoni* (Acari: Varroidae) in colonies of the honey bee *Apis mellifera* (Hymenoptera: Apidae) in a temperate climate. J. Econ. Entomol. 92, 526–533.

Calis, J.N.M., Boot, W.J., Beetsma, J., van den Eijnde, J.H.P.M., de Ruijter, A., van der Steen, J.J.M., 1998. Control of *Varroa* by combining trapping in honey bee worker brood with formic acid treatment of the capped brood outside the colony: putting knowledge on brood cell invasion into practice. J. Apicult. Res. 37 (3), 205–215.

Calis, J.N.M., Boot, W.J., Beetsma, J., van den Eijnde, J.H.P.M., de Ruijter, A., van der Steen, J.J.M., 1999a. Effective biotechnical control of *Varroa*: applying knowledge on brood cell invasion to trap honey bee parasites in drone brood. J. Apicult. Res. 38 (1–2), 49–61.

Calis, J.N.M., Fries, I., Ryrie, S.C., 1999b. Population modelling of *Varroa jacobsoni* Oud. Apidologie 30, 111–124.

Camazine, S., 1986. Differential reproduction of the mite, *Varroa jacobsoni* (Mesostigmata: Varroidae), on Africanized and European honey bees (Hymenoptera: Apidae). Ann. Entomol. Soc. Am. 79, 801–803.

Carneiro, F.E., Torres, R.R., Strapazzon, R., Ramirez, S.A., Guerra, J.C.V., Koling, D.F., Moretto, G., 2007. Changes in the reproductive ability of the mite *Varroa destructor* (Anderson and Trueman) in Africanized honey bees (*Apis mellifera* L.) (Hymenoptera: Apidae) colonies in southern Brazil. Neotrop. Entomol. 36 (6), 949–952.

Chandler, D., Davidson, G., Pell, J.K., Ball, B.V., Shaw, K., Sunderland, K.D., 2000. Fungal biocontrol of Acari. Biocontrol Sci. Technol. 10 (4), 357–384.

Chandler, D., Sunderland, K.D., Ball, B.V., Davidson, G., 2001. Prospective biological control agents of *Varroa destructor* n. sp., an important pest of the European honeybee, *Apis mellifera*. Biocontrol Sci. Technol. 11 (4), 429–448.

Charrière, J.D., Imdorf, A., 2002. Oxalic acid treatment by trickling against *Varroa destructor*: recommendations for use in central Europe and under temperate climate conditions. Bee World 83, 51–60.

Charrière, J.D., Imdorf, A., Bachofen, B., Tschan, A., 2003. The removal of capped drone brood: an effective means of reducing the infestation of *Varroa* in honey bee colonies. Bee World 84 (3), 117–124.

Charrière, J.D., Imdorf, A., Fluri, P., 1998. Potentiel et limites de l'acaricide oxalique pour lutter contre *Varroa*. Rev. Suisse d'apic. 95 (8), 311–316.

Chauzat, M.P., Carpentier, P., Martel, A.C., Bougeard, S., Cougoule, N., Porta, P., Lachaize, J., Madec, F., Aubert, M., Faucon, J.P., 2009. Influence of pesticide residues on honey bee (Hymenoptera: Apidae) colony health in France. Environ. Entomol. 38, 514–523.

Chen, Y.-P., Siede, R., 2007. Honey bee viruses. Adv. Virus Res. 70, 33–80.

Chiroudi, E., Rosenkranz, P., Aumeier, P., 1997. Altersabhängige und rassenspezifische Duftstoffmuster bei Arbeiterinnen der Honigbiene (*A. mellifera*). Mittlg. der dt. Ges. Allg. Angew. Entomol. 11, 179–182.

Colin, M.E., 1990. Essential oils of labiatae for controlling honey bee varroosis. J. Appl. Entomol. 110, 19–25.

Correa-Marques, M.H., De Jong, D., Rosenkranz, P., Gonçalves, L.S., 2002. *Varroa*-tolerant Italian honey bees introduced from Brazil were not more efficient in defending themselves against the mite *Varroa destructor* than Carniolan bees in Germany. Genet. Mol. Res. 1, 199–204.

Correa-Marques, M.H., Medina Media, L., Martin, S.J., De Jong, D., 2003. Comparing data on the reproduction of *Varroa destructor*. Genet. Mol. Res. 2, 1–6.

Cox-Foster, D.L., Conlan, S., Holmes, E.C., Palacios, G., Evans, J.D., Moran, N.A., Quan, P.L., Briese, T., Hornig, M., Geiser, D.M., Martinson, V., vanEngelsdorp, D., Kalkstein, A.L., Drysdale, A., Hui, J., Zhai, J.H., Cui, L.W., Hutchison, S.K., Simons, J.F., Egholm, M., Pettis, J.S., Lipkin, W.I., 2007. A metagenomic survey of microbes in honey bee colony collapse disorder. Science 318 (5848), 283–287.

Currie, R.W., Gatien, P., 2006. Timing acaricide treatments to prevent *Varroa destructor* (Acari: Varroidae) from causing economic damage to honey bee colonies. Can. Entomol. 138 (2), 238–252.

Currie, R.W., Tahmasbi, G.H., 2008. The ability of high- and low-grooming lines of honey bees to remove the parasitic mite *Varroa destructor* is affected by environmental conditions. J. Can. Zool. 86 (9), 1059–1067.

Davis, A.R., 2009. Regular dorsal dimples on *Varroa destructor* – damage symptoms or developmental origin? Apidologie 40 (2), 151–162.

De D'Aubeterre, J.P., Myrold, D.D., Royce, L.A., Rossignol, P.A., 1999. A scientific note of an application of isotope ratio mass spectrometry to feeding by the mite, *Varroa jacobsoni* Oudemans, on the honeybee, *Apis mellifera* L. Apidologie 30, 351–352.

DeGrandi-Hoffman, G., Curry, R., 2004. A mathematical model of *Varroa* mite (*Varroa destructor* Anderson and Trueman) and honeybee (*Apis mellifera* L.) population dynamics. Int. J. Acarol. 30 (3), 259–274.

De Guzman, L.I., Delfinado-Baker, M., 1996. A new species of *Varroa* (Acari: Varroidae) associated with *Apis koschevnikovi* (Apidae: Hymenoptera) in Borneo. Int. J. Acarol. 22, 23–27.

De Guzman, L.I., Rinderer, T.E., 1999. Identification and comparison of *Varroa* species infesting honey bees. Apidologie 30, 85–95.

De Guzman, L.I., Rinderer, T.E., Frake, A.M., 2007. Growth of *Varroa destructor* (Acari: Varroidae) populations in Russian honey bee (Hymenoptera: Apidae) colonies. Ann. Entomol. Soc. Am. 100 (2), 187–195.

de Guzman, L.I., Rinderer, T.E., Frake, A.M., 2008. Comparative reproduction of *Varroa destructor* in different types of Russian and Italian honey bee combs. Exp. Appl. Acarol. 44 (3), 227–238.

De Guzman, L.I., Rinderer, T.E., Stelzer, J.A., Anderson, D., 1998. Congruence of RAPD and mitochondrial DNA markers in assessing *Varroa jacobsoni* genotypes. J. Apicult. Res. 37, 49–51.

De Jong, D., 1996. Africanized honey bees in Brazil, forty years of adaptation and success. Bee World 77, 67–70.

De Jong, D., De Jong, P.H., Gonçalves, L.S., 1982. Weight loss and other damage to developing worker honeybees from infestation with *V. jacobsoni*. J. Apicult. Res. 21, 165–216.

De Jong, D., Gonçalves, L.S., Morse, R.A., 1984. Dependence of climate of the virulence of *Varroa jacobsoni*. Bee World 65, 117–121.

De Jong, D., Soares, A.E.E., 1997. An isolated population of Italian bees that has survived *Varroa jacobsoni* infestation without treatment for over 12 years. Am. Bee J. 137, 742–745.

Dekeyser, M.A., Downer, R.G.H., 1994. Biochemical and physiological targets for miticides. Pestic. Sci. 40 (2), 85–101.

Delaplane, K.S., Hood, W.M., 1999. Economic threshold for *Varroa jacobsoni* Oud. in the southeastern USA. Apidologie 30, 383–395.

De la Rua, P., Jaffe, R., DalÍOlio, R., Muñoz, I., Serrano, J., 2009. Biodiversity, conservation and current threats to European honeybees. Apidologie 40, 263–284.

Della Vedova, G., Milani, N., 1999. Efficacy against *Varroa jacobsoni* Oudemans and tolerability by bees of the product Apiguard®. Apidologie 30, 438–440.

De Miranda, J., Cordoni, G., Budge, G., 2010. The Acute Paralysis virus–Kashmere bee virus–Israeli acute paralysis virus complex. J. Invertebr. Pathol. S30–S47.

De Miranda J., Genersch E., 2010. Deformed wing virus. J. Invertebr. Pathol. S48–S61

Delfinado-Baker, M., Aggarwal, K., 1987. A new *Varroa* (Acari: Varroidae) from the nest of *Apis cerana* (Apidae). Int. J. Acarol. 13, 233–237.

Delfinado-Baker, M., Rath, W., Boecking, O., 1992. The phoretic bee mites and honeybee grooming behaviour. Int. J. Acarol. 18, 315–322.

De Ruijter, A., 1982. Tobacco smoke can kill *Varroa* mites. Bee World 63, 138.

De Ruijter, A., 1987. Reproduction of *Varroa jacobsoni* during successive brood cycles. Apidologie 18, 321–326.

De Ruijter, A., Calis, J.N.M., 1988. Distribution of *Varroa jacobsoni* female mites in honey bee worker brood cells of normal and manipulated depth. Entomol. Gen. 14, 107–109.

De Ruijter, A., Kaas, J.P., 1983. The anatomy of the *Varroa* mite. In: Cavalloro, R. (Ed.), *Varroa jacobsoni* Oud Affecting Honey Bees: Present Status and Needs. A.A. Balkema, Rotterdam, pp. 45–47.

Desneux, N., Decourtye, A., Delpuech, J.M., 2007. The sublethal effects of pesticides on beneficial arthropods. Annu. Rev. Entomol. 52, 81–106.

Dillier, F.-X., Fluri, P., Imdorf, A., 2006. Review of the orientation behaviour in the bee parasitic mite *Varroa destructor*: sensory equipment and cell invasion behaviour. Rev. Suisse Zool. 113 (4), 857–877.

Donovan, B.J., Paul, F., 2005. Pseudoscorpions: the forgotten beneficials inside beehives and their potential for management for control of *Varroa* and other arthropod pests. Bee World 86 (4), 83–87.

Donovan, B.J., Paul, F., 2006. Pseudoscorpions to the rescue? Indian pseudoscorpions kill *Varroa* and other arthropod enemies of bees inside hives. Am. Bee J. 146 (10), 867–869.

Donzé, G., Guerin, P.M., 1994. Behavioral attributes and parental care of *Varroa* mites parasitizing honeybee brood. Behav. Ecol. Sociobiol. 34, 305–319.

Donzé, G., Herrmann, M., Bachofen, B., Guerin, P.M., 1996. Effect of mating frequency and brood cell infestation rate on the reproductive success of the honeybee parasite *Varroa jacobsoni*. Ecol. Entomol. 21, 17–26.

Donzé, G., Schneyder-Candrian, S., Bogdanov, S., Diehl, P.A., Guerin, P.M., Kilchenmann, V., Monachon, F., 1998. Aliphatic alcohols and aldehydes of the honey bee cocoon induce arrestment behavior in *Varroa jacobsoni* (Acari: Mesostigmata), an ectoparasite of *Apis mellifera*. Arch. Insect. Biochem. Physiol. 37, 129–145.

Downey, D.L., Winston, M.L., 2001. Honey bee colony mortality and productivity with single and dual infestations of parasitic mite species. Apidologie 32, 567–575.

Drijfhout, F.P., Kochansky, J., Lin, S., Calderone, N.W., 2005. Components of honeybee royal jelly as deterrents of the parasitic *Varroa* mite, *Varroa destructor*. J. Chem. Ecol. 31, 1747–1764.

Duay, P., de Jong, D., Engels, W., 2002. Decreased flight performance and sperm production in drones of the honey bee (*Apis mellifera*) slightly infested by *Varroa destructor* mites during pupal development. Genet. Mol. Res. 1, 227–232.

Duay, P., de Jong, D., Engels, W., 2003. Weight loss in drone pupae (*Apis mellifera*) multiply infested by *Varroa destructor* mites. Apidologie 34, 61–65.

Echazarreta, C.M., Paxton, R., 1997. Comparative colony development of Africanized and European honey bees (*Apis mellifera*) in lowland Neotropical Yucatan, Mexico. J. Apicult. Res. 36, 89–103.

Eguaras, M., Marcangeli, J., Oppedisano, M., Fernández, N., 1994. Seasonal changes in *Varroa jacobsoni* reproduction in temperate climates of Argentina. Bee Sci. 3, 120–123.

Eguaras, M., Marcangeli, J., Oppedisano, M., Fernandez, N., 1995. Mortality and reproduction of *Varroa jacobsoni* in resistant colonies of honey bees (*Apis mellifera*) in Argentina. Bee Sci., 174–178.

Eischen, F.A., Wilson, T., 1998. The effect of natural product smoke on *Varroa jacobsoni*: an update. Am. Bee J. 138, 293.

Ellis, J.D., Delaplane, K.S., Hood, W.M., 2001. Efficacy of a bottom screen device, Apistan (TM), and Apilife VAR (TM), in controlling *Varroa destructor*. Am. Bee J. 141 (11), 813–816.

Ellis, A.M., Hayes, G.W., Ellis, J.D., 2009a. The efficacy of small cell foundation as a *Varroa* mite (*Varroa destructor*) control. Exp. Appl. Acarol. 47 (4), 311–316.

Ellis, A.M., Hayes, G.W., Ellis, J.D., 2009b. The efficacy of dusting honey bee colonies with powdered sugar to reduce *Varroa* mite populations. J. Apicult. Res. 48 (1), 72–76.

Elzen, P.J., Baxter, J.R., Spivak, M., Wilson, W.T., 1999a. Amitraz resistance in *Varroa*: new discovery in North America. Am. Bee J. 139, 362.
Elzen, P.J., Baxter, J.R., Spivak, M., Wilson, W.T., 2000. Control of *Varroa jacobsoni* Oud resistant to fluvalinate and amitraz using coumaphos. Apidologie 31, 437–441.
Elzen, P.J., Baxter, J.R., Westervelt, D., Causey, D., Randall, C., Cutts, L., Wilson, W.T., 2001. Acaricide rotation plan for control of *Varroa*. Am. Bee J. 141, 412.
Elzen, P.J., Eischen, F.A., Baxter, J.R., Elzen, G.W., Wilson, W.T., 1999b. Detection of resistance in US *Varroa jacobsoni* Oud. (Mesostigmata: Varroidae) to the acaricide fluvalinate. Apidologie 30, 13–17.
Emsen, B., Dodologlu, A., 2009. the effects of using different organic compounds against Honey Bee Mite (*Varroa destructor* Anderson and Trueman) on colony developments of honey bee (*Apis mellifera* L.) and residue levels in honey. J. Anim. Vet. Adv. 8 (5), 1004–1009.
Endris, J.J., Baker, R.T.C., 1993. Aktionspotentiale, abgeleitet am ersten Laufbein von *Varroa jacobsoni*, nach olfactorischer Stimulierung. Apidologie 24, 488–489.
Engels, W., Rosenkranz, P., Hertl, F., Staemmler, G., 1984. Effect of drone brood removal on *Varroa* infested honey bee colonies. Apidologie 15 (3), 246–248.
European Group for Integrated Varroa Control, 1999. Coordination in Europe of research on integrated control of *Varroa* mites in honey bee colonies. Meeting November 13–14, 1999, Merelbeke, Belgium. <http://www.apis.admin.ch/host/doc/pdfvarroa/Merelbeke.pdf> (accessed 20.10.05).
Evans, J.D., Spivak, M., 2010. Socialized medicine: Individual and communal disease barriers in honey bees. J. Invertebr. Pathol. 103, S62–S72.
Fahle, N., Rosenkranz, P., 2005. Mate choice in *Varroa destructor*: male mites prefer young females. In: IUSSI-Proceedings of the German Section Meeting at Halle, ISBN 3-901864-02-4.
Fakhimzadeh, K., 2001. Effectiveness of confectioner sugar dusting to knock down *Varroa destructor* from adult honey bees in laboratory trials. Apidologie 32 (2), 139–148.
Fassbinder, C., Grodnitzky, J., Coats, J., 2002. Monoterpenoids as possible control agents for *Varroa destructor*. J. Apicult. Res. 41 (3–4), 83–88.
Faucon, J.P., Chauzat, M.P., 2008. Varroosis and others honey bee diseases: major causes for colony mortality in France. Bull. Acad. Vet. France 161, 257–263.
Faucon, J.P., Drajnudel, P., Chauzat, M.P., Aubert, M., 2007. Control of the efficacy of APIVAR ND against *Varroa destructor*, a parasite of *Apis mellifera*. Rev. Med. Vet. 158 (6), 283–290.
Fernández, N., Coineau, Y., 2006. *Varroa* – The Serial Bee Killer Mite. Atlantica, Biarritz.
Fernández, N., Eguaras, M., Hernández, D., 1993. Distribution patterns of *Varroa jacobsoni* Oud. on *Apis mellifera* L during winter in Argentina. Apidologie 24, 397–401.
Floris, I., Satta, A., Cabras, P., Garau, V.L., Angioni, A., 2004. Comparison between two thymol formulations in the control of *Varroa destructor*: effectiveness, persistence, and residues. J. Econ. Entomol. 97 (2), 187–191.
Floris, I., Satta, A., Garau, V.L., Melis, M., Cabras, P., Aloul, N., 2001. Effectiveness, persistence, and residue of amitraz plastic strips in the apiary control of *Varroa destructor*. Apidologie 32, 577–585.
Frazier, M., Mullin, C., Frazier, J., Ashcraft, S., 2008. What have pesticides got to do with it? Am. Bee J. 148 (6), 521–523.
Fries, I., 1989. Short-interval treatments with formic acid for control of *Varroa jacobsoni* in honey bee (*Apis mellifera*) colonies in cold climates. Swed. J. Agric. Res. 19, 213–216.
Fries, I., 1991. Treatment of sealed honey-bee brood with formic-acid for control of *Varroa jacobsoni*. Am. Bee J. 131 (5), 313–314.
Fries, I., Bommarco, R., 2007. Possible host–parasite adaptations in honey bees infested by *Varroa destructor* mites. Apidologie 38 (6), 525–533.
Fries, I., Camazine, S., 2001. Implications of horizontal and vertical pathogen transmission for honey bee epidemiology. Apidologie 32 (3), 199–214.
Fries, I., Camazine, S., Sneyd, J., 1994. Population dynamics of *Varroa jacobsoni*: a model and a review. Bee World 75, 5–28.
Fries, I., Hansen, H., 1993. Biotechnical control of *Varroa* mites in cold climates. Am. Bee J. 133 (6), 435–438.
Fries, I., Hansen, H., Imdorf, A., Rosenkranz, P., 2003. Swarming in honey bees (*Apis mellifera*) and *Varroa destructor* population development in Sweden. Apidologie 34, 389–398.
Fries, I., Imdorf, A., Rosenkranz, P., 2006. Survival of mite infested (*Varroa destructor*) honey bee (*Apis mellifera*) colonies in a Nordic climate. Apidologie 37, 564–570.
Fries, I., Perez-Escala, S., 2001. Mortality of *Varroa destructor* in honey bee (*Apis mellifera*) colonies during winter. Apidologie 32, 223–229.
Fries, I., Rosenkranz, P., 1996. Number of reproductive cycles of *Varroa jacobsoni* in honey-bee (*Apis mellifera*) colonies. Exp. Appl. Acarol. 20, 103–112.
Fries, I., Wallner, K., Rosenkranz, P., 1998. Effects on *Varroa jacobsoni* from acaricides in beeswax. J. Apicult. Res. 37, 85–90.
Fries, I., Wie, H., Shi, W., Huazhen, S.X., 1996. Grooming behavior and damaged mites (*Varroa jacobsoni*) in *Apis cerana cerana* and *Apis mellifera ligustica*. Apidologie 34, 3–11.
Fuchs, S., 1990. Preference for drone brood cells by *Varroa jacobsoni* Oud. in colonies of *Apis mellifera carnica*. Apidologie 21, 193–196.
Fuchs, S., 1994. Non-reproducing *Varroa jacobsoni* Oud in honey bee worker cells – status of mites or effect of brood cells? Exp. Appl. Acarol. 18, 309–317.
Fuchs, S., Langenbach, K., 1989. Multiple infestation of *Apis mellifera* L. brood cells and reproduction in *Varroa jacobsoni* Oud. Apidologie 20 (3), 257–266.
Garcia-Fernandez, P., Rodriguez, R.B., Orantesbermejo, F.J., 1995. Influence of climate on the evolution of the population-dynamics of the *Varroa* mite on honeybees in the south of Spain. Apidologie 26 (5), 371–380.
Garcia-Fernandez, P., Santiago-Alvarez, C., Quesada-Moraga, E., 2008. Pathogenicity and thermal biology of mitosporic fungi as potential microbial control agents of *Varroa destructor* (Acari: Mesostigmata), an ectoparasitic mite of honey bee, *Apis mellifera* (Hymenoptera: Apidae). Apidologie 39 (6), 662–673.
Garedew, A., Schmolz, E., Lamprecht, I., 2003. Micro-calorimetric and respirometric investigation of the effect of temperature on the anti *Varroa* action of the natural bee product-propolis. Thermochim. Acta 399 (1–2), 171–180.
Garedew, A., Schmolz, E., Lamprecht, I., 2004. The energy and nutritional demand of the parasitic life of the mite *Varroa destructor*. Apidologie 35, 419–430.
Garrido, C. 2004. Reproduktionssteuerung bei der parasitischen Bienenmilbe *Varroa destructor* Anderson & Trueman (ehamals *Varroa jacobsoni*). Ph.D. Thesis at the Faculty of Biology at the University of Hohenheim, 82 pp.
Garrido, C., Rosenkranz, P., 2003. The reproductive program of female *Varroa destructor* mites is triggered by its host, *Apis mellifera*. Exp. Appl. Acarol. 31, 269–273.
Garrido, C., Rosenkranz, P., 2004. Volatiles of the honey bee larva initiate oogenesis in the parasitic mite *Varroa destructor*. Chemoecology 14, 193–197.
Garrido, C., Rosenkranz, P., Paxton, R.J., Gonçalves, L.S., 2003. Temporal changes in *Varroa destructor* fertility and haplotype in Brazil. Apidologie 34, 535–541.
Garrido, C., Rosenkranz, P., Stürmer, M., Rübsam, R., Büning, J., 2000. Toluidine blue staining as a rapid measure for initiation of oocyte growth and fertility in *Varroa jacobsoni* Oud. Apidologie 31, 559–566.
German Bee Monitoring Project, 2008. <http://www.ag-bienenforschung.de/>.
Glinski, Z.F., Jarosz, J., 1990. *Serratia marcescens*, artificially contaminating brood and worker honeybees, contaminates the *Varroa jacobsoni* mite. J. Apicult. Res. 29, 107–111.
Gnädinger, F., 1984. Auswinterungsverluste bei Bienenvölkern in Baden. Allg. Deut. Imkerz. 18, 297–299.
Goetz, B., Koeniger, N., 1993. The distance between larva and cell opening triggers broodcell invasion by *Varroa jacobsoni*. Apidologie 24, 67–72.
Gonzales, V.H., Mantilla, B., Mahnert, V., 2007. A new host record for Dasychernes inquilinus (Arachnida, Pseudoscorpiones, Chernetidae) with an overview of pseudoscorpion–bee relationships. J. Arachnol. 35 (3), 470–474.
Goodwin, R.M., Taylor, M.A., Mcbrydie, H.M., Cox, H.M., 2006. Drift of *Varroa destructor*-infested worker honey bees to neighbouring colonies. J. Apicult. Res. 45 (3), 155–156.
Gramacho, K., Gonçalves, L.S., Rosenkranz, P., 1997. Temperature measurements of living and killed ("pin test") honey bee brood (*Apis mellifera*). Apidologie 28, 205–207.
Gramacho, K., Gonçalves, L.S., Rosenkranz, P., De Jong, D., 1999. Influence of body fluid from pin-killed honey bee pupae on hygienic behaviour. Apidologie 30, 367–374.
Greatti, M., Milani, N., Nazzi, F., 1992. Reinfestation of an acaricide-treated apiary by *Varroa jacobsoni* Oud. Exp. Appl. Acarol. 16, 279–286.
Gregorc, A., Planinc, I., 2001. Acaricidal effect of oxalic acid in honeybee (*Apis mellifera*) colonies. Apidologie 32, 333–340.
Gregorc, A., Planinc, I., 2004. Dynamics of falling *Varroa* mites in honeybee (*Apis mellifera*) colonies following oxalic acid treatments. Acta Vet. Brno. 73, 385–391.
Gregorc, A., Poklukar, J., 2003. Rotenone and oxalic acid as alternative acaricidal treatments for *Varroa destructor* in honeybee colonies. Vet. Parasitol. 111, 351–360.
Gregorc, A., Smodis Skerl, M.I., 2007. Combating *Varroa destructor* in honeybee colonies using flumethrin or fluvalinate. Acta Veterinaria Brno 76 (2), 309–314.
Guzmán-Novoa, E., Sanchez, A., Page Jr., R.E., Garcia, T., 1996. Susceptibility of European and Africanized honeybees (*Apis mellifera* L.) and their hybrids to *Varroa jacobsoni* Oud. Apidologie 27, 93–103.
Guzmán-Novoa, E., Vandame, R., Arechavaleta, M.E., 1999. Susceptibility of European an Africanized honeybees (*Apis mellifera* L.) to *Varroa jacobsoni* Oud. in Mexico. Apidologie 30, 173–182.
Hadisoesilo, S., Otis, G.W., 1998. Differences in drone cappings of *Apis cerana* and *Apis nigrocincta*. J. Apicult. Res. 37, 11–15.
Harbo, J.R., Harris, J.W., 1999. Heritability in honey bees (Hymenoptera Apidae) of characteristics associated with resistance to *Varroa jacobsoni* (Mesostigmata: Varroidae). J. Econ. Entomol. 92, 261–265.
Harbo, J.R., Harris, J.W., 2001. Resistance to *Varroa destructor* (Mesostigmata: Varroidae) when mite-resistant queen honey bees (Hymenoptera: Apidae) were free-mated with unselected drones. J. Econ. Entomol. 94, 1319–1323.
Harbo, J.R., Harris, J.W., 2004. Effect of screen floors on populations of honey bees and parasitic mites (*Varroa destructor*). J. Apicult. Res. 43 (3), 114–117.
Harbo, J.R., Harris, J.W., 2005. Suppressed mite reproduction explained by the behaviour of adult bees. J. Apicult. Res. 44 (1), 21–23.
Harbo, J.R., Hoopingarner, R.A., 1997. Honey bees (Hymenoptera: Apidae) in the United States that express resistance to *Varroa jacobsoni* (Mesostigmata: Varroidae). J. Econ. Entomol. 90, 893–898.
Harizanis, P.C., 1991. Infestation of queen cells by the mite *Varroa jacobsoni*. Apidologie 22, 533–538.
Harris, J.W., 2007. Bees with *Varroa*-sensitive hygiene preferentially remove mite-infested pupae aged $\leqslant$5 days postcapping. J. Apicult. Res. 46, 134–139.
Harris, J.W., 2008. Effect of brood type on *Varroa*-sensitive hygiene by worker honey bees (Hymenoptera: Apidae). Ann. Entomol. Soc. Am. 101 (6), 1137–1144.
Harris, J.W., Harbo, J.R., 1999. Low sperm counts and reduced fecundity of mites in colonies of honey bees (Hymenoptera: Apidae) resistant to *Varroa jacobsoni* (Mesostigmata: Varroidae). J. Econ. Entomol. 92, 83–90.
Harris, J.W., Harbo, J.R., 2000. Changes in reproduction of *Varroa destructor* after honey bee queens were exchanged between resistant and susceptible colonies. Apidologie 31, 689–699.

Harris, J.W., Harbo, J.R., Villa, J.D., Danka, R.G., 2003. Variable population growth of *Varroa destructor* (Mesostigmata: Varroidae) in colonies of honey bees hymenoptera: Apidae) during a 10-year period. Environ. Entomol. 32 (6), 1305–1312.

Higes, M., Martin-Hernandez, R., Botias, C., Bailon, E.G., Gonzalez-Porto, A.V., Barrios, L., del Nozal, M.J., Bernal, J.L., Jimenez, J.J., Palencia, P.G., Meana, A., 2008. How natural infection by *Nosema ceranae* causes honeybee colony collapse. Environ. Microbiol. 10 (10), 2659–2669.

Higes, M., Meana, A., Suarez, M., Llorente, J., 1999. Negative long-term effects on bee colonies treated with oxalic acid against *Varroa jacobsoni* Oud. Apidologie 30 (4), 289–292.

Holt, M., Aumeier, P., Kirchner, W., in press. The enemy of my enemy...the impact of entomopathogenic fungi on *Apis mellifera* and *Varroa destructor*. Apidologie, in press.

Hoppe, H., Ritter, W., 1987. Experiments using combined heat therapy to control *Varroa* disease. Apidologie 18 (4), 383–384.

Hoppe, H., Ritter, W., Stephen, E., 1989. The control of parasitic bee mites: *Varroa jacobsoni, Acarapis woodi*, and *Tropilaelaps clareae* with formic acid. Am. Bee J. 129, 739–742.

Huang, Z., 2001. Mite zapper – a new and effective method for *Varroa* mite control. Am. Bee J. 141 (10), 730–732.

Ibrahim, A., Reuter, G.S., Spivak, M., 2007. Field trial of honey bee colonies bred for mechanisms of resistance against *Varroa destructor*. Apidologie 38 (1), 67–76.

Ibrahim, A., Spivak, M., 2006. The relationship between hygienic behavior and suppression of mite reproduction as honey bee (*Apis mellifera*) mechanisms of resistance to *Varroa destructor*. Apidologie 37, 31–40.

Ifantidis, M.D., 1983. Ontogenesis of the mite *Varroa jacobsoni* in worker and drone honey bee brood cells. J. Apicult. Res. 22, 200–206.

Ifantidis, M.D., 1990. Re-examination of some parameters concerning reproduction of the mite *Varroa jacobsoni* Oud. In: Proceedings of the International Symposium on Resent Research on Bee Pathology, Gent, Belgium, pp. 20–26.

Ifantidis, M.D., Karamanidou, A., Katikou, P., 1999. Juvenile mortality of the female descendants in the ectoparasitic mite *Varroa jacobsoni* in worker brood of *Apis mellifera*. J. Apicult. Res. 38 (1), 25–32.

Ifantidis, M.D., Thrashyvoulou, A., Pappas, M., 1988. Some aspects of the process of *Varroa jacobsoni* mite entrance into honey bee (*Apis mellifera*) brood cells. Apidologie 19, 387–396.

Imdorf, A., Bogdanov, S., Ochoa, R.I., Calderone, N.W., 1999. Use of essential oils for the control of *Varroa jacobsoni* Oud. in honey bee colonies. Apidologie 30 (2–3), 209–228.

Imdorf, A., Charriere, J., Maquelin, C., Kilchemann, V., Bachofen, B., 1996. Alternative *Varroa* control. Am. Bee J. 136, 189–193.

James, R., 2009. Microbial control for invasive arthropod pests of honey bees. In: Hajek, A.E., Glare, T.R., O'Callaghan M. (Eds.), Progress in Biological Control, Use of Microbes for Control and Eradication of Invasive Arthropods, vol. 6, pp. 4–15.

Joder, J., Sammataro, D., 2003. Potential to control *Varroa* mites (Acari: Varroidae) using chemical ecology. Int. J. Acarol. 29 (2), 137–143.

Johnson, R.M., Pollock, H.S., Berenbaum, M.R., 2009. Synergistic interactions between in-hive miticides in *Apis mellifera*. J. Econ. Entomol. 102 (2), 474–479.

Kanbar, G., Engels, W., 2003. Ultrastructure and bacterial infection of wounds in honey bee (*Apis mellifera*) pupae punctured by *Varroa* mites. Parasitol. Res. 90 (5), 349–354.

Kanga, L.H.B., Jones, W.A., Gracia, C., 2006. Efficacy of strips coated with *Metarhizium anisopliae* for control of *Varroa destructor* (Acari: Varroidae) in honey bee colonies in Texas and Florida. Exp. Appl. Acarol. 40 (3–4), 249–258.

Kanga, L.H.B., Jones, W.A., James, R.R., 2003. Field trials using the fungal pathogen, *Metarhizium anisopliae* (Deuteromycetes: Hyphomycetes) to control the ectoparasitic mite, *Varroa destructor* (Acari: Varroidae) in honey bee, *Apis mellifera* (Hymenoptera: Apidae) colonies. J. Econ. Entomol. 96 (4), 1091–1099.

Kirchner, W.H., 1993. Lichtsinn und Vibrationssinn der *Varroa*-Milbe. Apidologie 24, 490–491.

Koeniger, N., Koeniger, G., Wijayagunasekera, N.H.P., 1981. Observations on the adaptation of *Varroa jacobsoni* to its natural host *Apis cerana* in Sri Lanka. Apidologie 12, 37–40.

Korpela, S., Aarhus, A., Fries, I., Hansen, H., 1993. *Varroa jacobsoni* Oud. in cold climates: population growth, winter mortality and influence on survival of honey bee colonies. J. Apicult. Res. 31, 157–164.

Kralj, J., Brockmann, A., Fuchs, S., Tautz, J., 2007. The parasitic mite *Varroa destructor* affects non-associative learning in honey bee foragers, *Apis mellifera* L.. J. Compar. Physiol. A: Neuroethol. Sens. Neu. Behav. Physiol. 193 (3), 363–370.

Kralj, J., Fuchs, S., 2006. Parasitic *Varroa destructor* mites influence flight duration and homing ability of infested *Apis mellifera* foragers. Apidologie 37 (5), 577–587.

Kraus, B., 1993. Preferences of *Varroa jacobsoni* for honey bees *Apis mellifera* L. of different ages. J. Apicult. Res. 32, 57–64.

Kraus, B., 1994. Factors influencing host choice of the honey bee parasite *Varroa jacobsoni* Oud. Exp. Appl. Acarol. 18, 435–443.

Kraus, B., Berg, S., 1994. Effect of lactic acid treatment during winter in temperate climate upon *Varroa jacobsoni* Oud and the bee (*Apis mellifera*) colony. Exp. Appl. Acarol. 18, 459–468.

Kraus, F.B., Büchler, R., Siede, R., Berg, S., Moritz, R.F.A., 2007. Trade-off between survival and male reproduction in *Varroa destructor* infested honeybee colonies (*Apis mellifera*). Ethol. Ecol. Evol. 19 (4), 263–273.

Kraus, B., Hunt, G., 1995. Differentiation of *Varroa jacobsoni* Oud populations by random amplification of polymorphic DNA (RAPD). Apidologie 26, 283–290.

Kraus, B., Koeniger, N., Fuchs, S., 1986. Unterscheidung zwischen Bienen verschiedenen Alters durch *Varroa jacobsoni* Oud, und Bevorzugung von Ammenbienen im Sommerbienenvolk. Apidologie 17, 257–266.

Kraus, B., Koeniger, N., Fuchs, S., 1994. Screening of substances for their effect on *Varroa jacobsoni* – attractiveness, repellency, toxicity and masking effects of etherneal oils. J. Apicult. Res. 33 (1), 34–43.

Kraus, B., Velthuis, H.H.W., 1997. High humidity in the honey bee (*Apis mellifera* L.) brood nest limits reproduction of the parasitic mite *Varroa jacobsoni* Oud. Naturwissenschaften 84, 217–218.

Kuenen, L.P.S., Calderone, N.W., 1997. Transfers of *Varroa* mites from newly emerged bees: preferences for age- and function-specific adult bees. J. Insect Behav. 10, 213–228.

Kuenen, L.P.S., Calderone, N.W., 2000. *Varroa* mite infestations in elevated honey bee brood cells: effects of context and caste. J. Insect Behav. 13 (2), 201–215.

Laurent, J.C., Santas, L., 1987. Etude du development larvaire de *Varroa jacobsoni* Oud. Apidologie 18, 53–60.

Le Conte, Y., Arnold, G., 1987. Influence de l'âge des abeilles *Apis mellifera* L et de la chaleur sur le comportement de *Varroa jacobsoni* (Oudemans). Apidologie 18, 305–320.

Le Conte, Y., Arnold, G., 1988. Etude du thermopreferendum de *Varroa jacobsoni* Oud. Apidologie 19, 155–164.

Le Conte, Y., Arnold, G., Trouiller, J., Masson, C., 1990. Identification of a brood pheromone in honeybees. Naturwissenschaften 77, 334–336.

Le Conte, Y., Arnold, G., Trouiller, J., Masson, C., Chappe, B., Ourisson, G., 1989. Attraction of the parasitic mite *Varroa* to the drone larvae of honeybees by simple aliphatic esters. Science 245, 638–639.

Le Conte, Y., de Vaublanc, G., Crauser, D., Jeanne, F., Rousselle, J.-C., Bécard, J.-M., 2007. Honey bee colonies that have survived *Varroa destructor*. Apidologie 38 (6), 566–572.

Le Conte, Y., Navajas, M., 2008. Climate change: impact on honey bee populations and diseases. Revue scientifique et technique. Office Int. Epizoot. 27 (2), 499–510.

Le Conte, Y., Sreng, L., Trouiller, J., 1994. The recognition of larvae by worker honeybees. Naturwissenschaften 81, 462–465.

LeDoux, M.N., Pernal, S.F., Higo, H.A., Winston, M.L., 2000. Development of a bioassay to test the orientation behaviour of the honey bee ectoparasite *Varroa jacobsoni*. J. Apicult. Res. 39, 47–54.

Liebig, G., 2001. How many *Varroa* mites can be tolerated by a honey bee colony? Apidologie 32, 482–484.

Liebig, G., Aumeier, P., 2007. Helfen kleine Zellen gegen *Varroa*? Dtsch. Bienenjour. 04, 32–33.

Lindberg, C.M., Melathopoulos, A.P., Winston, M.L., 2000. Laboratory evaluation of miticides to control *Varroa jacobsoni* (Acari: Varroidae), a honey bee (Hymenoptera: Apidae) parasite. J. Econ. Entomol. 93 (2), 189–198.

Liu, T.P., Peng, Y.S., 1990. Palpal tarsal sensilla of the female mite *Varroa jacobsoni* Oudemans (Acari: Varroidae). Can. Entomol. 122, 295–300.

Lodesani, M., 2004. Control strategies against *Varroa mites*. Parassitologia 46 (1–2), 277–279.

Lodesani, M., Colombo, M., Spreafico, M., 1995. Ineffectiveness of Apistan treatment against the mite *Varroa jacobsoni* Oud. in several districts of Lombardy (Italy). Apidologie 26, 67–72.

Lodesani, M., Costa, C., Serra, G., Colombo, R., Sabatini, A.G., 2008. Acaricide residues in beeswax after conversion to organic beekeeping methods. Apidologie 39 (3), 324–333.

Lodesani, M., Crailsheim, C., Moritz, R.F.A., 2002. Effect of some characters on the population growth of mite *Varroa jacobsoni* in *Apis mellifera* L. colonies and results of a bi-directional selection. J. Appl. Entomol. 126, 130–137.

Marcangeli, J.A., Eguaras, M.J., Fernandez, N.A., 1992. Reproduction of *Varroa jacobsoni* (Acari: Mesostigmata: Varroidae) in temperate climates of Argentina. Apidologie 23, 57–60.

Martel, A.C., Zeggane, S., Aurieres, C., Drajnudel, P., Faucon, J.P., Aubert, M., 2007. Acaricide residues in honey and wax after treatment of honey bee colonies with Apivar (R) or Asuntol (R) 50. Apidologie 38 (6), 534–544.

Martin, S.J., 1994. Ontogenesis of the mite *Varroa jacobsoni* Oud. in worker brood of the honeybee *Apis mellifera* L. under natural conditions. Exp. Appl. Acarol. 18, 87–100.

Martin, S.J., 1995a. Ontogenesis of the mite *Varroa jacobsoni* Oud. in drone brood of the honeybee *Apis mellifera* L. under natural conditions. Exp. Appl. Acarol. 19, 199–210.

Martin, S.J., 1995b. Reproduction of *Varroa jacobsoni* in cells of *Apis mellifera* containing one or more mother mites and the distribution of these cells. J. Apicult. Res. 34, 187–196.

Martin, S., 1998. A population model for the ectoparasitic mite *Varroa jacobsoni* in honey bee (*Apis mellifera*) colonies. Ecol. Model. 109, 267–281.

Martin, S.J., 2001a. The role of *Varroa* and viral pathogens in the collapse of honeybee colonies: a modelling approach. J. Appl. Ecol. 38 (5), 1082–1093.

Martin, S., 2001b. *Varroa destructor* reproduction during the winter in *Apis mellifera* colonies in UK. Exp. Appl. Acarol. 25, 321–325.

Martin, S.J., Hogarth, A., van Breda, J., Perrett, J., 1998. A scientific note on *Varroa acobsoni* Oudemans and the collaps of *Apis mellifera* L. colonies in the United Kingdom. Apidologie 29, 369–370.

Martin, S., Holland, K., Murray, M., 1997. Non-reproduction in the honeybee mite *Varroa jacobsoni*. Exp. Appl. Acarol. 21, 539–549.

Martin, S.J., Kemp, D., 1997. Average number of reproductive cycles performed by *Varroa jacobsoni* in honey bee (*Apis mellifera*) olonies. J. Apicult. Res. 36, 113–123.

Martin, S.J., Kryger, P., 2002. Reproduction of *Varroa destructor* in South African honey bees: does cell space influence *Varroa* male survivorship? Apidologie 33 (1), 51–61.
Martin, S.J., Medina, L.M., 2004. Africanized honey bees have unique tolerance to *Varroa* mites. Trends Parasitol. 20, 112–114.
Martin, C., Provost, E., Bagneres, A.G., Roux, M., Clement, J.L., Le Conte, Y., 2002. Potential mechanism for detection by *Apis mellifera* of the parasitic mite *Varroa destructor* inside sealed brood cells. Physiol. Entomol. 27, 175–188.
Martin, C., Provost, E., Roux, M., Bruchou, C., Crauser, D., Clement, J.-L., Le Conte, Y., 2001a. Resistance of the honey bee, *Apis mellifera* to the acarian parasite *Varroa destructor*: behavioural and electroantennographic data. Physiol. Entomol. 26 (4), 362–370.
Martin, C., Salvy, M., Provost, É.M., Bagnéres, A.G., Roux, M., Crauser, D., Clement, J.L., Le Conte, Y., 2001b. Variations in chemical mimicry by the ectoparasitic mite *Varroa jacobsoni* according to the developmental stage of the host honey bee *Apis mellifera*. Insect Biochem. Mol. Biol. 31, 365–379.
Martin-Hernandez, R., Higes, M., Perez, J.L., Nozal, M.J., Gomez, L., Meana, A., 2007. Short term negative effect of oxalic acid in *Apis mellifera* iberiensis. Span. J. Agr. Res. 5 (4), 474–480.
Mattila, H.R., Otis, G.W., Daley, J., Schulz, T., 2000. of Apiguard, a thymol-based miticide Part 2. Non-target effects on honey bees. Am. Bee J. 140 (1), 68–70.
Maul, V., Klepsch, A., Assmannwerthmuller, U., 1988. The trapping comb technique as part of bee management under strong infestation by *Varroa jacobsoni* Oud. Apidologie 19 (2), 139–154.
Medina, L., Martin, S.J., 1999. A comparative study of *Varroa jacobsoni* reproduction in worker cells of honey bees (*Apis mellifera*) in England and Africanized bees in Yucatan, Mexico. Exp. Appl. Acarol. 23, 659–667.
Medina, L., Martin, S.H., Espinosa-Montaño, L., Ratnieks, F.L.W., 2002. Reproduction of *Varroa destructor* in worker brood of Africanized honey bees (*Apis mellifera*). Exp. Appl. Acarol. 26, 1–10.
Meikle, W.G., Mercadier, G., Holst, N., Girod, V., 2008. Impact of two treatments of a formulation of *Beauveria bassiana* (Deuteromycota: Hyphomycetes) conidia on *Varroa* mites (Acari: Varroidae) and on honeybee (Hymenoptera: Apidae) colony health. Exp. Appl. Acarol. 46 (1–4), 105–117.
Melathopoulos, A.P., Winston, M.L., Whittington, R., Higo, H., Le Doux, M., 2000. Field evaluation of neem and Canola oil for the selective control of the honey bee (Hymenoptera: Apidae) mite parasites *Varroa jacobsoni* (Acari: Varroidae) and Acarapis woodi (Acari: Tarsonemidae). J. Econ. Entomol. 93 (3), 559–567.
Message, D., Gonçalves, L.S., 1995. Effect of size of worker brood cells of Africanized honey bees on infestation and reproduction of the ectoparasitic mite *Varroa jacobsoni*. Apidologie 26, 381–386.
Milani, N., 1994. Possible presence of fluvalinate-resistant strains of *Varroa jacobsoni* in northern Italy. In: Proc. Intern. Meet. "New perspectives on *Varroa*", Řež presso Praga, 1993, IBRA, Cardiff, 87.
Milani, N., 1995. The resistance of *Varroa jacobsoni* Oud. to pyrethroids – a laboratory assay. Apidologie 26, 415–429.
Milani, N., 1999. The resistance of *Varroa jacobsoni* Oud. to acaricides. Apidologie 30, 229–234.
Milani, N., 2001a. Activity of oxalic and citric acids on the mite *Varroa destructor* in laboratory assays. Apidologie 32, 127–138.
Milani, N., 2001b. Management of the resistance of *Varroa* mites to acaricides. In: Delaplane, K.S., Webster, T. (Eds.), Mites of the Honey Bee. Dadant, Sons, Hamilton, USA, pp. 241–250.
Milani, N., Barbattini, R., 1988. Effectiveness of Apistan (Fluvalinate) in the control of *Varroa jacobsoni* Oudemans and its tolerance by *Apis mellifera* Linnaeus. Apicoltura 4, 39–58.
Milani, N., Chiesa, F., 1990. Some factors affecting the reproduction of *Varroa jacobsoni* Oud. under laboratory conditions. Apicoltura 6, 33–42.
Milani, N., Della Vedova, G., 1996. Determination of the LC50 in the mite *Varroa jacobsoni* of the active substances in Perizin® and Cekafix®. Apidologie 27, 175–184.
Milani, N., Della Vedova, G., 2002. Decline in the proportion of mites resistant to fluvalinate in a population of *Varroa destructor* not treated with pyrethroids. Apidologie 33, 417–422.
Milani, N., Della Vedova, G., Nazzi, F., 2004. (Z)-8-Heptadecene reduces the reproduction of *Varroa destructor* in brood cells. Apidologie 35, 265–273.
Milani, N., Lob, M., 1998. Plastic strips containing organophosphorous acaricides to control *Varroa jacobsoni*. Am. Bee J. 138, 612–615.
Milani, N., Nannelli, R., 1988. The tarsal sense organ in *Varroa jacobsoni* Oud.: SEM observations. In: Proceedings of a Meeting of EC-Experts'Group, Udine, Italy, pp. 71–82.
Mondragón, L., Martin, S., Vandame, R., 2006. Mortality of mite offspring: a major component of *Varroa destructor* resistance in a population of Africanized bees. Apidologie 37, 67–74.
Mondragón, L., Spivak, M., Vandame, R., 2005. A multifactorial study of the resistance of honeybees *Apis mellifera* to the mite *Varroa destructor* over one year in Mexico. Apidologie 36 (3), 345–358.
Moretto, G., 2002. Mortality of *Varroa destructor* in broodless Africanized and Carnica honey bee (*Apis mellifera* L.) colonies. Interciencia 27, 702–704.
Moretto, G., Gonçalves, L.S., De Jong, D., 1993. Heritability of Africanized and European honey bee defensive behavior against the mite *Varroa jacobsoni*. Rev. Brasil. Genet. 16, 71–77.
Moretto, G., Gonçalves, L.S., De Jong, D., 1995. Analysis of the F1 generation, descendants of Africanized bee colonies with differing defense abilities against the mite *Varroa jacobsoni*. Rev. Brasil. Genet. 18, 177–179.
Moretto, G., Gonçalves, L.S., De Jong, D., 1997. Relationship between food availability and the reproductive ability of the mite *Varroa jacobsoni* in Africanized bee colonies. Am. Bee J. 137, 67–69.
Moretto, G., Gonçalves, L.S., De Jong, D., Bichuette, M.Z., 1991. The effects of climate and bee race on *Varroa jacobsoni* Oud. infestations in Brazil. Apidologie 22, 197–203.
Moritz, R.F.A., 1988. A reevaluation of the 2-locus model for hygienic behavior in honeybees (*Apis mellifera* L.). J. Hered. 79 (4), 257–262.
Moritz, R.F.A., Kraus, F.B., Kryger, P., Crewe, R.M., 2007. The size of wild honeybee populations (*Apis mellifera*) and its implications for the conservation of honeybees. J. Insect Conserv. 11, 391–397.
Moritz, R.F., Mautz, D., 1990. Development of *Varroa jacobsoni* in colonies of *Apis mellifera* capensis and *Apis mellifera* carnica. Apidologie 21, 53–58.
Muñoz, I., Garrido-Bailón, E., Martín-Hernández, R., Meana, A., Higes, M., De la Rúa, P., 2008. Genetic profile of *Varroa destructor* infesting *Apis mellifera iberiensis* colonies. J. Apicult. Res. 47 (4), 310–313.
Nanetti, A., Büchler, R., Charriere, J.D., Fries, I., Helland, S., Imdorf, A., Korpela, S., Kristiansen, P., 2003. Oxalic acid treatments for *Varroa* control (Review). Apiacta 38, 81–87.
Nannelli, R., 1985. Ulteriori conoscenze sulla morfologia e lo sviluppo, della larva e delle ninfe di *Varroa jacobsoni* Oud (Mesostigmata: Varroidae). Estratto da REDIA, vol. LXVII, pp. 287–303.
Nasr, M., Wallner, K., 2003. Residues in honey and wax. Implications and safety. In: Proc. of the North American Apicultural Research Symposium. Am. Bee J., 40, p. 322.
Nation, J.L., Sanford, M.T., Milne, K., 1992. Cuticular hydrocarbons from *Varroa jacobsoni*. Exp. Appl. Acarol. 16, 331–344.
Navajas, M., Migeon, A., Alaux, C., Martin-Magniette, M.L., Robinson, G.E., Evans, J.D., Cros-Arteil, S., Crauser, D., Le Conte, Y., 2008. Differential gene expression of the honey bee *Apis mellifera* associated with *Varroa destructor* infection. BMC Genom. 9, 301.
Nazzi, F., Bortolomeazzi, R., dela Vedova, G., del Piccolo, F., Annoscia, D., Milani, N., 2009. Octanoic acid confers to royal jelly *Varroa*-repellent properties. Naturwissenschaften 96, 309–314.
Nazzi, F., Milani, N., 1996. The presence of inhibitors of the reproduction of *Varroa jacobsoni* Oud. (Gamasida: Varroidae) in infested cells. Exp. Appl. Acarol. 20, 617–623.
Nazzi, F., Milani, N., dela Vedova, G., 2004. A semiochemical from larval food influences the entrance of *Varroa destructor* into brood cells. Apidologie 35, 403–410.
Nazzi, F., Milani, N., dela Vedova, G., Nimis, M., 2001. Semiochemicals from larval food affect the locomotory behaviour of *Varroa destructor*. Apidologie 32, 149–155.
Nguyen, B.K., Saegerman, C., Pirard, C., Mignon, J., Widart, J., Thirionet, B., Verheggen, F.J., Berkvens, D., De Pauw, E., Haubruge, E., 2009. Does imidacloprid seed-treated maize have an impact on honey bee mortality? J. Econ. Entomol. 102 (2), 616–623.
Oldroyd, B.P., 1999. Coevolution while you wait: *Varroa jacobsoni*, a new parasite of western honeybees. Trends Ecol. Evol. 14, 312–315.
Oldroyd, B.P., 2007. What's killing American honey Bees? PLOS Biol. 5 (6), 1195–1199.
Oudemans, A.C., 1904. On a new genus and species of parasitic acari. Notes from the Leyden Museum 24, 216–222.
Pätzold, S., Ritter, W., 1989. Studies on the behaviour of the honey-bee mite *Varroa jacobsoni* O., in a temperature gradient. J. Appl. Ent. 107, 46–51.
Peng, Y.S., Fang, Y., Xu, S., Ge, L., 1987a. The resistance mechanism of the Asian honey bee, *Apis cerana* Fabr., to an ectoparasitic mite *Varroa jacobsoni* Oudemanns. J. Invertebr. Pathol. 49, 54–60.
Peng, Y.S., Fang, Y., Xu, S., Ge, L., Nasr, M.E., 1987b. Response of foster Asian honey bee (*Apis cerana* Fabr.) colonies to the brood of European honey bee (*Apis mellifera* L.) infested with parasitic mite *Varroa jacobsoni* Oudemanns. J. Invertebr. Pathol. 49, 259–264.
Perez-Sato, J.A., Chaline, N., Martin, S.J., Hughes, W.O.H., Ratnieks, F.L.W., 2009. Multi-level selection for hygienic behaviour in honeybees. Heredity 102 (6), 609–615.
Pernal, S.F., Baird, D.S., Birmingham, A.L., Higo, H.A., Slessor, K.N., Winston, M.L., 2005. Semiochemicals influencing the host-finding behaviour of *Varroa destructor*. Exp. Appl. Acarol. 37 (1–2), 1–26.
Pettis, J.S., Shimanuki, H., 1999. A hive modification to reduce *Varroa* populations. Am. Bee J. 139, 471–473.
Piccirillo, G.A., De Jong, D., 2003. The influence of brood comb cell size on the reproductive behavior of the ectoparasitic mite *Varroa destructor* in Africanized honey bee colonies. Genet. Mol. Res. 2, 36–42.
Piccirillo, G.A., De Jong, D., 2004. Old honey bee brood combs are more infested by the mite *Varroa destructor* than are new brood combs. Apidologie 35, 359–364.
Rademacher, E., Harz, M., 2006. Oxalic acid for the control of varroosis in honey bee colonies – a review. Apidologie 37 (1), 98–120.
Rademacher, E., Imdorf, A., 2004. Legalization of the use of oxalic acid in *Varroa* control. Bee World 85 (4), 70–72.
Ramm, D., Böckeler, W., 1989. Ultrastrukturelle Darstellungen der Sensillen in der Vordertarsengrube von *Varroa jacobsoni* (Acari). Zool. JB. Anat. 119, 221–236.
Randy, O., 2008. Powdered sugar dusting – sweet and safe, but does it really work? Am. Bee J., 1077–1080.
Rath, W., 1992. The key to *Varroa* – the drones of *Apis cerana* and their cell cap. Am. Bee J. 132 (5), 329–331.
Rath, W., 1999. Co-adaptation of *Apis cerana* Fabr. and *Varroa jacobsoni* Oud. Apidologie 30, 97–110.

Rehm, S.M., Ritter, W., 1989. Sequence of the sexes in the offspring of *Varroa jacobsoni* and resulting consequences for the calculation of the developmental period. Apidologie 20, 339–343.

Renz, M., Rosenkranz, P., 2001. Infestation dynamics and reinvasion of *Varroa destructor* mites in honey bee colonies kept isolated and in groups. Apidologie 32, 492–494.

Ribiere, M., Olivier, V., Blanchard, P., Schurr, F., Celle, O., Drajnudel, P., Faucon, J.-P., Thiery, R., Chauzat, M.-P., 2008. The collapse of bee colonies: the CCD case ("Colony collapse disorder") and the IAPV virus (Israeli acute paralysis virus). Virologie 12 (5), 319–322.

Rice, N.D., Winston, M.L., Higo, H.A., 2004. Integrated pest management for the parasitic mite *Varroa destructor* (Anderson and Trueman) in colonies of honey bees (*Apis mellifera*). Am. Bee J. 144, 791–795.

Richard, D., Colin, M.-E., L'homme, M., 1990. Anatomical organization of the tracheal system of *Varroa jacobsoni*. Exp. Appl. Acarol. 9, 63–72.

Rickli, M., Diehl, P.A., Guerin, P.M., 1994. Cuticle alkanes of honeybee larvae mediate arrestment of bee parasite *Varroa jacobsoni*. J. Chem. Ecol. 20, 2437–2453.

Rickli, M., Guerin, P.M., Diehl, P.A., 1992. Palmitic acid released from honeybee worker larvae attracts the parasitic mite *Varroa jacobsoni* on a servosphere. Naturwissenschaften 79, 320–322.

Rinderer, T.E., De Guzman, L.I., Delatte, G.T., Harper, C., 2003. An evaluation of ARS Russian honey bees in combination with other methods for the control of *Varroa* mites. Am. Bee J. 143 (5), 410–413.

Rinderer, T.E., De Guzmann, L.I., Delatte, G.T., Stelzer, J.A., Lancaster, V.A., Kuznetsov, V., Beaman, L., 2001. Resistance to the parasitic mite *Varroa destructor* in honey bees from far-eastern Russia. Apidologie 32 (4), 381–394.

Rinderer, T.E., De Guzman, L.I., Harris, J., Kuznetsov, V., Delatte, G.T., Stelzer, J.A., Beaman, L., 2000. The release of ARS Russian honey bees. Am. Bee J. 140, 305–307.

Rinderer, T., De Guzman, L., Sylvester, H.A., 2004. Re-examination of the accuracy of a detergent solution for *Varroa* mite detection. Am. Bee J. 144 (7), 560–562.

Ritter, W., 1988. Medications registered in Western Europe for *Varroa* tosis control. Apidologie 19 (2), 113–116.

Rosenkranz, P., 1987. Thermobehandlung verdeckelter Arbeiterinnen-Brutwaben als Möglichkeit der *Varroa* tose-Kontrolle. Apidologie 18, 385–388.

Rosenkranz, P., 1988. Temperaturpräferenz der *Varroa*-Milbe und Stocktemperaturen in Bienenvölkern an Tropenstandorten (Acarina: Varroidae/Hymenoptera: Apidae). Entomol. Gener. 14, 123–132.

Rosenkranz, P., 1993. A bioassay for the test of the host finding behaviour of *Varroa jacobsoni*. Apidologie 24, 486–488.

Rosenkranz, P., 1999. Honey bee (*Apis mellifera* L.) tolerance to *Varroa jacobsoni* Oud. in South America. Apidologie 30, 159–172.

Rosenkranz, P., Bartalszky, H., 1996. Reproduction of *Varroa* females after long broodless periods of the honey bee colony during summer. Apidologie 27, 288–289.

Rosenkranz, P., Engels, W., 1994a. Infertility of *Varroa jacobsoni* females after invasion into *Apis mellifera* worker brood as a tolerance factor against *Varroa* tosis. Apidologie 25, 402–411.

Rosenkranz, P., Engels, W., 1994b. Genetic and environmental influences on the duration of preimaginal worker development in eastern (*Apis cerana*) and western (*Apis mellifera*) honey bees in relation to *Varroa* tosis. Rev. Brasil. Genet. 17, 383–391.

Rosenkranz, P., Fries, I., 2005. Does a four year selection in a closed honey bee population lead to *Varroa* tolerance? Test of queens deriving from surviving colonies. In: IUSSI-Tagungsband, ISBN 3-901864-02-4, Halle.

Rosenkranz, P., Fries, I., Boecking, O., Stürmer, M., 1997. Damaged *Varroa* mites in the debris of honey bee (*Apis mellifera* L.) colonies with and without hatching brood. Apidologie 28, 427–437.

Rosenkranz, P., Kirsch, R., Renz, R. 2006. Population dynamics of honey bee colonies and *Varroa* tolerance: a comparison between Uruguay and Germany In: Santana, Lobo, Hartfelder (Eds.), Proceedings 7th Encontro Sobre Abelhas, USP, Ribeirão Preto, Brazil.

Rosenkranz, P., Renz, M., 2003. *Varroa destructor* infestation of adult bees, worker brood and drone brood during the season and consequences for treatment concepts. Apidologie 34, 509–510.

Rosenkranz, P., Stürmer, M., 1992. Ernährungsabhängige Fertilität der *Varroa*-Weibchen in Arbeiterinnenbrut von *Apis mellifera carnica* und *Apis mellifera capensis*, vol. 47. Univ. Mariae Curie, Sklodowska, Lublin-Poland, Sectio DD, pp. 55–60.

Rosenkranz, P., Tewarson, N.C., Rachinsky, A., Strambi, A., Strambi, C., Engels, W., 1993a. Juvenile hormone titer and reproduction of *Varroa jacobsoni* in capped brood stages of *Apis cerana indica* in comparison to *Apis mellifera ligustica*. Apidologie 24, 375–382.

Rosenkranz, P., Tewarson, N.C., Singh, A., Engels, W., 1993b. Differential hygienic behaviour towards *Varroa jacobsoni* in capped worker brood of *Apis cerana* depends on alien scent adhering to the mites. J. Apicult. Res. 32, 89–93.

Rothenbuhler, W., 1964. Behavior genetics of nest cleaning behavior in honeybees I. Response of four inbred lines to disease killed brood. Anim. Behav. 12, 578–583.

Ruano, M.V., Fernandez, F.M., Ochoa, A.C., Valenzuela, 1991. *Varroa* sis disturbs the orientation of bees its influence on parasitosis development. Vida Apicola 48, 55–57.

Ruttner, F., Marx, H., Marx, G., 1984. Beobachtungen über eine mögliche Anpassung von *Varroa jacobsoni* an *Apis mellifera* in Uruguay. Apidologie 15, 43–62.

Ruttner, F., Ritter, W., 1980. Das Eindringen von *Varroa jacobsoni* nach Europa im Rückblick. Allg. Deut. Imkerz. 14, 130–134.

Sakofski, F., Koeniger, N., Fuchs, S., 1990. Seasonality of honey-bee colony invasion by *Varroa jacobsoni* Oud. Apidologie 21, 547–550.

Salvy, M., Martin, C., Bagnéres, A.G., Provost, E., Roux, M., Le Conte, Y., Clement, J.L., 2001. Modification of the cuticulaer hydrocarbon profile of *Apis mellifera* worker bees in the presence of the ectoparasitic mite *Varroa jacobsoni* in brood cells. Parasitology 122, 145–159.

Sammataro, D., Finley, J., Underwood, R., 2008. Comparing oxalic acid and sucrocide treatments for *Varroa destructor* (Acari: Varroidae) control under desert conditions. J. Econ. Entomol. 101 (4), 1057–1061.

Sammataro, D., Hoffman, G.D., Wardell, G., Finley, J., Ostiguy, N., 2004. Testing of a combination of control tactics to manage *Varroa destructor* (Acari: Varroidae) population levels in honey bee (Hymenoptera: Apidae). Int. J. Acarol. 30, 71–76.

Sammataro, D., Untalan, P., Guerrero, F., Finley, J., 2005. The resistance of *Varroa* mites (Acari: Varroidae) to acaricides and the presence of esterase. Int. J. Acarol. 31 (1), 67–74.

Satta, A., Floris, I., Caboni, P., Cabras, P., Eguaras, M., Velis, G., 2008. New experimental data on use of rotenone as an acaricide for control of *Varroa* destructor in honey bee colonies. J. Econ. Entomol. 101 (4), 1075–1080.

Satta, A., Floris, I., Eguaras, M., Cabras, P., Garau, V.L., Melis, M., 2005. Formic acid-based treatments for control of *Varroa destructor* in a mediterranean area. J. Econ. Entomol. 98 (2), 267–273.

Schatton-Gadelmayer, K., Engels, W., 1988. Blood proteins and body weight of newly-emerged worker honeybees with different levels of parasitization of brood mites. Entomol. Gener. 14, 93–101.

Schneider, P., Drescher, W., 1987. Einfluss der Parasitierung durch die Milbe *Varroa jacobsoni* aus das Schlupfgewicht, die Gewichtsentwicklung, die Entwicklung der Hypopharynxdrusen und die Lebensdauer von *Apis mellifera*. Apidologie 18, 101–106.

Schroeder, A., Wallner, K., Weber, D., 2004. Amitraz als *Varroa* zid – Einfluss auf die Honigqualität. Apidologie 35 (5), 535–536.

Seeley, T.D., 2007. Honey bees of the Arnot Forest: a population of feral colonies persisting with *Varroa destructor* in the northeastern United States. Apidologie, 19–29.

Shaddel-Telli, A.A., Maheri-Sis, N., Aghajanzadeh-Golshani, A., Asadi-Dizaji, A., Cheragi, H., Mousavi, M., 2008. Using medicinal plants for controlling *Varroa* mite in honey bee colonies. J. Anim. Vet. Adv. 7 (3), 328–330.

Shaw, K.E., Davidson, G., Clark, S.J., Ball, B.V., Pell, J.K., Chandler, D., Sunderland, K.D., 2002. Laboratory bioassays to assess the pathogenicity of mitosporic fungi to *Varroa destructor* (Acari: Mesostigmata), an ectoparasitic mite of the honeybee, *Apis mellifera*. J. Biol. Contr. 24, 266–276.

Shimanuki, H., Calderone, N.W., Knox, D.A., 1994. Parasitic mite syndrome: the symptoms. Am. Bee J. 134, 117–119.

Skinner, J.A., Parkman, J.P., Studer, M.D., 2001. Evaluation of honey bee miticides, including temporal and thermal effects on formic acid gel vapours, in the central south-eastern USA. J. Apicult. Res. 40, 81–89.

Solignac, M., Cornuet, J.-M., Vautrin, D., Le Conte, Anderson, D., Evans, J., Cros-Arteil, S., Navajas, M., 2005. The invasive Korea and Japan types of *Varroa destructor*, ectoparasitic mites of the Western honey bee (*Apis mellifera*), are two partly isolated clones. Proc. Roy. Soc. Lond. Ser. B: Biol. Sci. 272, 411–419.

Solignac, M., Vautrin, D., Pizzo, A., Navajas, M., Le Conte, Y., Cornuet, J.M., 2003. Characterization of microsatellite markers from the apicultural pest *Varroa destructor* (Acari: Varroidae) and its relatives. Mol. Ecol. Notes 3, 556–559.

Spivak, M., 1996a. Response of hygienic honey bees to *Varroa* mites. Resist. Pest Manag., 42–44.

Spivak, M., 1996b. Honey bee hygienic behavior and defense against *Varroa jacobsoni*. Apidologie 27, 245–260.

Spivak, M., Reuter, G.S., 1998. Performance of hygienic honey bee colonies in a commercial apiary. Apidologie 29, 291–302.

Spivak, M., Reuter, G.S., 2001. *Varroa destructor* infestation in untreated honey bee (Hymenoptera: Apidae) colonies selected for hygienic behavior. J. Econ. Entomol. 94, 326–331.

Steiner, J., 1993. Verteilung von *Varroa jacobsoni* im drohnenfreien Bienenvolk (*Apis mellifera carnica*). Apidologie 24 (1), 45–50.

Steiner, J., Diehl, P.A., Vlimant, M., 1995. Vitellogenesis in *Varroa jacobsoni*, a parasite of honey bees. Exp. Appl. Acarol. 19 (7), 411–422.

Steiner, J., Dittmann, F., Rosenkranz, P., Engels, W., 1994. The first gonocycle of the parasitic mite (*Varroa jacobsoni*) in relation to preimaginal development of its host, the honey bee (*Apis mellifera carnica*). Invertebr. Rep. Develop. 25, 175–183.

Tarpy, D.R., Summers, J., Keller, J.J., 2007a. Comparison of parasitic mites in Russian-hybrid and Italian honey bee (Hymenoptera: Apidae) colonies across three different locations in North Carolina. J. Econ. Entomol. 100 (2), 258–266.

Tarpy, D.R., Summers, J., Keller, J.J., Hensey, W., 2007b. Comparing pairs of Russian and Italian colonies by new beekeepers in North Carolina. Am. Bee J. 147 (2), 149–152.

Taylor, M.A., Goodwin, R.M., McBrydie, H.M., Cox, H.M., 2008. The effect of honey bee worker brood cell size on *Varroa destructor* infestation and reproduction. J. Apicult. Res. 47 (4), 239–242.

Tewarson, N.C., Engels, W., 1982. Undigested uptake of non-host proteins by *Varroa jacobsoni*. J. Apicult. Res. 21, 222–225.

Trouiller, J., 1998. Monitoring *Varroa jacobsoni* resistance to pyrethroids in Western Europe. Apidologie 29, 537–546.

Trouiller, J., Arnold, G., Chappe, B., Le Conte, Y., Billion, A., Masson, C., 1994. The kairomonal esters attractive to the *Varroa jacobsoni* mite in the queen brood. Apidologie 25, 314–321.

Trouiller, J., Arnold, G., Chappe, B., Le Conte, Y., Masson, C., 1992. Semiochemical basis of infestation of honey bee brood by *Varroa jacobsoni*. J. Chem. Ecol. 18 (11), 2041–2053.

Trouiller, J., Arnold, G., Le Conte, Y., Masson, C., Chappe, B., 1991. Temporal pheromonal and kairomonal secretion in the brood of honeybees. Naturwissenschaften 78, 368–370.

Trouiller, J., Milani, N., 1999. Stimulation of *Varroa jacobsoni* Oud. oviposition with semiochemicals from honeybee brood. Apidologie 30, 3–12.

Tsagou, V., Lianou, A., Lazarakis, D., Emmanouel, N., Aggelis, G., 2004. Newly isolated bacterial strains belonging to Bacillaceae (*Bacillus* sp.) and Micrococcaceae accelerate death of the honey bee mite, *Varroa destructor* (*V. jacobsoni*) in laboratory assays. Biotechnol. Lett. 26, 529–532.

Van der Geest, L.P.S., Elliot, S.L., Breeuwer, J.A.J., Beerling, E.A.M., 2000. Diseases of mites. Exp. Appl. Acarol. 24, 497–560.

vanEngelsdorp, D., Hayes Jr., J., Underwood, R.M., Pettis, J., 2008a. A survey of honey bee colony losses in the US, fall 2007 to spring 2008. PLoS ONE 3, e4071.

vanEngelsdorp, D., Meixner, M.D., 2010. A historical review of managed honey bee populations in Europe and the United States and the factors that may affect them. J. Invertebr. Pathol. 103, S80–S95.

vanEngelsdorp, D., Underwood, R.M., Cox-Foster, D.L., 2008b. Short-term fumigation of honey bee (Hymenoptera: Apidae) colonies with formic and acetic acids for the control of *Varroa destructor* (Acari: Varroidae). J. Econ. Entomol. 101 (2), 256–264.

Vandame, R., Colin, M.E., Morand, S., Otero-Colina, G., 2000. Levels of compatibility in a new host–parasite association: *Apis mellifera/Varroa jacobsoni*. Can. J. Zool. 78, 2037–3044.

Vandame, R., Morand, S., Colin, M.E., Belzunces, L.P., 2002. Parasitism in the social bee *Apis mellifera*: quantifying costs and benefits of behavioral resistance to *Varroa destructor* mites. Apidologie 33, 433–445.

Vetharaniam, I., Barlow, N.D., 2006. Modelling biocontrol of *Varroa destructor* using a benign haplotype as a competitive antagonist. N. Z. J. Ecol. 30 (1), 87–102.

Villa, J.D., Bustamante, D.M., Dunkley, J.P., Escobar, L.A., 2008. Changes in honey bee (Hymenoptera: Apidae) colony swarming and survival pre- and postarrival of *Varroa destructor* (Mesostigmata: Varroidae) in Louisiana. Ann. Entomol. Soc. Am. 101 (5), 867–871.

Villa, J.D., Rinderer, T.E., 2008. Inheritance of resistance to *Acarapis woodi* (Acari: Tarsonemidae) in crosses between selected resistant Russian and selected susceptible US honey bees (Hymenoptera: Apidae). J. Econ. Entomol. 101 (6), 1756–1759.

Vitzthum, H.G., 1931. In: Kükenthal, W., Krumbach, T. (Eds.), Handbuch der Zoologie. De Gruyter, Leipzig.

Wakonigg, G., Eveleigh, L., Arnold, G., Crailsheim, K., 2000. Cuticular hydrocarbon profiles reveal age-related changes in honey bee drones (*Apis mellifera carnica*). J. Apicult. Res. 39, 137–141.

Wallner, K., 1999. *Varroa* cides and their residues in bee products. Apidologie 30, 235–248.

Wallner, K., 2000. *Varroa* zide im Bienenwachs. Die aktuelle Situation in 10 europäischen Ländern. Apidologie 31, 613–615.

Wallner, K., 2005. Foundation causing honeybee brood damage. In: ICPBR 9. International Symposium York, p. 30.

Walter, D., Procter, H., 1999. Mites: Ecology, Evolution and Behavior. CABI Publishing, Wallingford, Oxon, UK.

Ward, K., Danka, R., Ward, R., 2008. Comparative performance of two mite-resistant stocks of honey bees (Hymenoptera: Apidae) in Alabama beekeeping operations. J. Econ. Entomol. 101 (3), 654–659.

Warrit, N., Smith, D.R., Lekprayoon, C., 2006. Genetic subpopulations of *Varroa* mites and their *Apis cerana* hosts in Thailand. Apidologie 37, 19–30.

Weller, S. 2008. Populationsdynamik der parasitischen Bienenmilbe *Varroa destructor* in vorselektierten Bienenvölkern (*A. mellifera* L.) unter besonderer Berücksichtigung der Reproduktion. Master Thesis at the Faculty of Biology at the University of Hohenheim, 97 pp.

Wilde, J., Fuchs, S., Bratkowski, J., Siuda, M., 2005. Distribution of *Varroa destructor* between swarms and colonies. J. Apicult. Res. 44 (4), 190–194.

Working group of German Bee Institutes, 2003. Das Kooperationsprojekt "Primorski". Allg. Dtsch. Imkerztg. 37 (3), 6–11.

Yang, X., Cox-Foster, D., 2007. Effects of parasitization by *Varroa destructor* on survivorship and physiological traits of *Apis mellifera* in correlation with viral incidence and microbial challenge. Parasitology 134, 405–412.

Yoder, J., Sammataro, D., 2003. Potential to control *Varroa* mites (Acari: Varroidae) using chemical ecology. Int. J. Acarol. 29 (2), 137–143.

Yue, C., Genersch, E., 2005. RT-PCR analysis of deformed wing virus in honeybees (*Apis mellifera*) and mites (*Varroa destructor*). J. Gen. Virol. 86, 3419–3424.

Zetlmeisl, K., Rosenkranz, P., 1994. *Varroa* females in a bioassay: host recognition of honey bee larvae and adult bees. Apidologie 25, 507–508.

Ziegelmann, B., Steidle, H., Lindenmayer, A., Rosenkranz, P., 2008. Sex pheromones trigger the mating behaviour of *Varroa destructor*. Apidologie 39, 598.