Review article

Invasion behaviour of *Varroa jacobsoni* Oud.: from bees into brood cells

Joop Beetsma[†], Willem Jan Boot*, Johan Calis

Department of Entomology, Agricultural University of Wageningen,
PO Box 8031, 6700 EH Wageningen, the Netherlands

(Received 8 September 1998; accepted 11 February 1999)

Abstract – *Varroa jacobsoni* mites may invade worker or drone brood cells when worker bees bring them in close contact with these cells. The attractive period of drone brood cells is two to three times longer than that of worker brood cells. The attractiveness of brood cells is related to the distance between the larva and the cell rim and the age of the larva. The moment of invasion of the mite into a brood cell is not related to the duration of its stay on adult bees. The fraction of the phoretic mites that invade brood cells is determined by the ratio of the number of suitable brood cells and the size of the colony. The distribution of mites over worker and drone brood in a colony is determined by the specific rates of invasion and the numbers of both brood cell types. Knowledge of mite invasion behaviour has led to effective biotechnical control methods. © Inra/DIB/AGIB/Elsevier, Paris

Apis mellifera / *Varroa jacobsoni* / invasion / brood cell type / biotechnical control

1. INTRODUCTION

The parasitic mite *Varroa jacobsoni* Oudemans (Acari: Varroidae) is a harmful pest of the European honeybee races. Up to now most beekeepers have applied acaricides to control this mite in their colonies. However, the use of acaricides has two major disadvantages: 1) contamination of honeybee products [63], and 2) the occurrence of mite resistance [29, 40, 44]. There-

fore, biotechnical control methods should be preferred. Adult female *V. jacobsoni* feed on the haemolymph of both adult bees and brood. While staying on adult bees, they can survive up to several months; for example, during the broodless period in colonies in a temperate climate. This ability allows the mites to wait for an opportunity to invade a brood cell. Invasion into a worker or drone brood cell before cell capping is essential for mite reproduction [39, 50]. Studying the

* Correspondence and reprints

E-mail: janboot@users.ento.wav.nl

[†] After an active life filled with curiosity about bees, beekeeping beekeepers and researchers, we lost Joop Beetsma as he passed away on 26 March, 1999 after a sudden and short illness

process of invasion into brood cells is important for two reasons. First, invasion is directly related to reproduction and therefore defines population growth. Second, the results of these studies have led to the improvement of biotechnical control methods in which trapping combs are used. In this paper, current knowledge on the process of invasion behaviour is reviewed.

2. INVASION BEHAVIOUR OF INDIVIDUAL MITES

Boot et al. [10] studied invasion behaviour of individual mites in small, heavily infested colonies. Experiments were carried out in a specially designed observation hive using a 'half-comb' frame [2]. Generally, two frames, both containing a 'half-comb', one on top of the other, were used to maintain a brood nest large enough for observations. The 'half-comb' consisted of one layer of cells of which the cell bottoms had been replaced by a transparent sheet. Two movable video cameras were used to monitor the opening and the bottom of a group of cells simultaneously. The side of the cell openings was illuminated with infrared light which penetrated the whole cell including the larva. When mites invaded brood cells, they crawled between the cell wall and the larva until they reached the bottom of the cell, where they were trapped in the larval food [8, 24, 38]. The observations suggested that the movement of a mite from the cell opening to the bottom took about 1 min. When studying the recordings of the position of the bees at the cell opening over 3 min before the mite reached the cell bottom, Boot et al. [10] concluded that it was not necessary for the bee to place its head and thorax into the brood cell for mite invasion. Apparently, mites left bees when brought in close proximity to a brood cell. Because mites were never observed to walk across the comb surface, Boot et al. [10] suggested that mites went directly from the ventral side of the bee into the brood cell.

When using the 'half-comb' frames, the

bees blocked the view on the cell opening. Therefore, a frame of cells with transparent side walls was constructed. Mites could be observed through opposite transparent perspex cell walls of vertical rows of cells [2] into which larvae had been grafted. When the larvae were large enough to attract mites, two video cameras were placed at opposite sides of a few cells to record invasion of mites. After many attempts, the complete movement and several parts of the movement from the bee to the brood cell bottom could be recorded. The mite walked over the side of the abdomen of the bee, left the bee and moved onto a cell capping and entered the adjacent cell, walked on the surface of the larva and crawled between the larva and the cell wall to the bottom of the cell. Boot et al. [10] concluded that mites only invade brood cells when the distance between the mite on the bee and the cell opening is small. Ten minutes after the recorded invasion, eight other mites were seen on bees passing the recently invaded cell, but they did not invade this cell. Since infested brood cells seem to be just as attractive to mites as non-infested ones [30], the distance between these mites and the cell may have been too long for invasion. In addition, mites positioned between the abdominal sternites [41, 48] may not respond to stimuli from the brood cell. The mites were never seen walking on the comb, or entering and leaving the brood cells to select a cell for invasion. In cells with attractive larvae, the mites have to cover a distance of 4–7 mm from cell opening to the larva [13, 34]. Therefore, the signal to decide whether to stay on the bee or to enter the brood cell is perceived at a distance of at least 4 mm from the larva and not after direct contact with the larva.

3. ATTRACTIVENESS OF BROOD CELLS

Preference of mites to drone larvae was found first in tests outside the colony [42, 45, 52], but whether mites could discriminate

between drone and worker brood cells in a natural environment had not yet been shown. Therefore, Boot et al. [8] compared the invasion of mites into worker brood cells with that into drone brood cells in small highly infested colonies kept in an observation hive, using half-combs [2]. For each cell, records were made of the time that a mite appeared at the transparent cell bottom and the time at which the cell had been capped. Invasion into worker and drone brood cells was studied in separate experiments. Invasion into worker brood cells could be recorded from 15–20 h before cell capping, and in drone brood cells from 40–50 h before cell capping. Because the ratio between the number of phoretic mites and available brood cells changed gradually within each experiment, the rate of invasion of mites into brood cells must have been affected [11]. Therefore, this experiment gave information only about the duration of the attractive period of each cell, and not on the rate of invasion within the attractive period. When comparing brood cells containing at least five mites, Boot et al. [8] concluded that brood cells can be invaded during the whole invasion period. The number of mites invading worker brood cells per hour remained more or less constant until cell

capping, but decreased before capping of drone brood cells. Boot et al. [8] attributed the decreasing rate of invasion into drone brood cells to a limited number of mites in relation to the number of drone brood cells in the small experimental colony. The attractive period of drone brood cells was two to three times longer than that of worker brood cells (*figure 1*). This was in agreement with the results of a similar study by Wieting and Ferenz [64] and earlier results based on indirect criterions [33, 38].

Comparison of the rates of invasion of worker and drone brood cells simultaneously in one colony is not practical because of the differential time of capping of both cell types and because of the longer period of attractiveness of drone brood cells. If worker and drone larvae are of the same age at the start of the experiment, after all worker brood cells have been capped, invasion into drone brood cells continues while the density of mites on the bees has decreased.

A different distribution of mites has been found in different types of cells containing the same type of larva. De Jong and Morse [23] found more mites in worker cells protruding above the comb surface than in neighbouring worker cells. De Ruijter and

Figure 1. Cumulative relative number of mites invading worker and drone brood cells preceding cell capping. Invasion into worker and drone brood cells was studied in separate small colonies in an observation hive. n = the number of mites invaded [9].

Calis [27] found more mites in worker brood cells with artificially raised bottoms. Calis et al. [17] and Ramon et al. [46] found more mites in smaller cells, when brood attractiveness to mites was tested in cells differing in diameter. Calis et al. [17] and Goetz and Koeniger [34] also found more mites in shortened worker brood cells.

Boot et al. [13] measured the period that brood cells are attractive to mites, the distribution of mites over different cell types, and the distance between larva and cell rim of different cell types, in relation to the time preceding cell capping. The attractive period of brood cells was again measured in half-combs [2, 9]. Two half-combs, clamped together with adjacent transparent sheets, were introduced into a heavily infested colony. The times of mite invasion and cell capping were recorded on transparent sheets. Invasion was recorded in normal worker and drone brood cells, shortened worker and drone brood cells, elongated worker brood cells, drone cells provided with a worker larva, and worker cells provided with a drone larva. The distance between larva and cell rim was measured with a probe, as used by Goetz and Koeniger [34]. To compare the attractiveness for mites between untreated, shortened or elongated cells or worker cells with a drone larva and vice versa, Boot et al. [13] used cells with the same width containing larvae of the same age in one test colony. Therefore, the relationship between the estimated distances between the cell rim and the nearest surface of the coiled larva producing an attractant would give the same result as estimating the volume of the unoccupied part of the cells.

Shortening of both worker and drone brood cells always resulted in a longer attractive period than control brood cells. Elongated worker brood cells were attractive to the mites for a shorter period than control worker brood cells. Drone cells containing a worker larva seemed to be attractive to mites during a shorter period than control worker brood cells, and drone lar-

vae in worker cells seemed to be attractive during a longer period than control drone brood cells.

The cell type strongly affected the number of mites that invaded. In shortened worker brood cells, two to three times as many mites were found per cell compared to the control cells. In elongated worker brood cells and in drone cells containing a worker larva 1/6 and 1/2 of the number of mites in control cells were found, respectively. In shortened drone brood cells, one and a half to two times as many mites were found as in control drone brood cells. No significant difference was found in the number of mites per cell between worker cells containing a drone larva and control drone brood cells.

The distance between the larva and the cell rim decreased linearly in cells containing a worker larva during the 30 h preceding cell capping. Control worker brood cells were capped when this distance was about 5.5 mm. In elongated worker brood cells the same relationship between time before capping and distance from larva to cell rim was found, but this distance was about 3 mm more than that of control cells at the same time before cell capping, corresponding to the distance by which the cells had been elongated. In drone cells with a worker larva, the distance from larva to cell rim was also much longer (about 2–3 mm) than in control worker brood cells. In artificial conical worker brood cells (ANP-comb) with a wider cell bottom [64] this distance was 0.5–1 mm more than in control worker cells. In drone brood cells, the distance between the larva and the cell rim remained the same, on average 7 mm, during the 35 h preceding cell capping. Before that period, a decrease in this distance was found.

In general, the distance between larva and cell rim decreased with time. Hence, the critical distance at which mites begin to invade brood cells may be estimated by taking the distance found at the beginning of the attractive period. Similar values were found for the following critical distances:

between 6.9 and 7.9 mm for control worker brood cells, between 7.2 and 7.8 mm for control drone brood cells and 6.9 mm for artificial (ANP) worker cells. However, the critical distances for invasion into elongated worker brood cells and for invasion into drone brood cells containing a worker larva were estimated to be longer (from 8.2–9.0 mm).

The mites probably use a signal coming from the larva, such as heat production or the production of volatile substances, and the distance between larva and cell rim may affect the strength of the signal as it reaches a mite on a bee. To perceive this signal, the distance between the mite staying on the bee and the larva may have to be within a critical distance. In elongated worker brood cells and drone cells containing a worker larva, the critical distance at which invasion starts was estimated to be greater than in control worker brood cells. Since the attractive period was shorter in these cases, the larva was older when invasion of mites began. Possibly, the critical distance for invasion is greater when the larva is older, because the strength of a signal coming from the larva may increase with age (Calis et al., unpublished data).

Le Conte et al. [42] claimed that odours of a few aliphatic esters, especially methyl palmitate (MP), are the signals a mite uses to invade brood cells. Each of these esters, which had been extracted from the larval cuticle, attracted mites in an olfactometer. The experiment indicated that these esters can at least be perceived by the mites. Trouiller et al. [60] extracted a maximum of 17 and 320 ng of MP from the cuticle of a worker and a drone larva, respectively. In drone larvae the aliphatic esters were secreted over a longer period preceding cell capping than in worker larvae [61].

Although these data correlate with the differential invasion of worker and drone brood cells, Boot et al. [6] did not find an increased attractiveness of mites to worker brood cells after application of 2 μ L of acetone containing 172, 17.2 or 1.72 ng of MP

per larva. Application of 17.2 and 1.72 ng of MP, or only acetone, did not affect the attractive period of the cells and the number of mites per cell. Only in one experiment in which 1.72 ng of MP were applied, was the number of invaded mites higher than in control cells; however, the length of the attractive period was similar. All larvae died after application of 172 ng of MP. Treatment with 17.2 ng caused some mortality, and treatment with 1.72 ng or acetone alone did not cause mortality.

Calis et al. (unpublished data) measured the attractiveness of worker larvae of different honey bee races and of different ages. Brood combs with eggs 0–1 day of age [7] were produced in colonies of different honeybee races and introduced into strong colonies for nursing the brood. When the larvae were 6–7 days of age the combs were placed into a strong mite-free colony to prevent infestation of these cells. After the first cells had been capped, the combs were introduced into the middle of the brood nest of a heavily infested colony. In contrast to the previous experiment [8], brood of different ages was simultaneously exposed to mite invasion over 3 h in a highly infested colony. It was assumed that the density of the mites on the bees did not change within such a short period. After 3 h, the combs were removed from the infested colony, the capped cells were marked on transparent sheets, and the combs were returned to the mite-free colony. Newly capped brood cells were marked in 3-h intervals. After six to seven intervals the combs were taken from the colony and the number of capped cells per interval and the number of invaded mites were recorded. After the data of three experiments were weighted to the number of brood cells and the number of mites it appeared that the relative numbers of mites per cell increased with the age of the larva (figure 2).

Few differences were found between races (Calis et al., unpublished data). On the other hand after Büchler [16] introduced

Figure 2. The relative attractiveness of *A. m. carnica* worker brood cells increases during 3-h intervals before cell capping. Brood of different ages was exposed simultaneously to mite invasion in a heavily infested colony for 3 h (Calis et al., unpublished data).

one frame with nine subunits containing dated (1–2 days) worker brood of different races or a Buckfast strain in a highly infested colony, he found differences in the rate of infestation between races. The average infestation per brood cell of pieces of brood of the same size was lowest in *A. m. mellifera* brood when compared to that of *A. m. carnica* or Buckfast brood.

Queen cells are usually not infested by mites. However, when rearing queens (1 500) under different conditions, Harizanis [36] found differential rates of infestation. In queen rearing colonies with open and sealed brood, an average of 2 % of the queen cells were infested. When only sealed brood or no brood was present the percentages of infested queen cells increased to 4 and 9 %, respectively. In colonies without brood, only five mites were found with offspring in queen cells. The oldest offspring was a mobile protonymph. Because the capped stage of queen cells is relatively short (8 days) [49], this offspring never could

become adult. The low attractiveness of queen cells for mites could be due to a weaker attractive signal. Trouiller et al. [62] explain this weak attractivity of queen cells as follows: queen larvae produce only half the amount of methyl palmitate, methyl linolenate and ethyl palmitate, which are attractants for *V. jacobsoni* [42], as worker larvae. In addition queen larvae produce much more methyl oleate, a substance repellent to mites, than worker larvae.

4. DOES INVASION AND REPRODUCTION DEPEND ON THE HISTORY OF THE MITES?

The composition of the *V. jacobsoni* population on adult bees varies constantly. Phoretic mites differ in age and in the duration of their stay on adult bees. These mites may be callow or have reproduced once or several times [26]. In addition these mites

may have a different origin owing to transfer by drifting of drones or inexperienced forager bees [35, 54], or by robber bees [53]. Some of the mites may have escaped from brood cells when the bees removed infested brood [3–5]. When invading a brood cell for the second time, oviposition of these mites had probably already been initiated before or during the first 2 days [1] or the first day [59] of their interrupted stay in a capped brood cell which will affect the start and the rate of egg-laying of the mites [25].

Several authors have assumed that young mites have to mature and old mites have to prepare for reproduction in a brood cell while staying on adult bees [1, 30, 57]. In that case, one would expect that the stay on adult bees would affect the moment of invasion into a brood cell, the start of oviposition or the reproductive success of the mite. De Ruijter and Pappas [28] collected young and old mites from brood cells 10 days after cell capping. Both categories of mites were introduced into recently sealed brood cells, either immediately, or after a stay of 1 week on adult bees. Ten days later, the offspring of both categories of mites had attained a more advanced stage of development when their mothers had been in contact with adult bees; oviposition of these mites began earlier than in mites without previous contact with adult bees. On the other hand, it appeared that contacts with adult bees by the mites are not necessary for the initiation of oviposition [26, 28]. In colonies of hybrids between *Apis mellifera intermissa* and introduced European races, Beetsma and Zonneveld [1] collected swollen mites (in which the dorsal and ventral shields were clearly separated) and non-swollen mites from adult bees, and introduced them into recently capped worker brood cells. The average number of offspring of swollen mites was similar to that of naturally invaded mites, but the non-swollen mites produced significantly fewer offspring. Swollen mites might have escaped from capped brood cells which had been opened by bees and therefore demonstrate an increased rate of egg lay-

ing. De Ruijter [25] demonstrated this effect when transferring mites 24 or 48 h after cell capping into another series of recently capped worker brood cells. In addition, mites transferred after a stay of 48 h in a capped brood cell did not produce male offspring. When Beetsma and Zonneveld [1] collected non-swollen mites from brood cells, and introduced them into Eppendorf test tubes provided with a stretched larva (one in the process of spinning a cocoon) every 12 days, these mites did not reproduce over 35 days. However, when the swollen mites were introduced into recently sealed brood cells, the number of offspring produced was similar to that of naturally invading mites. Therefore, Beetsma and Zonneveld [1] suggested that oviposition could be stimulated both by a preceding stay on adult bees or in a brood cell in which the mites did not reproduce.

Boot et al. [9] placed a broodless and mite-free colony in an isolated place to prevent reinfestation by mites. They introduced heavily infested emerging brood for 1 day to provide the colony with a large number of young and older mites that started their phoretic phase on the same day. Boot et al. [9] measured invasion of these mites into brood cells during a maximum of 20 days. A comb containing 500 worker larvae 3–4 days of age was introduced daily and removed after 3 days. Each day all capped cells were marked on transparent sheets to register the invasion time of mites. Finally all mites remaining on adult bees were killed and counted. With these data the number of phoretic mites and the number of mites that invaded brood cells could be calculated for each day. In three replicates with colonies of different sizes, it appeared that mites began to invade brood cells on the first day of their phoretic stage and continued to invade brood cells at a constant rate, although this rate and the number of bees differed between the replicates (figure 3).

Previously assumed differences in invasion time between, for example, young and old mites could not be demonstrated. Boot et

Figure 3. Calculated percentage of mites residing on adult bees. Mite-free broodless colonies were infested by introducing emerging infested brood for 1 day. Five hundred dated worker larvae were introduced daily. After capping the combs were removed to count the number of invaded mites [10].

al. [12] also demonstrated that the time spent on adult bees did not affect the fraction of mites without offspring, the number of offspring, the number of viable daughters and the fraction of mites with only male offspring. On the other hand, Schmidt-Bailey and Fuchs [55] found that the time spent on adult bees increased the trapping efficiency of drone brood cells. When groups of 50 drone brood cells were introduced, 1, 2, 3 and 4 weeks after formation of separate infested broodless nuclei in Kirchhain mating boxes, their trapping efficiency increased.

5. EFFECT OF THE BROOD/BEE RATIO ON INVASION

Explanations for the differences in the rate of invasion between the replicates of the experiments of Boot et al. [9] became clear from the results of a similar experiment in which the size of the colony or the number of brood cells suitable for invasion was changed. Boot et al. [11] demonstrated that the rate of invasion increased with the number of suitable brood cells and decreased with the number of bees. When the surface area of suitable brood cells increases, more bees will come close to a brood cell and the phoretic mites have more opportunities to

leave the bee and enter a brood cell. Conversely, with a mite population of the same size, the density of mites on bees will decrease with increasing colony size and therefore their opportunities to come close to a brood cell will decrease. The rate of invasion also decreased when young brood, not yet attractive to mites, was introduced. The addition of brood probably forced the bees to spread over more combs and therefore fewer mites were present in the direct vicinity of the attractive brood cells [11].

After the experiments on invasion into worker brood cells [9], Boot et al. [14] studied the invasion into drone brood cells in relation to the size of the colony using a similar design. In these experiments, a comb containing 50 drone larvae 3–4 days of age was introduced each day. In six replicates it appeared that the rate of invasion of mites into drone brood cells was correlated with the number of drone brood cells per kg of bees, but not with the duration of their stay on adult bees, similar to the situation in worker brood cells [11]. However, drone brood cells were invaded 11.6 times more frequently than worker brood cells. Note, in these experiments the invasion into worker or drone brood cells was tested in separate colonies (cf. the experiments by Fuchs [31]).

Part of this higher frequency of invasion may be due to the longer attractive period of drone cells [8, 38]. When invasion into a brood cell depends on the frequency with which a bee brings a mite close enough to a brood cell to invade, the number of mites that invade per cell is expected to be two to three times higher in drone brood cells, provided that the number of mites on the bees remains the same. In addition, when the frequency with which a bee brings a mite close enough to a brood cell for invasion is proportional to the surface of a brood cell, 1.7 times more mites are expected per drone brood cell owing to their 1.7 times larger surface. Combining these two factors would result in drone brood cells being invaded 3.4–5.1 times more frequently than worker brood cells. However, it was found that drone brood cells were invaded 11.6 times more frequently. Thus, the rate of invasion per cell is increased an additional two to four times by the presence of a drone larva instead of a worker larva. Martin [43] added a third factor to explain the higher number of mites in drone brood cells when compared to worker brood cells. The weights of drone and worker larvae are 346 and 140 mg, respectively, yielding a proportion of 2.47. Including this factor would lead to a range of 8.4–12.6 times more frequent invasions in drone brood cells than in worker brood cells. However, this factor is probably not related to a higher number of bee visits to drone brood cells as suggested by Martin [43], because Boot et al. [10] demonstrated that mite invasion was not related to feeding or cell capping. It is more likely that the weight of the larva is related to the strength of the signal causing mite invasion [42].

6. DISTRIBUTION OF MITES OVER WORKER AND DRONE BROOD CELLS

Schulz [57] and Fuchs [31] found more mites in drone brood cells than in worker brood cells. De Jong [22], Rozenkranz et

al. [52] and Otten and Fuchs [45] suggested that mites prefer drone brood to worker brood and Schulz [57], Ifantidis [37] and Fuchs and Langenbach [32] suggested that this preference is due to the higher reproductive success of mites in drone brood cells. The larger number of mites generally found in drone brood cells is thought by these authors to be the result of selection of 'drone brood mites'. This preference, however, could not be found in individual mites. When Radtke [47] collected adult mites from worker and drone brood cells, marked each group of mites distinctly, and introduced them into a colony, he found no indication of a selection of 'worker brood mites' or 'drone brood mites'. In fact, he recovered about the same numbers of mites in both categories of marked mites in worker and drone brood cells that had been capped in the same period.

The differential distribution of mites over different ratios of drone and worker brood cells within one colony can be calculated according to Boot et al. [14] using only the relative rates of invasion per drone and worker brood cell per day and the numbers of both brood cell types without making further assumptions. The relative rates of invasion per brood cell per day are 0.56 and 6.49 for worker and drone brood, respectively. These values are the result of all possible factors that affect brood cell invasion.

Fuchs [31] studied the invasion of worker and drone brood cells simultaneously in the same colony. He carried out this experiment in 68 colonies containing only one comb with worker brood and one comb with drone brood. The numbers of worker and drone brood cells varied between the colonies from mainly worker brood to mainly drone brood. After all brood cells had been capped, Fuchs [31] counted the number of mites that invaded the two types of brood cells. The relationship between the percentage of the mites in drone brood cells and the percentage of drone brood cells in the experiments of Fuchs [31] is presented in *figure 4*. The

average number of mites per drone brood cell was 8.3 times higher than that per worker brood cell. This distribution (drone brood cell preference, cf. Fuchs [31]) was not affected by the rate of infestation of the colony nor by the total number of available brood cells. However, the distribution was affected by the percentage of drone brood cells. The average percentage of mites per drone brood cell was 12.1 times higher than that per worker brood cell when the percentage of drone brood cells varied between 5 and 15 (situation found in untreated colonies).

On the basis of the data provided by Dr Fuchs, nearly the same relationship between the percentage of mites in drone brood cells to the percentage of drone brood cells could be predicted using only the relative rates of invasion into worker and drone brood [14], and the numbers of worker and drone brood

cells provided by Dr Fuchs (figure 4). The observed distributions were congruent with the theory on invasion [14] which assumed that invasions of worker and drone brood cells are independent events. Or, the decision of the mites to invade a brood cell is determined by the signal they receive from the brood cell in their direct vicinity.

7. CONCLUSION

Although many aspects of invasion behaviour have been revealed, it is still unclear which substances the mites are attracted to when invading a brood cell. These attractive substances could differ in quantity or even in quality between worker and drone larvae. In addition mites of populations of different origin (East Russia or Japan) could respond differently to these substances. Invasion behaviour of mites in

Figure 4. The relationship between the percentages of *Varroa jacobsoni* in drone brood cells and the percentages of drone brood cells as observed and calculated by Fuchs [31] and as predicted by using the relative rates of invasion per day per worker or drone brood cell [13] and the numbers of worker and drone brood cells provided by Dr Fuchs.

A. mellifera and in *A. cerana* colonies cannot yet be compared because few data are available on the behaviour of the Asian mite in colonies of its original host. The results so far obtained provide possibilities for further studies. The estimation of the relative rates of invasion per day per worker and drone brood cell has made it possible to answer the question as to why it is advantageous for the mite to invade both worker and drone brood cells while reproductive success in drone brood cells is higher [15].

The population growth of *V. jacobsoni* depends entirely on that of the honey bee colony. Since it is known that the rate of invasion of the mite depends on the size of the colony and the number of worker and drone brood cells suitable for mite invasion, simulation models of the mite population could be improved [21, 43].

V. jacobsoni can effectively be trapped when using large numbers of worker brood cells. The finding that mites invade drone brood cells in larger numbers than worker brood cells [14, 31, 57] inspired several authors [19, 51, 58] to develop biotechnical control methods in which mites are trapped in drone brood combs that are subsequently removed from the colony. From the experiments on the process of invasion, it follows that in a colony of given size the number of phoretic mites that can be trapped depends mainly on the number of cells used for trapping. The methods developed by Calis et al. [19] are already effective with relatively small amounts of drone brood cells. Boot et al. [14] calculated that in a broodless colony of 1 kg of bees only 462 drone brood cells are needed to trap 95 % of the mites. To obtain the same result, however, 5 357 worker brood cells would be needed. The principle of trapping mites in broodless colonies with drone brood has led to the development of several biotechnical control methods [18, 56]. Without tests in the field, the effectiveness of biotechnical control methods can now be predicted using the simulation model developed by Calis et al. [20].

ACKNOWLEDGEMENT

We thank Dr S. Fuchs for kindly providing the data he collected in 1987.

Résumé – Le comportement d'invasion de *Varroa jacobsoni* Oud. : des abeilles aux cellules de couvain. L'acarien *Varroa jacobsoni* (Acari : Varroidae) peut envahir les cellules de couvain d'ouvrières (cco) ou de mâles (ccm) d'abeilles (*Apis mellifera* L.) lorsque les ouvrières le mettent en contact étroit avec ces cellules. Les acariens passent du flanc de l'abdomen de l'abeille sur le rayon et pénètrent immédiatement dans la cellule de couvain adjacente, grimpent à la surface de la larve et se glissent entre la larve et la paroi de la cellule jusqu'au fond de celle-ci. On n'a jamais vu d'acariens se déplacer sur le rayon ni entrer dans des cellules de couvain et en ressortir pour choisir une cellule à envahir [10].

À l'aide de « demi-rayons », Boot et al. [8] ont pu enregistrer le moment où un acarien apparaissait au fond de la cellule transparente et le moment où la cellule était operculée. L'invasion des acariens dans les cco s'est produite entre 15 et 20 h avant l'operculation de la cellule, alors que dans les ccm elle a commencé 45 à 50 h avant l'operculation. La période d'attractivité des ccm est donc 2 à 3 fois plus longue que celle des cco. Boot et al. [13] ont mesuré i) la période d'attractivité des cellules de couvain, ii) la répartition des acariens sur les différents types de cellules, et iii) la distance entre la larve et le bord de la cellule de divers types de cellules, en relation avec la durée qui a précédé l'operculation. La période d'attractivité des cco et des ccm raccourcies a été plus longue et on y a trouvé 1,5 à 3 fois plus d'acariens que dans les cellules témoins. La période d'attractivité des cco allongées a été plus courte et elles ne renfermaient qu'un sixième des acariens présents dans les cellules témoins. Les cellules de mâles avec une larve d'ouvrière semblent avoir eu une période d'attractivité plus courte et ne ren-

fermaient que la moitié des acariens trouvés dans les cco témoins. Les cellules d'ouvrières avec une larve de mâle semblent avoir eu une période d'attractivité plus longue, mais le nombre d'acariens ne différait pas de celui trouvé dans les ccm témoins.

L'attractivité des cellules de couvain semble être en rapport avec la distance entre la larve et le bord de la cellule. On a estimé la distance critique à laquelle les acariens envahissaient les cellules de couvain, en mesurant cette distance au début de la période d'attractivité. Dans les cco allongées et dans les ccm enfermant une larve d'ouvrière, la distance critique était plus grande que dans les cco témoins. Puisque la période d'attractivité était plus courte dans ces deux cas là, les larves étaient plus âgées lorsque les acariens ont commencé à envahir les cellules.

À partir de colonies indemnes d'acariens, Calis et al. [20] ont obtenu des rayons de couvain daté. Lorsque les premières cellules de couvain ont commencé à être operculées, les rayons ont été placés durant 3 h dans une colonie fortement infestée, puis remis dans les colonies indemnes. L'operculation des cellules de couvain a été observée toutes les 3 h. Le nombre relatif d'acariens qui envahissaient les cellules a augmenté avec l'âge de la larve.

Boot et al. [9] ont introduit un grand nombre d'acariens jeunes et vieux dans une colonie indemne et les ont laissé une journée. Les acariens ont commencé à envahir les cellules de couvain au premier jour du stade phorétique et ont continué à le faire à un taux constant, bien que ce taux et le nombre d'abeilles aient varié d'une répétition à l'autre. Quand on introduisait chaque jour un grand nombre de cellules de couvain, la même proportion d'acariens phorétiques envahissait chaque jour une cellule de couvain. L'invasion d'une cellule de couvain n'était pas liée à la durée de leur séjour sur les abeilles adultes. Le temps passé sur les abeilles adultes n'influence donc pas le succès reproductif [12].

Le taux d'invasion est déterminé par le rapport du nombre de cellules de couvain appro-

priées à la taille de la colonie. Plus le nombre de cellules de couvain attractives est grand, plus grand est le taux d'invasion et plus la taille de la colonie est grande, plus faible est la densité des acariens sur les abeilles et, donc, plus faible est le taux d'invasion. Boot et al. [14] ont établi ces rapports en utilisant des colonies sans couvain dans lesquelles ils introduisaient chaque jour un nombre connu de cellules de couvain de mâles daté. Les ccm ont été envahies 11,6 fois plus souvent que les cco.

Boot et al. [14] ont calculé la répartition des acariens dans une colonie sur le couvain d'ouvrières et le couvain de mâles. La répartition est déterminée par les taux spécifiques d'invasion par jour et les nombre de cellules des deux types. Les répartitions observées par Fuchs [34] concordent avec la théorie sur l'invasion [14].

L'étude du comportement d'invasion de *V. jacobsoni* a permis de mettre au point des méthodes de lutte biotechniques efficaces, qui utilisent le piégeage du couvain de mâles dans des colonies sans couvain [21, 58]. Calis et al. [18] ont mis au point un modèle de simulation qui permet de prédire l'efficacité des méthodes biotechniques. Avec ce modèle il n'est plus nécessaire de tester les variations de ces méthodes au champ.
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***Apis mellifera* / *Varroa jacobsoni* / comportement d'invasion / lutte biotechnique**

Zusammenfassung – Von den Bienen in die Brutzellen: Ein Überblick über das Eindringverhalten von *Varroa jacobsoni*.

Sobald Arbeiterinnen die Varroamilben in nahen Kontakt zu Arbeiterinnen – oder Drohnenbrutzellen brachten, konnten diese in sie eindringen. Die Milben bewegten sich hierbei von der Seite des Abdomens der Biene auf die Wabe, wobei sie sofort in eine nahegelegene Brutzelle eindringen. Dann liefen sie auf der Oberfläche der Larve herum und krochen zwischen der Larve und der Zellwand hindurch bis zum Boden der

Zelle. Es wurde niemals beobachtet, daß die Milben auf der Wabenoberfläche herumlaufen oder daß sie Zellen betreten und wieder verließen um eine Zelle für den Befall auszusuchen [10].

Durch die Verwendung von 'Halbwaben' konnten Boot et al. [8] feststellen, zu welchem Zeitpunkt die Milben auf dem durchsichtigen Zellboden erschienen und wann diese Zellen verdeckelt wurden. In verschiedenen Völkern begann der Befall der Arbeiterinnenbrutzellen 15–20 Stunden, der der Drohnenbrutzellen 40–50 Stunden vor der Verdeckelung der Zellen. Der Zeitraum, in dem die Zellen attraktiv wirken, ist daher bei den Drohnenbrutzellen 2–3 mal länger als bei den Arbeiterinnenbrutzellen.

Boot et al. [13] bestimmten: 1) die attraktive Zeit der Brutzellen, 2) die Verteilung der Milben zwischen verschiedenen Brutzellen, und 3) den Abstand zwischen der Larve und dem Zellrand bei den verschiedenen Zelltypen in Beziehung zu der Zeit bis zur Zellverdeckelung. Die attraktive Zeit gekürzter Arbeiterinnen- und Drohnenbrutzellen war verlängert, dies führte zu im Vergleich zu Kontrollzellen 1,5 bis 2 mal höheren Anzahlen von Milben in diesen Zellen. Demgegenüber war die attraktive Zeit von verlängerten Zellen kürzer, in diesen Zellen fanden sich im Vergleich zu Kontrollzellen nur 1/6 der Milbenzahlen. Drohnenzellen, die eine Arbeiterinnenlarve enthielten, wiesen eine kürzere attraktive Zeit auf und enthielten halb so viele Milben wie die Kontrollgruppe von Arbeiterinnenbrutzellen. Arbeiterinnenbrutzellen mit einer Drohnenlarve waren eine längere Zeit attraktiv, der Befall mit Milben unterschied sich aber nicht von den Kontrollgruppe mit Drohnenzellen.

Die Attraktivität der Brutzellen schien mit dem Abstand zwischen der Larve und dem Zellrand zusammenzuhängen. Der kritische Abstand, ab dem die Milben in die Brut einzudringen beginnen, kann zu Beginn der attraktiven Periode bestimmt werden. In verlängerten Arbeiterinnenbrutzellen und in Drohnenzellen, die eine Arbeiterinnenlarve enthielten, war dieser gegenüber den Kon-

trollzellen verlängert. Da die attraktive Zeit in diesen Fällen verkürzt war, waren die Larven zum Zeitpunkt des Beginnes des Zellbefalls bereits älter.

Calis et al. [20] entnahmen Waben mit datierter Brut aus milbenfreien Völkern. Sobald die Verdeckelung der ersten Zellen begann, wurden diese drei Stunden lang in hochbefallene Völker eingebracht und danach wieder in die milbenfreien Völker zurückgebracht. Danach wurde in Abständen von drei Stunden die Verdeckelung der Zellen verfolgt. Offensichtlich nahmen mit steigendem Alter der Larve die relativen Anzahlen von Milben zu, die die Zellen befallen hatten.

Boot et al. [9] setzten eine große Anzahl jüngerer und älterer Milben in ein milbenfreies Volk ein. Die Milben begannen bereits am ersten Tag ihres phoretischen Stadiums die Brutzellen zu befallen, danach drangen sie mit konstanter Befallsrate in die Brutzellen ein. Diese Befallsrate war zwischen den Versuchen allerdings unterschiedlich. Sobald jeden Tag die gleiche Anzahl von Brutzellen eingebracht wurde, befiel jeden Tag ein gleichbleibender Anteil der Milben die Brut. Der Befall der Zellen stand nicht mit dem Alter der Milben im Zusammenhang. Die Zeit, die diese auf Bienenarbeiterinnen verbrachten, stand in keinem Zusammenhang mit ihren Reproduktionserfolg [12].

Die Befallsrate wird von dem Verhältnis zwischen geeigneten Brutzellen und der Größe des Volkes bestimmt. Je größer die Anzahl attraktiver Brutzellen ist, desto höher ist auch die Befallsrate. Je größer das Volk ist, desto geringer ist die Dichte der Varroamilben auf den Bienen und daher auch die Befallsrate. Boot et al. [14] ermittelten diesen Zusammenhang, indem sie täglich eine bestimmte Menge von Drohnenbrutzellen in ansonsten bruttfreie Völker einbrachten. Hieraus bestimmten sie, daß Drohnenbrutzellen 11,6 mal mehr befallen werden als Arbeiterinnenbrutzellen.

Boot et al. [14] berechneten die Verteilung von Milben zwischen Arbeiterinnenbrut und

Drohnenbrut in einem Volk. Diese Verteilung wird von den spezifischen Befallsraten beider Bruttypen bedingt. Die von Fuchs [34] beobachteten Verteilungen stimmten mit dieser Theorie des Befallsverhaltens überein [14].

Die Untersuchung des Befallsverhaltens von Brut durch *Varroa jacobsoni* ermöglichte die Entwicklung wirksamer biotechnischer Bekämpfungsmethoden unter Verwendung von Fangwaben in brutlosen Völkern [29, 58]. Calis et al. [18] entwickelten ein Simulationsmodell, das Voraussagen der Wirksamkeit dieser Methoden ermöglicht. Hierdurch ist es nicht länger nötig, Varianten dieser Methoden in Feldversuchen zu testen. © Inra/DIB/AGIB/Elsevier, Paris

***Apis mellifera* / *Varroa jacobsoni* /
Eindringverhalten / Brutzellentyp /
Biotechnische Bekämpfung**

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