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Further observations on the correlation between attractiveness of honey bee brood cells to *Varroa jacobsoni* and the distance from larva to cell rim

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Abstract

Varroa jacobsoni Oudemans (Acari: Varroidae) was studied with respect to invasion into different types of honeybee, *Apis mellifera* L., brood cells. Different cell types were obtained by shortening and elongating of cells, grafting worker larvae into drone cells and *vice versa*. The type of cell strongly affected the number of mites per cell, and the attractive period of the cells to the mites. The type of cell also affected the distance from larva to cell rim preceding cell capping. When this distance was larger in comparison to control cells of the same age, the attractive period of the brood cells was shorter and *vice versa*. Since in all cell types the distance from larva to cell rim continuously decreased preceding cell capping, this negative correlation is in agreement with the hypothesis that there is a critical larva-rim distance under which brood cells are attractive to mites. Then, the length of the attractive period of brood cells depends on the moment this critical distance is reached. The distribution of mites over different cell types in turn results from differences in the attractive period.

Introduction

Varroa jacobsoni Oudemans, worldwide a major pest of *Apis mellifera* L., parasitizes both adult bees and honeybee brood, but only reproduces in the capped brood cells (Ifantidis & Rosenkranz, 1988). Since invasion into brood cells is crucial for reproduction of the mites, this aspect has been studied frequently, especially the resulting distribution of mites over different cell types. A well known example is the more frequent occurrence of mites in drone cells when offered the choice between worker and drone cells (e.g. Fuchs, 1990). This phenomenon may be explained as a differential response to the two types of larvae. However, non-random distributions of mites over different cell types have also been found when the type of larva was the same. De Jong & Morse (1988) and de Ruijter & Calis (1988) found more mites in worker cells protruding above the comb surface than in neighbouring worker cells. Another example is given by P. Rosenkranz

(Meeting EC-Experts Group, Thessaloniki 1984, pers. comm.), Calis *et al.* (1993), and Ramon *et al.* (1993) who found more mites in the smaller cells, when brood cell attractiveness to mites was tested in cells differing in diameter. Finally, Calis *et al.* (1993) and Goetz & Koeniger (1993) found more mites in shortened worker cells.

Why do Varroa mites invade certain types of brood cells more frequently than others? The distribution of mites over cells depends on the way the mites select a cell for invasion. Brood cells are invaded during a certain period preceding cell capping: c. 1 day for worker brood cells, and c. 2 days for drone brood cells (Ifantidis, 1988; Boot *et al.*, 1992). To find a suitable brood cell Varroa mites do not walk over the comb nor go in and out the cells. They move directly from the bee into the selected cell, and probably use a chemical or physical signal like heat production to decide whether to stay on the bee or to invade the cell (Boot *et al.*, 1994a). When signal strength decreases with increas-

ing distance between larva and cell rim, the response to a signal coming from the brood cell may well be correlated to this distance. Since larvae grow and the length of their cells remains more or less the same, the distance from larva to cell rim probably decreases during development of the larva. Hence, there may be a critical distance between larva and cell rim under which brood cells become attractive to the mites. The type of cell may determine how many hours before cell capping this critical distance is reached, thus defining the length of the attractive period. In addition, it is expected that more mites will invade per cell when cells are attractive for a longer time span, since the probability for a mite to invade a cell is constant per time unit (Boot *et al.*, 1993; Boot *et al.*, 1994b).

In the above referred studies, the biased distribution of mites over various cell types possibly occurred because the type of cell affected the moment at which the critical distance between larva and cell rim was reached. As a result of shortening the cells (Calis *et al.*, 1993; Goetz & Koeniger, 1993), the distance between larva and cell rim was shortened as well. A critical distance would be reached earlier. Assuming that the moment of capping depends on the age of larvae and that the moment of capping is not much affected by shortening of the cells, the attractive period would thus be extended. In cells that protrude above the comb surface after cell capping (de Jong & Morse, 1988; de Ruijter & Calis, 1988), the critical distance may also have been reached earlier than in other cells. Protruding cells had possibly been lengthened by the bees just before capping, whereas the cells had already become attractive to the mites at that time. Hence, the distance from larva to cell rim may have been shorter in the period that the cells were about to become attractive, which resulted in the critical distance being reached earlier. Finally, in cells with a smaller diameter than others (P. Rosenkranz, pers. comm.; Calis *et al.*, 1993; Ramon *et al.*, 1993), the distance between larva and cell rim was probably smaller as well, because after the larva has completely covered the cell bottom, its body can expand only in the direction of the cell opening. If so, then the critical distance would also be reached earlier in development of the larva.

These observations lead to the hypothesis that the length of the attractive period depends on the moment a critical distance from larva to cell rim is reached, and that the distribution of mites over different cell types in turn results from differences in the attractive period. In this study we intend to subject this *a posteriori* hypothesis to a more precise test by studying not only

the distribution of mites over various cell types, but also the length of the attractive period and the distance from larva to cell rim.

Materials and methods

All experiments were carried out in 10-frame hives with common Dutch honeybees, *Apis mellifera* L. Three kinds of experiments were carried out: (1) to estimate the period that brood cells are attractive to mites, (2) to determine the distribution of mites over different cell types, and (3) to measure the distance from larva to cell rim of different cell types in relation to the time preceding cell capping. Some of the results have been published before in a preliminary report (Calis *et al.*, 1993).

Determination of the attractive period of brood cells. In these experiments 'half-combs' from which the bottoms of the cells had been replaced by a transparent sheet, were used (Boot *et al.*, 1992; Beetsma *et al.*, 1993). Two of these 'half-combs', one of them containing a patch of brood, were clamped together and placed in the middle of a bee colony, heavily infested with mites. Other combs containing open brood were removed from the colony. Mites could therefore only invade cells of the patch of brood introduced for the experiment.

Invasion of mites was recorded by removing the test comb from the colony, brushing the adhering bees into a bucket, separating the two 'half-combs', and holding the 'half-comb' with brood against the light. Mites could easily be seen through the transparent cell bottoms. Invasion of mites was recorded every two hours. For each cell, records were made when a mite had appeared and when the cell had been capped. These data were later used to calculate how many hours preceding cell capping each mite had invaded into a cell. Subsequently, the 'half-combs' were clamped together, put into the colony again, and the bees collected in the bucket were returned to the colony by shaking them on top of the test comb. Other combs were kept covered with cloth during hive manipulations, to minimize disturbance of the colony. After finishing the observations, the capped cells were opened to check the number of mites in cells.

Invasion of mites was recorded in normal worker and drone cells, shortened worker and drone cells, elongated worker cells, drone cells with worker larvae, and worker cells with drone larvae. Shortened cells were made by carefully cutting the cell rims from

one half of a patch of brood by using electrically heated wire as a knife. This was done 10–20 h before the cells were normally expected to become invaded by mites (Boot *et al.*, 1992). The other half of the brood patch was used as a control. After cutting the cell rims, the bees started rebuilding the cells. This process was monitored by emptying 8 evenly distributed cells in the brood patch, 4 in the shortened part and 4 in the control part, and measuring cell depth every two hours during inspections. Elongated cells were made indirectly as follows. A droplet of melted wax was put into all six adjacent cells of the brood cell to be elongated. This droplet of wax raised the bottom of the cells about 3 mm. Subsequently, the comb was put into a colony and the queen was allowed to oviposit into the cells. Eggs in the cells to be elongated were removed. The bees elongated the cells containing brood due to the raised cell bottom. Consequently, the cells enclosed were elongated to the same height as that of the surrounding cells, but the cells were 3 mm deeper. Young larvae, less than one day old, were grafted into the elongated cells. Only one half of the 'half-comb' was used to record invasion into elongated cells. The other half was used as control, whereas the control brood cells were alternated with capped brood cells in the same pattern as for the elongated cells.

To monitor invasion of mites into drone cells with worker larvae and worker cells with drone larvae, young larvae, less than one day old, were grafted into the cells. Invasion into drone cells with worker larvae and *vice versa* was not directly compared with control cells, because when control cells were present the bees did not nurse the manipulated brood cells well enough, and many larvae died.

Distribution of Varroa mites over different cell types.

The number of mites invading various brood cell types was determined and compared with control brood cells. A comb containing both a brood patch of a certain cell type and a patch of control brood cells, was placed into a heavily infested colony that had their own combs with open brood removed. Every four hours, capping of both manipulated and control cells was marked on transparent sheets. After capping of most of the brood cells, the comb was removed from the colony and the cells were checked for mites. To compare the number of mites per cell, only those 4-h intervals were used during which 10 or more mites had invaded. Differences from a random distribution between manipulated and control cells were tested with the chi-square test. The ratio of mites per manipulated cell to their num-

Fig. 1. Invasion of mites into shortened and control drone brood cells. Example of the data collected during the experiments to determine the attractive period of brood cells: cumulative number of mite invasions (A), cell depth (B), and cell capping (C).

ber per control cell was calculated for each interval. Subsequently, the average ratio was calculated from the ratio's in the separate intervals, weighted to the number of mites that had invaded.

The number of mites in shortened worker cells, elongated worker cells, and drone cells with worker larvae, were compared with the number in control worker cells. The number of mites in shortened drone cells and worker cells with drone larvae were compared with control drone cells. Brood patches of various cell types were obtained using the same methods as for the experiment to determine the attractive period of brood cells.

Distance from larva to cell rim. The distance from larva to cell rim was determined in relation to the time preceding cell capping. A brood comb with many old larvae, the cells of which were capped by the bees within 30 to 50 h, was taken from a colony. The distances from these larvae to the cell rims were measured with a probe, as used by Goetz & Koeniger (1992). The brood comb was put into the colony again, and subsequently every two hours a transparent sheet was placed over the brood area on which newly capped cells were marked.

In this way, the distance to the cell rim in relation to the time preceding cell capping was measured for control worker and drone cells, worker larvae in elongated cells, worker larvae in drone cells, and worker larvae in an artificial worker comb (Wieting & Ferenz, 1991). This artificial comb has plastic cells of which the bottom is as wide as a drone cell and the opening as wide as a worker cell. Because of the conical shape, a different distance from larva to cell rim was expected. Worker larvae in elongated cells and worker larvae in drone cells were obtained as before.

Results

Attractive period of brood cells. In the experiments to determine the attractive period of brood cells, records were made of mite invasion into brood cells and capping of cells. In addition, differences in cell depth between control and shortened brood cells were monitored. Figure 1 shows an example of the experiment with the highest number of mites invaded. Cell capping of control and manipulated cells always occurred during the same period (Fig. 1c), but mite invasions into manipulated cells started later or earlier than in control cells (Fig. 1a). After cutting the rims from the cells in the experiments with shortened cells, the bees quickly started rebuilding, although the cells remained shorter than control cells for a long time (Fig. 1b). The cell rims were therefore cut for a second time when no mites had invaded after 6 h, to maintain a marked difference between control cells and shortened cells at the moment at which invasion started.

For each mite the time of invasion was calculated in relation to cell capping. Sometimes, one or a few mites invaded much earlier before capping than the others. To reduce the effect of an accidental early invasion on the estimate of the attractive period of brood cells, the attractive period was arbitrarily defined as the period preceding cell capping during which 90% of the mites had invaded. Tables 1 and 2 summarize the results.

Shortening of both worker and drone brood cells always resulted in a longer attractive period when compared to control brood cells. Elongated worker cells were attractive to the mites during a shorter period than the control ones. Drone cells with worker larvae seemed to be attractive to mites during a shorter period than control worker brood cells, and drone larvae in worker cells seemed to be attractive during a longer period than control drone brood cells, although the attractive period of these cell types could not be com-

pared directly with that of control cells. After assessing the real number of mites in the cells, the percentage of mites overlooked appeared to be less than 15% in 14 of the 16 brood patches recorded. In elongated worker cells however, the percentage of mites overlooked was very high: 43%.

Distribution of Varroa mites over different cell types.

The cell type strongly affected the number of mites that invaded. In shortened worker brood cells, 2 to 3 times as many mites were found per cell when compared with control cells (Table 3). In elongated worker cells and in drone cells with worker larvae, fewer mites were found per cell when compared with control cells: in elongated worker cells about 1/6, and in drone cells with worker larvae about 1/2 of the number in control cells. Shortening of drone cells also resulted in more mites per cell: about 1.5 to 2 times as many mites as in control drone cells (Table 4). Between worker cells with drone larvae and control drone brood cells no significant difference was found in the number of mites per cell.

The distance from larva to cell rim. In the 30 h preceding cell capping, the distance from larva to cell rim decreased linearly in cells with worker larvae (Fig. 2). Control worker cells were capped when this distance was about 5.5 mm (Fig. 2a). In elongated worker 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 capping (Fig. 2b), corresponding to the distance by which the cells had been elongated. In drone cells with worker larvae, the distance from larva to cell rim was also much larger than in control worker cells: about 2 to 3 mm (Fig. 2c). In the artificial worker cells, the distance from larva to cell rim was about 0.5 to 1 mm more than in control worker cells.

Drone brood cells showed a different relationship between the distance from larva to cell rim and the time preceding cell capping (Fig. 3). From about 35 h preceding cell capping, the distance from larva to cell rim remained on average about 7 mm. Only before 35 h preceding cell capping a decrease of this distance was found in relation to time.

In general, the distance between larva and cell rim decreased with time. Hence, the critical distance at which mites start to invade the cells may be estimated by taking the distance found at the start of the attractive period. Figure 4 shows such estimates, based on the

Table 1. Differences in the period attractive to *Varroa* mites between various cell types containing worker larvae and control worker cells. The attractive period is defined as the period preceding cell capping during which 90% of the mites invaded

Treatment ¹	Number of mites	Percentage of mites overlooked ²	Attractive period (h)
Shortened worker cells***	110	3.5	26
Control	92	1.1	20
Shortened worker cells***	70	2.8	24
Control	31	11.4	14
Shortened worker cells***	95	4.0	30
Control	49	10.9	18
Elongated worker cells***	16	42.9	6
Control	114	6.6	14
Drone cells with worker larvae	45	13.5	12
Drone cells with worker larvae	24	29.4	3 ³
Drone cells with worker larvae	28	6.7	7 ³

¹ Differences in the distribution of invasions over time between shortened or elongated cells and control cells were tested with the Kolmogorov-Smirnov Two Sample test, *** = $P < 0.001$

² The percentage of mites overlooked was determined by opening the capped cells after observations and counting the real number of mites in the cells. This number was compared with the number of mite invasions observed.

³ Invasion of mites was recorded every hour instead of every 2 h.

Table 2. Differences in the period attractive to *Varroa* mites between various cell types containing drone larvae and control drone cells. The attractive period is defined as the period preceding cell capping during which 90% of the mites invaded

Treatment ¹	Number of mites	Percentage of mites overlooked ²	Attractive period (h)
Shortened drone cells***	244	5.8	52
Control	265	5.7	40
Shortened drone cells***	143	3.4	48
Control	79	9.2	34
Worker cells with drone larvae	35	10.3	64

¹ Differences in the distribution of invasions over time between shortened cells and control cells were tested with the Kolmogorov-Smirnov Two Sample test, *** = $P < 0.001$

² The percentage of mites overlooked was determined by opening the capped cells after observations and counting the real number of mites in the cells. This number was compared with the number of mite invasions observed.

Fig. 2. The distance between larva and cell rim in relation to the time before cell capping of worker larvae in control worker cells (A), in elongated worker cells (B), in drone cells (C), and in artificial worker cells (D).

attractive periods found in this study and in two other studies, and based on the regression lines from Figure 2 for cells with worker larvae and the average distance from larva to cell rim from Figure 3 for cells with drone larvae. Estimates of critical distances ranged between 6.9 and 7.9 mm for control worker cells and between 7.2 and 7.8 mm for control drone cells. The critical distance for artificial worker cells (Wieting & Ferenz, 1991) was estimated to be 6.9 mm, within the range for control worker cells. The critical distances for invasion into elongated worker cells and for invasion into drone cells with worker larvae were estimated to be larger: between 8.2 and 9.0 mm.

Discussion

The type of brood cell strongly affected the number of mites per cell (Tables 3 and 4), and the differences in the number of mites found per cell were related to the length of the attractive period to mites (Tables 1 and 2). When the attractive period was longer, more mites invaded. Because a longer attractive period implies that more cells are available, this positive relationship is in agreement with earlier results showing that more mites will invade when more brood cells are available (Boot *et al.*, 1993; Boot *et al.*, 1994b). The results show that the size of cells has to be taken into account when attractivity of brood cells to *Varroa* mites is compared

Table 3. Number of mites which invaded various cell types containing worker larvae in comparison with control worker cells. The number of time intervals in which mite invasion was compared, the total number of brood cells that were capped, the total number of mites that invaded, and the average ratio of mites per cell of a type of cell to their number in control cells, are shown

Treatment	Number of intervals	Total number of cells	Total number of mites	Average ratio to control cells ¹
Shortened worker cells	8	526	203	2.17***
Shortened worker cells	3	270	70	2.85**
Shortened worker cells	4	74	122	2.85***
Elongated worker cells	3	137	127	0.16***
Drone cells with worker larvae	3 ²	411	69	0.49**
Drone cells with worker larvae	4 ²	310	124	0.44***

¹ Differences from a random distribution over cells of various types and control cells were tested with Chi²-test, ** = P<0.01, *** = P<0.001

² Intervals of 6 h instead of 4 h.

Table 4. Number of mites which invaded various cell types containing drone larvae in comparison with control drone cells. The number of time intervals in which mite invasion was compared, the total number of brood cells that were capped, the total number of mites that invaded, and the average ratio of mites per cell of a type of cell to their number in control cells, are shown

Treatment	Number of intervals	Total number of cells	Total number of mites	Average ratio to control cells ¹
Shortened drone cells	4	397	185	1.84**
Shortened drone cells	7	271	542	1.68***
Worker cells with drone larvae	4 ²	156	534	1.20 ^{NS}

¹ Differences from a random distribution over cells of various types and control cells were tested with Chi²-test, NS = not significant, ** = P<0.01, *** = P<0.001

² Intervals of 6 h instead of 4 h

between various honey bee strains or races. Brood of small-sized bees may for instance be less attractive to the mites than brood of large-sized bees, when compared in standard combs. Standard combs will be relatively large for the small bees and relatively small for

the large bees. Differences in brood attractivity may in such cases be solely caused by differential attractive periods of the brood cells due to relative differences in cell size.

Fig. 3. The distance between larva and cell rim in relation to the time before cell capping in control drone cells.

In addition to the relationship between the attractive period and the number of mites per cell, a relationship between the attractive period and the distance from the larva to the cell rim was found. Cell types with a larger distance in comparison to control cells of the same age, had a shorter attractive period and *vice versa*. Since the distance from larva to cell rim continuously decreased preceding cell capping, this negative relationship is in agreement with the hypothesis that mites start to invade cells when the distance from larva to cell rim drops below a threshold. In normal brood cells, this critical distance for invasion appeared to be 7 to 8 mm, both in worker and drone cells (Fig. 4). Goetz & Koeniger (1993) found a similar distance at which invasion into worker brood cells starts: between 7 and 7.5 mm. In Wieting & Ferenz's study (1991) a shorter attractive period was found for artificial worker cells than for control cells: 6 h and 12 h, respectively. No explanation was provided for this difference in attractive period. Our results show that at the same time before cell capping the distance from larva to cell rim is larger in the artificial cells than in control cells (Fig. 2a, d). Hence, in the artificial cells the critical distance is reached at a later moment in the development of the larva, resulting in a shorter attractive period. Based on the attractive periods of 6 and 12 h for the artificial and control cells respectively (Wieting & Ferenz, 1991), both periods indeed give the same estimate for the critical distance: 6.9 mm (Fig. 4). Thus, the shorter attractive period of the artificial cells may be caused by the differential distance from larva to cell rim. This distance may be larger in the artificial cells, because these cells are conical with a bottom that has the same width as a drone cell. Hence, the larva can expand

more without being forced in the direction of the cell opening. The same explanation may be valid for the larger distance from larva to cell rim found in drone cells with worker larvae.

The effect of distance from larva to cell rim on invasion implies that this distance interferes with the way mites select brood cells. In theory, mites may measure the distance from larva to cell rim, whereas they use this distance as a correlate for cell suitability. However, this is unlikely because the mites cannot estimate the distance visually and because they do not select brood cells by walking in and out cells but select cells while they stay on an adult bee (Boot *et al.*, 1994a). Thus they probably use a signal coming from the larva like heat production or production of volatile chemicals, whereas the distance from larva to cell rim affects the strength of the signal as it reaches a mite on a bee.

In elongated worker cells and drone cells with worker larvae, the critical distance at which invasion starts was estimated to be larger than in control brood cells (Fig. 4). Since the attractive period was shorter for elongated worker cells and for drone cells with worker larvae, the larva was older when invasion by mites began. Possibly, the critical distance for invasion is larger when the larva is older, because the strength of a signal coming from the larva may increase with larval age. This may also explain why invasion did not always start immediately after shortening of cells, though the distance from larva to cell rim was clearly shorter than 7 mm. The signal coming from these young larvae may have been too weak for invasion to occur.

Of the mites that invaded elongated worker cells, 43% was overlooked (Table 1). This high percentage may be due to the short attractive period of such cells. A larger part of the mites is then expected to invade shortly before capping. Because cells were inspected at 2-hourly intervals, the cells invaded during the preceding 2 h were often already capped and the larva had stretched to start spinning (Jay, 1963). At this stage, mites do not stay on the bottom of the cell anymore. They may be hidden behind the larva, and the chance for a mite to be overlooked increases. The shorter attractive period may also be the reason for the relatively high percentages of mites overlooked in drone cells with worker larvae. Although in some cases a considerable part of the mites was overlooked, the estimates for the attractive period may still be reliable, provided that overlooked mites invaded within the same period as the others.

Fig. 4. Critical distance from larva to cell rim at which invasion into brood cells is estimated to start in different cell types.

Our results are in agreement with the hypothesis that the length of the attractive period depends on the moment a critical distance from larva to cell rim is reached, and that the distribution of mites over different cell types in turn results from differences in the attractive period. The number of mites that eventually invade in different cells is still difficult to quantify, however, because the number of mites present on the adult bees in a colony is never constant. This number varies strongly due to invasion into open brood cells and emergence from capped brood cells. In this study, the number of mites per cell were therefore compared between types of cells that had been capped during the same time interval. Since the attractive period of these cells was different however, the cells compared were still not exposed to the same number of mites on adult bees. Furthermore, the rate of invasion per cell may vary during the attractive period and between cells of different types. In any case, there seems to be an important difference in the rate of invasion into cells with worker larvae and cells with drone larvae. The rate of invasion per drone brood cell was found to be about 12 times as high as the rate of invasion per worker brood cell (Boot *et al.*, 1995). This higher rate of invasion per cell is partly due to the 2–3 times longer attractive period of drone cells and, when the area of brood determines the rate of invasion rather than the number of cells, to the 1.7 times larger area of drone

cells on the comb's surface in comparison with worker cells. Taken together this would result in a 3.4–5.1 times higher rate of invasion per drone cell, which is not enough to explain the 12 times higher rate found. Thus, the rate of invasion per cell is another 2–4 times increased by the presence of a drone larva versus a worker larva.

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