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Behaviour of *Varroa* mites invading honey bee brood cells

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ABSTRACT

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Key words: *Varroa jacobsoni*, *Apis mellifera*, brood cells, invasion behaviour.

Invasion behaviour of *Varroa jacobsoni* into honey bee brood cells was studied using an observation hive. The mites were carried close to a suitable brood cell by the bees. Subsequently, the mites moved from the bees to the rim of the cell, walked quickly inside, crawled between the larva and the cell wall, and moved onto the bottom of the cell. *Varroa* mites were never seen walking across the comb, and entering and leaving brood cells as has been described for *Tropilaelaps clareae*. Differences in invasion strategies between *V. jacobsoni* and *T. clareae* are discussed.

INTRODUCTION

The parasitic mite *Varroa jacobsoni* is currently the most important pest of *Apis mellifera*, worldwide. *Varroa* mites parasitize both adult bees and bee brood. They feed on the haemolymph of adult bees and additionally use the bees as transport vehicles within the colony as well as for dispersal from colony to colony. Reproduction of the mites only takes place while residing on honey bee brood. Consequently, the mites have to leave the bees and invade the brood cells (Ritter, 1981; Ifantidis and Rosenkranz, 1988).

Since invasion into brood cells is indispensable for reproduction, knowledge about invasion behaviour and the factors affecting this behaviour may provide a basis for development of new control methods. For example, the finding that *Varroa* mites invade drone cells in larger numbers than worker cells (e.g. Fuchs, 1990), prompted a biotechnical control method in which mites are trapped in drone

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cells and subsequently removed from the colony (Schulz *et al.*, 1983; Rosenkranz and Engels, 1985).

Invasion has been studied primarily at the population level. Studies have been done on the distribution of mites over different types of brood cells (*e.g.* Ruijter and Calis, 1988; Büchler, 1989; Fuchs, 1990), and on the distribution of mites over adult bees and brood cells (*e.g.* Woyke, 1987; Boot *et al.*, 1993; Boot *et al.*, 1994). In these studies the resulting distribution was studied, whereas the underlying behaviour was reconstructed indirectly by inference. Direct studies on behaviour of individual mites have been carried out in artificial settings (*e.g.* Otten and Fuchs, 1988; Le Conte *et al.*, 1989; Rickli *et al.*, 1992) because manipulations to see individual mite behaviour are difficult in a bee hive. Such studies are useful to provide answers to specific questions, *e.g.* whether mites react to certain odours (Le Conte *et al.*, 1989; Rickli *et al.*, 1992), but the relevance of these observations to the behaviour of mites under realistic conditions is not immediately obvious. In this study mite behaviour was observed in a more realistic setting to identify which factors and conditions may play a role during invasion of mites, and to help interpretation of observations in artificial settings.

MATERIALS AND METHODS

Invasion behaviour was observed in small, heavily infested *Apis mellifera* colonies. A specially designed observation hive and two types of frames were used, the design of which was recently described in detail by Beetsma *et al.* (1993). Below, the frame types are described to clarify the nature of observations on mite behaviour.

Observations with a 'half-comb' frame

The cell walls of newly constructed worker combs were cut from the bottom of a comb and melted carefully onto a transparent sheet. Subsequently, this sheet was fixed into a frame of 22 × 35.5 cm. The frame thus held only half a comb, allowing observations through the cell openings as well as through the cell bottoms. Two movable cameras were positioned on either side of the comb in such a way that events at the opening and at the bottom of the same cells were recorded simultaneously. The hive was illuminated with infra-red light, using a ring of 50 light-emitting diodes (LED's), placed at the side of the cell openings. At this side, the mites, being red brown under natural light, appeared white in the recordings with infra-red light, contrasting strongly to the dark bees on which the mites resided. The infra-red light transmitted through the bee larvae covering the cell bottoms caused the mites in the cells to be visible as dark spots on the video screen due to absorption of part of the light. The cell bottom side of the comb was not illuminated directly, because mites and bee brood are both white under infra-red light, and cannot be distinguished. Generally, two hive parts, both containing a 'half-comb' frame, were connected to each other because in a larger colony more brood can be nursed.

Observations using a frame of cells with transparent side walls

A considerable percentage of the mites reside on the ventral side of the bees (Kraus *et al.*, 1986). When the 'half-comb' frame was used for observations, bees walking over the comb surface presented their dorsal aspect to the camera and the mites on the ventral side of the bee could not be recorded. In addition, bees blocked the view on the cell opening, thereby hindering observation of invasion behaviour. Hence, another frame type was constructed in which mite invasion could be observed through opposite transparent Perspex cell walls of vertical rows of cells (Beetsma *et al.*, 1993). Larvae were grafted into the cells and, when the larvae were large enough, events were recorded with two cameras directed towards the same cells from opposite sides. Again the observation hive was composed of two hive parts, one containing the frame with the transparent side walls, and the other containing a 'half-comb' frame to provide ample space for honey and pollen storage, and for oviposition by the queen. The larvae in the cells with the transparent cell walls were nursed well by the bees, and therefore this setting was assumed to be realistic. However, manipulations of the brood may have interfered with invasion of the mites.

RESULTS

Observations with a 'half-comb' frame

When *Varroa* mites invaded brood cells, they crawled between the cell wall and the larva until they reached the bottom of the cell, where they stayed immobilized (Ifantidis, 1988; Boot *et al.*, 1992). Mites were visible from the moment they reached the cell bottom, but some time elapsed between their entering into the cell and their appearance at the cell bottom. Our observations suggested that this movement required about one minute. Therefore, the position of the bees present at the cell opening of the invaded cells was observed during three minutes preceding appearance of the mite at the cell bottom, because within that period the mite probably invaded the cell (Fig. 1).

Positions of the bees were divided into three classes: (1) no bee present in front of the cell opening, (2) bee at least partly covering the cell opening and (3) bee present in the invaded cell. Bees often moved their head towards the cell opening; apparently for a quick inspection, but this was classified as 'bee in front of the cell opening'. Only when the head and thorax of the bee were in the cell was it classified as 'bee in the cell'. In such cases the bee probably fed the larva, which takes 10 seconds up to a few minutes (Brouwers *et al.*, 1987).

Moving into the cell by the bee was not necessary for mite invasion to occur, because only in 7 out of 15 mite invasions was a bee present in the cell during part of the 3-minute-period preceding mite appearance (Fig. 1). The mites probably invaded the cells when a bee was present in front of the cell opening. In all 15 cases observed, this position was found most frequently during the 3-minute-period preceding mite appearance. Mites were never observed walking across the comb

Fig. 1. Position of the bees at the cell opening of 15 invaded cells during the three minutes preceding mite appearance at the bottom of these cells. The position of the bees was divided into three classes: (1) no bee present in front of the cell opening, (2) bee present in front of the cell opening and (3) bee in the cell. The time distribution over these three classes is shown.

surface, suggesting that the mites went directly from the ventral side of the bee into the cells.

When the 'half-comb' frame was used, the dorsum of bees walking over the comb surface was recorded. Consequently, even a glimpse of the mites was rare at the cell opening, as the bees blocked the view. Mite invasion was observed once, however, when the bee on which the mite resided fortuitously moved away from the cell opening. This mite went from the bee to the cell rim, and immediately entered the cell, after which it could no longer be observed at the cell opening. After 67 seconds the mite reappeared at the bottom of the cell.

Observations using cells with transparent side walls

With the transparent side wall type of frame, only 4–5 cells were observed simultaneously because a large magnification was needed. Additionally, not all cells

observed were attractive to mites simultaneously, and since invasion into a particular cell was a rather rare event, only three mite invasions were recorded despite our efforts. One of these mite invasions could be followed clearly (Fig. 2). First the mite walked over the abdomen of the bee (1–2). The mite then left the bee and went to the cell rim/cap of the adjacent cell (2), moved quickly around over the cap and entered the cell (3). The mite subsequently walked for 3 seconds on the surface of the larva (4–6), before it crawled between the larva and the cell wall (7) and then moved on slowly to the bottom of the cell (8–10). After 34 seconds from the time of entering the cell the mite had covered half the distance from the surface of the larva to the cell bottom (9; this could easily be marked as the moment the mite moved in front of the gut of the larva), and 65 seconds after entering the cell the bottom was reached (10), which matches with the 67 seconds period needed to reach the cell bottom in the observation with the other frame type.

The other two observations of mite invasion were less clear. The mites could only be observed from the moment of cell invasion, because the large number of bees present near the cell opening hindered observation. After invasion, the mites walked for 4 and 2 seconds, respectively, over the larva before crawling between the larva and the cell wall. The sites chosen by the mites to crawl between the larva and the cell wall could not be observed clearly, and therefore the moment the mites reached the cell bottom was not determined. In one of the two recorded invasions, the mite had moved half-way the larva after 31 seconds since entering the cell.

DISCUSSION

In principle, *Varroa* mites should invade brood cells as quickly as possible because they cannot reproduce while on adult bees. Still the mites may reside several weeks and longer on adult bees, depending on the number of brood cells that are available for invasion (Boot *et al.*, 1993; Boot *et al.*, 1994). Probably invasion into brood cells is relatively slow because the distance between the mite on the bee and the brood cell has to be small before invasion can occur. For instance, during the ten minutes after invasion of the single mite as described in Fig. 2, eight other mites were seen on the bees passing the recently invaded cell, but they did not invade the cell. Since infested cells seem to be just as attractive to mites as non-infested cells (Fuchs, 1985), the distance between mite and cell may have been too large for invasion. In addition, some of the mites on adult bees are positioned between the abdominal sternites (Kraus *et al.*, 1986; Rath, 1993). Since they are positioned deep between the sternal plates, these mites may be unable to react to stimuli coming from the brood cell that play a role in invasion.

When mites leave a bee to invade a brood cell, they do so without having had prior contact with the larva. The mites have to cover the distance from the cell rim to the larva, which measures 4–7 mm in cells that are attractive to mites (Goetz and Koeniger, 1993). Thus, information to decide whether to stay on the bee or to invade a brood cell is acquired at a distance from the larva, possibly by a chemical signal

or by differences in temperature. It has been shown that *Varroa* mites in artificial settings react to a number of chemicals (Rickli *et al.*, 1992; Le Conte *et al.*, 1989). However, reaction of mites to these chemicals should also be studied while the mites stay on bees, because the mites go directly from the bees into the brood cell. When not residing on a bee, mites may be motivated to find an adult bee rather than a larva. Kraus (1993) recently showed that *Varroa* mites indeed prefer the scent of adult bees over the scent of larvae when tested in an olfactometer.

The mites were never seen walking on the comb, or entering and leaving the brood cells to select a cell for invasion. This strategy is used by *Tropilaelaps clareae* (Laigo and Morse, 1968; Woyke, 1989), another parasitic mite of honey bees, which also has to invade brood cells for reproduction. Both mite species recently started to parasitize *A. mellifera*, *A. cerana* being the original host of *Varroa* and *A. dorsata* being the original host of *T. clareae* (De Jong *et al.*, 1982). Walking across the comb to select a brood cell has two advantages for *T. clareae*. First, they can reach a new brood cell quickly enough to survive because, in contrast to *Varroa*, *T. clareae* cannot survive on adult bees for more than two days (Woyke, 1984). Secondly, by reaching a new brood cell faster, they can reproduce earlier than *Varroa*, which is probably one of the main causes of the higher growth rate of the *T. clareae* population when compared to *Varroa* in *A. mellifera* colonies (Woyke, 1987). However, in colonies of the original host of the *Varroa* mite, *A. cerana*, walking across the comb to select a brood cell for invasion may be a risky strategy. *A. cerana* was observed to kill *Varroa* mites while they were on adult bees (Peng *et al.*, 1987; Büchler *et al.*, 1992). Nevertheless, *Varroa* mites still survive for long periods outside brood cells in *A. cerana* colonies, probably by hiding in relatively safe sites on the adult bees (Rath, 1993). Possibly, *Varroa* mites minimize exposure to adult bees in not walking across the comb to select a brood cell.

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