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ORIGINAL PAPER

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Cannibalism and early capping: strategy of honeybee colonies in times of experimental pollen shortages

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Abstract We observed the impact of bad pollen supply (non-foraging due to artificial rain and pollen removal under poor-foraging conditions) on the survival of honey bee larvae, and on the total development time from egg-laying to the capping of a larval cell. Five days of non-foraging led to cannibalism of larvae younger than 3 days old and to a shortening of the time until larvae were sealed, but 4- and 5-day-old larvae survived even worse pollen supply situations. Manual pollen removal and reduction of income (pollen trap) induced cannibalism of younger larvae. The larvae's mean capping age significantly correlated with the mean pollen income: the less pollen was stored by the hive during the larvae's development, the earlier the larvae were capped. Both behavioral patterns lead to a quick reduction in the amount of unsealed older brood in response to a shortage of available protein. Older larvae have the highest pollen demand, so this strategy compensates for a shortage of supply by reducing demand. Additionally worker jelly gets enriched by protein gained from cannibalism, and the early capping of older larvae saves the oldest part of the brood, which represents the highest broodcare investment.

Keywords Honeybees · Cannibalism · Survival rates · Pollen shortages · Unsealed brood

Introduction

In a honey bee colony, most of the protein income is used for feeding unsealed brood. The hive's main protein source is pollen. So we can expect that the hive's ability to raise brood strongly depends on its current pollen supply. Many studies have shown the relationship between brood rearing and pollen foraging (Filmer 1932; Al-Tikrity et al. 1972; Webster et al. 1985; Winston and Fergusson 1986; Camazine 1993; Camazine et al. 1998; Pankiw et al. 1998) and the influence of available pollen stores on foraging activity (Barker 1971).

Hellmich and Rothenbuhler (1986) showed that the presence of older larvae causes a stronger increase in pollen foraging activity than the presence of younger larvae. Doull (1974) showed that pollen stored near the broodnest has a higher attraction to nurse bees than pollen stored elsewhere in the hive. If pollen stores are near areas of older brood, the pollen is consumed more quickly (Taber 1973). Underfed worker larvae have a higher risk of developmental failure and develop into dwarf adults (Jay 1963). From these facts we can conclude that older brood is much more dependent on a good pollen supply than younger brood.

Although the hive keeps a reserve of pollen, the amount of stored pollen decreases quickly when the bees are prevented from collecting pollen for several consecutive days in summer (Blaschon et al. 1999). A few days of rainy or windy weather can almost empty a hive's pollen stores.

Szabo (1980) noticed a negative effect of weather factors on colony development and mass gain. Haydak (1935) showed that a honey bee colony can raise brood without pollen for only a short time, and Dietz and Stephenson (1975) demonstrated the importance of the availability of fresh pollen for successful brood rearing. Dustmann and Ohe (1988) proved that repeated periods of pollen shortage have a negative effect on a colony's brood development, the effects of which can be measured even some generations later. However, although the bees need pollen for brood care, they manage somehow to continue their nursing activities even in times of bad pollen supply (Wille 1984).

How can bees keep up their brood nursing – at least for a certain time – if the colony is low on pollen? The study of Blaschon et al. (1999) gives us a hint: The

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number of older unsealed larvae decreased significantly by the end of a 5-day non-foraging period. They discussed changes in developmental speed of larvae, direct cannibalism of larvae and changes of the oviposition rate as possible reasons. They reported a quite stable oviposition rate during non-foraging periods. We think that such a short-term effect could not be caused by a change in the egg-laying rate of the queen (that would take at least 6 days to directly affect the number of older larvae); therefore, we can assume that something happened with the existing larvae.

Some experiments have shown that a percentage of the larvae disappear during the development process (Merrill 1924; Garofalo 1977; Woyke 1988) and some authors (Newton and Michl 1974; Woyke 1977; Weiss 1984) have mentioned a shortage of pollen as possibly inducing brood cannibalism. Brood cannibalism may be a reaction to a decrease in the amount of available pollen below the minimum level needed to meet the demands of the brood (Haydak 1970) – in contrast to egg eating (Myser 1952), worker policing (Ratnieks 1993), and the elimination of diploid drone brood (Woyke 1963a, 1963b). Some studies (Webster and Peng 1987; Webster et al. 1987) have demonstrated that the protein gained by brood cannibalism can indeed be used for producing jelly fed to other larvae.

We assume that nurse bees start to eat some of their unsealed larvae when pollen gets scarce. The older the larvae eaten, the bigger the gain of protein per cannibalized larva, but also the higher the investment "lost" because older larvae have already received more nursing than younger ones. So one key question is: do the bees cannibalize younger or older ages of uncapped larvae, or do they treat both groups the same?

Another possibility is that the number of unsealed older larvae is reduced by capping some larvae at an earlier age than usual. It might be a good strategy in times of bad pollen supply to try to bring larvae more quickly to the "safe" (capped) stage of larval development. To understand the possible pollen-shortage strategies of honey bees, we performed two experiments that examined the survival and development of larvae in times of non-foraging and poor-foraging conditions by experimentally shorten pollen supply and/or lowering foraging efficiency.

Materials and methods

General methods

We observed colonies of *Apis mellifera carnica* Pollmann housed in observation hives. For each test cycle, an area inside the broodnest (25 cm×25 cm) was cleared of sealed and unsealed brood and a cage was introduced that prevented the queen from entering this area. Worker bees could pass through the cage and prepare cells for egg-laying. After 3 days we caged the queen in this area for 2 h, then we removed her to another part of the hive. The cage remained around the area for another 3 days to allow the worker bees to attend the cells and the eggs, but the queen could not enter this area to lay additional eggs there. This created a cohort of brood of known age.

Each day a map of eggs, larvae and pupae was drawn in our observation area on transparent sheets against the glass walls of the hive. These daily mappings continued for 9 days until the last larva in the cohort was sealed. We indicated each individual's developmental stages: "Egg1" to "Egg3" for the 3 days in the egg stage, "L1d" through "L5d" for the 5-day larval period, and "C" for capped larvae. Larvae that disappeared were presumed to have been eaten by adult bees, because daily inspections of the hives bottom and the entrance never showed intact or parts of removed larvae.

During colony manipulation we often observed larvae being eaten but never being removed. The data from these maps were used to calculate total (final) and daily mortality of observed larvae in each observation period. The capping of the larvae was filmed on video under red-light conditions to measure the exact time between the laying of the eggs and the capping of each larval cell. Because the laying time of all eggs was not recorded for each egg separately, we assumed the mean time value of the two-hour capping phase as the egg-laying time of all eggs, which leads to a maximal error of ± 1 h in the calculations of the uncapped time span.

Setup 1: non-foraging periods

For this experiment (performed in 1998 in Graz, Austria), we used an eight-frame observation hive, housing a colony of about 13,000 bees. We simulated periods of heavy, continuous rainfall with a "rain-machine" (Riessberger and Crailsheim 1997) at the entrance of the hive. This machine provides a shower of cooled water in a shaded box in front of the entrance. The water, the shading and the temperature in this box (9–11°C) prevent the bees from leaving the hive and let the bees behave like they normally do during rain (in contrast to just blocking the entrance, which results in absolute intracolonial chaos after some time). After some test runs (which are not included in the data presented here), the bees did not try to leave the hive, so we assume they accepted our artificial rain as real. This treatment lead to non-foraging conditions (like in normal rain), but does not include barometric changes in the hive.

We alternated periods of non-foraging (5 consecutive days each) with foraging periods (without simulated rain, 6 consecutive days each). Each evening during a non-foraging period (after the sun went down) we stopped the showering for half an hour to allow the bees to get out of the hive and defecate. Each day we mapped the whole hive for pollen cells on transparency media ("whole-hive maps"). The caging of the queen and the start of foraging/non-foraging periods were timed so that the larvae in a cohort were one day old on the 1st day of a 5-day non-foraging period or a 6-day foraging period.

Setup 2: manual pollen reduction and poor-foraging periods

In this experiment (performed in 1999 in Graz, Austria) we checked if the effects observed in the rain-machine experiment could be explained by changes in the amount of stored pollen. We manipulated the pollen stores and the pollen income without preventing the bees from leaving the hive. This eliminated possible side-effects due to the bees' inability to collect honey, and the temperature effects due to cooled water in front of the entrance.

We used a three-frame observation hive housing a colony of about 7,000 bees and prevented the queen from reaching the lowest frame by placing a "queen excluder" between the lowest frame and the middle frame. Home-coming pollen foragers do not like to pass through a queen excluder with their loads, so they stored almost all collected pollen on the lowest frame of the hive. Thus, when we replaced the lowest frame with a pollenless one we removed almost all pollen from the hive. We followed the larvae of a cohort during such a period of severe pollen reduction, starting before day 1 of larval development, then followed the next cohort through a period without pollen reduction.

In each pollen-deprived period the adult bees faced a time with larvae to feed and almost no pollen stores, and started to collect pollen on the 1st day. To slow down the process of restoring the pollen stores in the hive, we placed a double pollen trap in front of the hive entrance. Contrary to the previous rain-machine experiment (which causes non-foraging conditions), this pollen trap setup simulates poor-foraging conditions in times of low pollen stores (pollen removal).

In this experiment, we recorded eggs, young larvae (1–3 days old), old larvae (more than 3 days old), capped larvae, pollen and honey on our whole-hive maps. Twenty-four hours after the capping of the cells, the larvae were removed from them. We measured the fresh weight of each larva as well as its protein content (Lowry et al. 1951). In total, 97 larvae were measured in this way. 45 of them were reared in pollen reduction periods, 52 in no-reduction periods.

Statistics

We used two-tailed Mann-Whitney *U*-tests to test for significant differences between mean values. For testing for significant correlations between observed variables we used a Spearman rank test. We set alpha to 0.05 in these tests, only in the section concerning the physical parameters of larvae we lowered alpha to 0.01 as multiple-test correction. The survival rates of trials with different treatments were compared with χ^2-tests and χ^2-values were compared to a $\chi^2_{.05[1]}$-value of 3.842.

Results

Experiment 1: non-foraging periods (rain-machine)

Development of pollen stores

The experimental conditions produced a steady decrease of pollen stores in non-foraging periods and a steady increase of pollen stores in foraging periods (see Fig. 1). Thus, we created a situation in which the pollen supply got worse with increasing age of the larvae in non-foraging periods, whereas in foraging periods 1-day-old larvae faced a low pollen supply but the supply got better as the larvae got older.

Survival of larvae

In non-foraging periods a much smaller percentage of larvae was reared successfully than in foraging periods (see Fig. 2a). Of 140 1-day-old larvae tracked in non-foraging periods, only 45 (32%) reached the final capping stage. Of 103 1-day-old larvae tracked in foraging periods, 82 (80%) were capped at the end of the observation cycles. In two of the non-foraging trials, none of the larvae survived to the capped stage. The first seven of eight observed periods (foraging periods always alternated with non-foraging periods) showed significant influence of our treatment in consecutive periods (χ^2 values: 44.2; 48.5; 25.7; 23.9; 16.6; 5.6; 1.2; $\chi^2_{.05[1]} = 3.842$). While comparison of all foraging periods against each other revealed no significant differences in final survival ($0.016 \leq \chi^2 \geq 2.8$); only two combinations of the non-foraging periods were not significantly distinguishable (periods 2 + 4 and 6 + 8; see Fig. 2a). Considering the final survival and disappearing of all foraging and all non-foraging periods, significantly less larvae survived in non-foraging periods ($\chi^2 = 68.4$) than in foraging periods.

For larvae raised under non-foraging conditions, median daily mortality was highest on the third day of larval development (58%). Figure 2b shows, that 2- and 3-day-old larvae show a high daily mortality, so we pooled the survival data of these two ages and compared them in foraging and non-foraging periods.

The median daily mortality of 2- and 3-day-old larvae was more than four times higher ($n_1 = 7$, $n_2 = 8$, $P = 0.02$; two-tailed Mann-Whitney *U*-test) in non-foraging (31%) than in foraging periods (7%). The daily mortality of young larvae (L1d–L3d) was significantly greater than those of old larvae (L4d and older), both in non-foraging periods ($n_1 = 11$, $n_2 = 6$, $P = 0.009$; two-tailed Mann-Whitney *U*-test) and in foraging periods ($n_1 = 12$, $n_2 = 12$, $P = 0.002$; two-tailed Mann-Whitney *U*-test).

Larvae that survived to the "critical age" of 3 days were cannibalized very rarely (3 instances out of 131 larvae tracked beyond age 3 days), even though pollen stores continued to decrease as the larvae grew from 3 days old to 5 days old.

Time until capping

As shown in Fig. 3, the time between the laying of an egg and the capping of the cell of the larva that grew from that egg was, on average, 6 h shorter in non-foraging periods than in foraging periods ($n_1 = 45$, $n_2 = 81$, $P = 2.20 \times 10^{-16}$; two-tailed Mann-Whitney *U*-test).

Experiment 2: manual pollen reduction and poor-foraging periods (pollen trap)

Development of pollen stores

In this experiment we created conditions of almost no pollen in the hive at the beginning (day 1) of each pol-

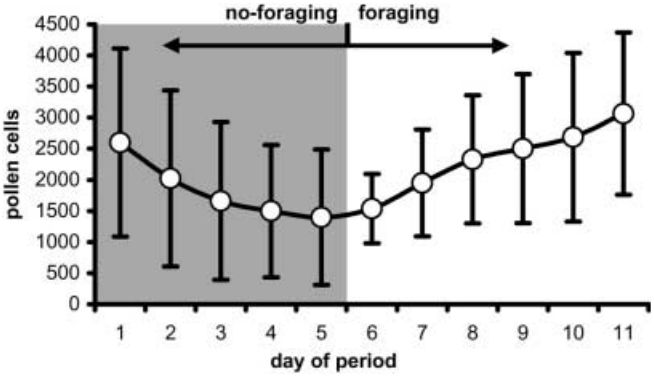

Fig. 1 As shown here, the mean number of pollen cells varied greatly during different trials, but all trials produced the same tendency: a steady decrease of pollen stores during non-foraging periods, and a steady increase during foraging periods. $n = 4$ foraging and $n = 4$ non-foraging periods. Graph shows mean values and standard deviation

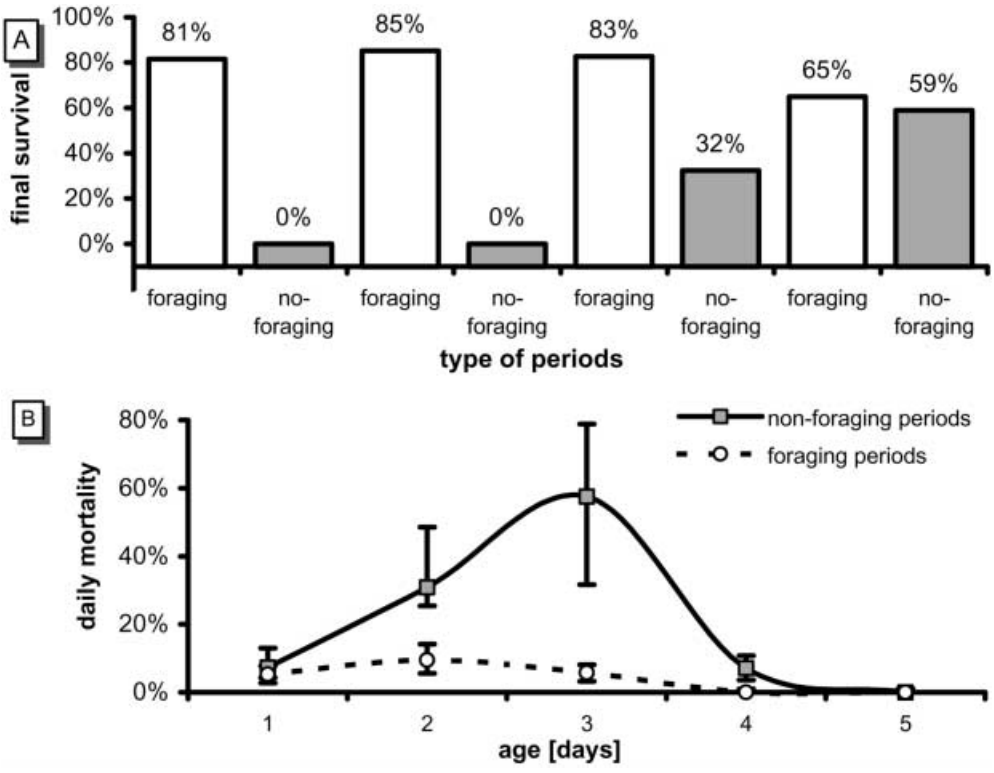

Fig. 2 **a** The mean survival rate of larvae reared in non-foraging periods (32%) was much lower than the rate in foraging periods (80%). In two of the four non-foraging periods, all of the larvae we were tracking disappeared and were presumed eaten before reaching the 4th day of larval development. **b** In non-foraging periods, 3-day-old larvae showed the highest daily mortality. The median daily mortality for 2- and 3-day-old larvae (raw data pooled) was more than four times higher in non-foraging periods (31%) than in foraging periods (7%). For significance levels see text

len-reduction period. On each day after day 1, the bees brought in much pollen, and the pollen stores increased day by day. The no-reduction periods started with a higher level of pollen stores (120–500 cells) on day 1, but the pollen buildup on subsequent days was not as great as in the pollen-reduction periods. So both groups of tracked larvae faced a pollen supply that got better each day of their larval development, but larvae reared in pollen-reduction periods had hatched from eggs a few hours after a severe pollen deprivation (see Fig. 4).

Survival of larvae

In all six trials, fewer larvae survived in periods of manual pollen reduction than in periods without pollen reduction (see Fig. 5a). Of 133 larvae tracked after manual pollen reduction, 70 (=53%) survived to the capped stage. Without pollen reduction, 72 out of 87 (=83%) survived. Five of six observed periods (always reduction periods alternated with no-reduction periods) showed significant influence of our treatment in consecutive periods (χ^2 values: 0.8; 11.9; 4.8; 17.1; 15.1; $\chi^2_{.05[1]} = 3.842$). While comparison of all no-reduction periods against each other revealed no significant differences in final survival ($0.003 \le \chi^2 \ge 1.5$), all combinations of periods with pollen reduction were significantly distinguishable ($7.7 \le \chi^2 \ge 24.3$). Considering the final survival and disappearing of all reduction and all no-reduction periods, significantly less larvae survived in reduction periods ($\chi^2 = 18.2$) than in no-reduction periods.

In periods of pollen reduction, the median daily mortality was higher in the first three days of larval development (L1d: 24%; L2d: 21%; L3d: 10%) than in the next 2 days. Figure 5b shows, that 1- to 3-day-old larvae show a high daily mortality, so we again pooled the survival data of these three ages and compared them in foraging and non-foraging periods. The daily mortality for larvae 3 days old or younger was more than ten times higher in pollen reduced periods than in periods without pollen reduction (21% versus 2%), and this difference was highly significant ($n_1 = 9$, $n_2 = 9$, $P = 0.009$; two-tailed Mann-Whitney U-test). In daily mortality there was a significant difference between young larvae (L1d–L3d) and old larvae (L4d and older) in both pollen-reduction

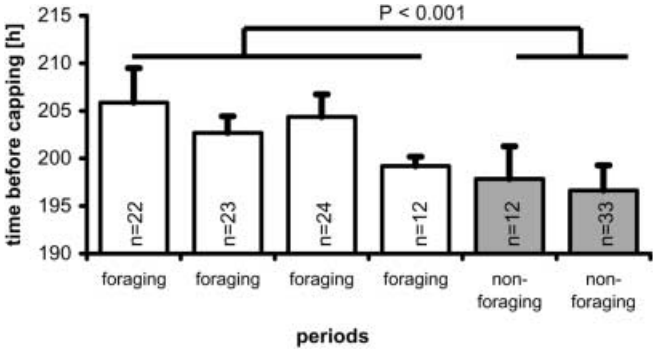

Fig. 3 The mean time between egg-laying and the capping of the larval cell was 6 h shorter in non-foraging periods than in foraging periods. (The maximum possible error in this time-span calculation is ±1 h.)

periods ($n_1 = 9$, $n_2 = 9$, $P = 1.33 \times 10^{-4}$; two-tailed Mann-Whitney U-test) and in no-reduction periods ($n_1 = 9$, $n_2 = 9$, $P = 0.012$; two-tailed Mann-Whitney U-test). None of the larvae disappeared after the 4th day of larval development in pollen-reduction periods, and none after the 3rd day in periods without pollen reduction.

The survival of larvae was not correlated with the mean number of pollen cells in the hive. Also, the time between the laying of the egg and the capping of the cell was not correlated with the mean number of pollen cells in the hive. The mean time span from the first to the last capping event in each trial was 12.6 h.

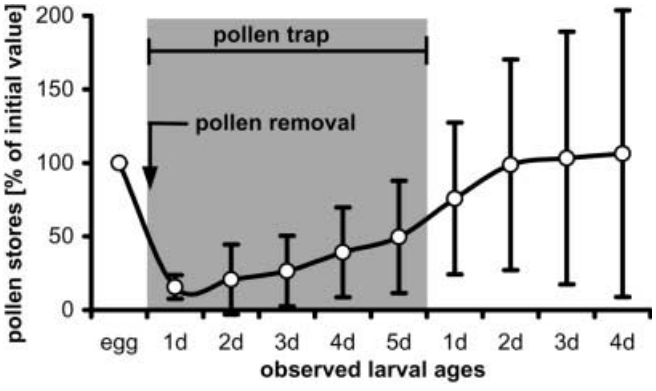

Fig. 4 Twenty-four hours after manual pollen reduction, the mean amount of pollen stores was 15.68% of the pollen amount before the reduction. During the 5 days with a pollen trap in front of the entrance, pollen stores built up to 49.63% of the original level. After we removed the pollen trap, the mean amount of pollen stores reached about 100% of the original level after 2 days

As Fig. 6 shows, the mean time between the laying of an egg and the capping of the larval cell was positively correlated ($n = 124$, $r = 0.57$, $P = 2.92 \times 10^{-12}$; Spearman rank test) with the gain in pollen stores in the hive during the first 4 days of larval development. Data from pollen reduction periods and non-reduction periods were considered here.

Physical condition of larvae

Because we performed five correlation tests between physiological parameters and pollen levels, we lowered alpha to 0.01 as multiple test correction. Neither the

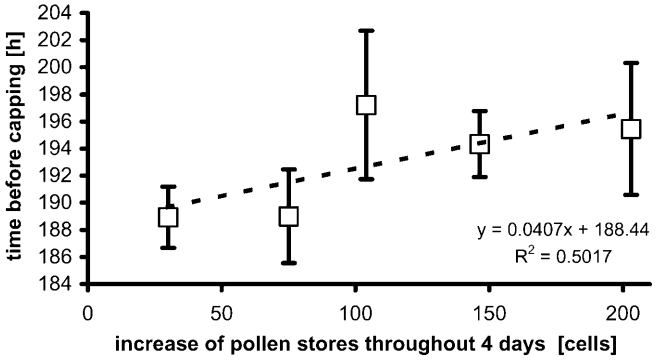

Fig. 6 The time from egg-laying to the capping of larval cells in an observation period was correlated with the absolute increase in the number of pollen cells during the period. (The maximum possible error in this time-span calculation is ±1 h)

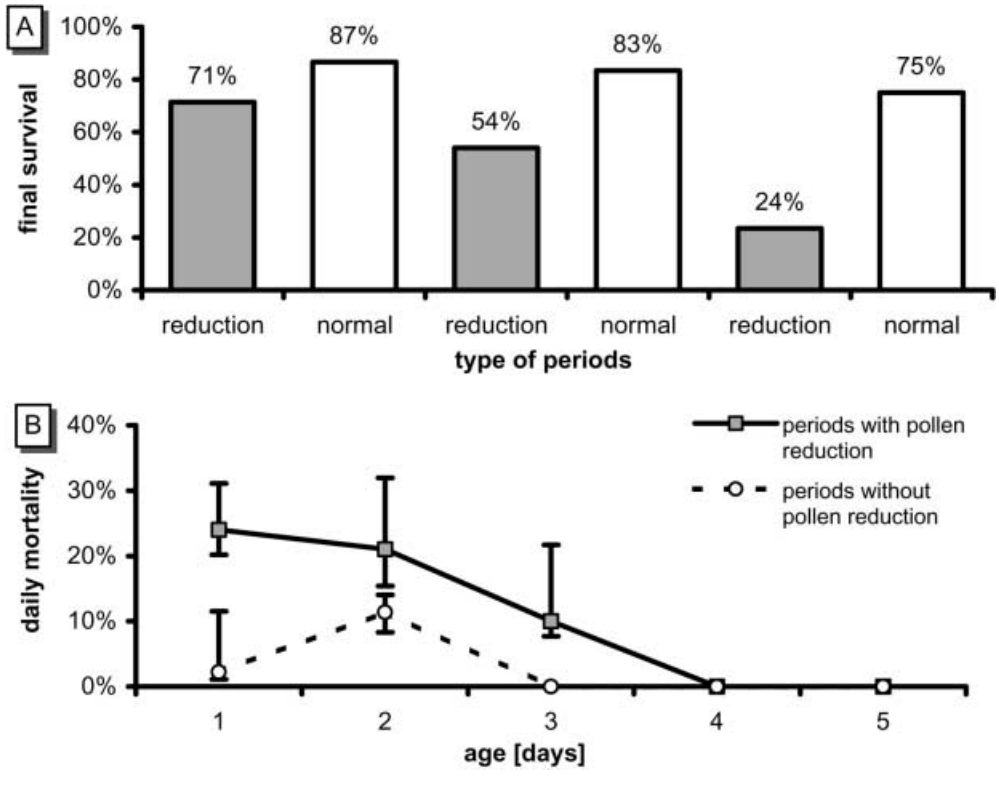

Fig. 5 **a** Only 53% of the tracked larvae survived in periods of manual pollen reduction, compared to 83% in periods without this treatment. **b** Daily mortality of larvae was higher in periods with pollen reduction than in normal periods. In pollen-reduced periods, the younger the larva, the higher the daily mortality was. All larvae that reached the 4th day of larval development survived. For significance levels see text

fresh weight (142.67 mg ± 14.99 mg; $n = 97$, $r_s = 0.08$, $P = 0.2029$; Spearman rank test) nor the dry weight (35.28 mg ± 3.63 mg; $n = 97$, $r_s = 0.15$, $P = 0.0779$; Spearman rank test) of the larvae that survived to the capped stage was significantly correlated with the mean number of cells of stored pollen during larval development.

The percentage of protein in the fresh weight of larvae (the "relative protein content") was positively correlated with the mean amount of pollen stores during larval development ($n = 97$, $r_s = 0.29$, $P = 0.002$; Spearman rank test) as well as the total protein content of the larvae ($n = 97$, $r_s = 0.29$, $P = 0.0019$; Spearman rank test). During observation periods with very small amounts of stored pollen (mean 185 cells throughout the period), the mean relative protein content was 7.69%, and during observation periods with high levels of pollen stores (mean 1219 cells throughout the period) the relative protein content was 8.51%. The percentage of protein in the dry weight was not correlated (due to our correction of alpha) with the mean amount of pollen stores in the hive ($n = 97$, $r_s = 0.20$, $P = 0.0227$; Spearman rank test).

Discussion

Our treatment of generating non-foraging periods using our "rain-machine" led to a severe and steady loss of pollen stores. Although bees try to forage in times of real rainfall (if demand is high), they are not very efficient under these circumstances. So our technical approach to generate a rain-like non-foraging situation reflects a colonies storage situation in times of bad weather periods. The subsequent decrease of pollen stores in non-foraging periods was comparable to data published (Blaschon et al. 1999). Sudden changes in environmental conditions and related shortages of nutrients induce a cascade of behavioral reactions in the honeybee colony. First the colony increases foraging intensity (Barker 1971), but if this is impossible or ineffective, nurses start to use their body reserves (Haydak 1970) and adjust nursing intensity (Schmickl and Crailsheim 2000). Cannibalism might be the next step in this behavioral hierarchy (Weiss 1984).

Non-foraging periods led to a severe decrease of final survival of larvae. Especially middle aged larvae (2 and 3 days old) were cannibalized in this treatment. We assume that 1-day-old larvae were seldom cannibalised, because pollen levels were still high then and nurse bees need time to process pollen into jelly (Moritz and Crailsheim 1987; Crailsheim 1990; Crailsheim et al. 1992), what causes a time lag between the storage of pollen and the utilization of proteins. The 2nd and 3rd day of foraging and non-foraging showed only small differences in the absolute pollen amount between both types of periods, but contrary pollen dynamics, which seems to influence cannibalistic rates of middle-aged larvae markedly.

Older larvae were cannibalized very rarely, though the pollen supply was much worse at the end of non-foraging periods and those larvae have a higher protein demand due to their higher mass and volume (Wang 1965). We conclude that bees that engage in cannibalizing behavior during non-foraging periods and preferentially eat younger larvae.

Larvae were capped significantly earlier during non-foraging periods, what apparently increased the number of older larvae that reached the "secure" capped stage. These two findings – cannibalism of middle-aged larvae and early capping of older larvae – explain why the number of older unsealed brood decreases rapidly at the end of longer periods with rain-machine treatment.

In the second experiment, we lowered the pollen stores (by pollen removal and pollen traps) without preventing the bees from leaving the hive. Although the bees could forage, they could not increase pollen stores very much (="poor-foraging periods"), what simulates conditions with little pollen available in the environment. This time, pollen stores showed a contrary dynamic compared to the first experiment. Young larvae faced a severe pollen shortage and throughout the reduction periods pollen stores showed a low but steady increase.

As in the rain-machine experiment, we observed a severe decrease in the survival rates of larvae in reduction periods compared to no-reduction periods. Again, it was the young and middle-aged larvae that were preferentially eaten, while older larvae showed almost no mortality. The highest daily loss of larvae was of 1-day-old larvae, what verifies our assumption that also larvae of this age are eaten if pollen situation is bad.

Both experiments – although different types of treatment were used to reduce the pollen supply – showed a severe impact on cannibalism rates and developmental speed of larvae. The results of both experiments are consistent with larval population data collected by Blaschon et al. (1999) with a setup similar to our experiment 1.

The uncapped time span of the larvae correlated positively with the pollen income through the larvae's developmental time, which explains also the shorter uncapped time span in non-foraging periods (with zero pollen income then). We cannot say whether the time until capping depends also on the total amount of pollen in the hive, because we only measured the number of pollen cells without taking into consideration how fully filled they were. However, there was no correlation with the number of pollen cells in the hive.

We assume that the unsealed broodnest works like a protein buffer for the colony. In times when available pollen is becoming scarce, they start to empty the "brood-battery", decreasing the number of unsealed brood. Younger larvae are not as valuable to the hive as older ones, because a shorter period of brood care (=less energy) has been invested in them (Lindauer 1952).

From an economic point of view it is better for the hive to make the older larvae safe (by early capping) and sacrifice younger ones (through cannibalism), what both quickly decreases the total larval demand. Although the older larvae survive under bad pollen supply conditions and the nurse bees try to provide adequate nutrition for some of the larvae by cannibalizing others, we found that the pollen shortage had a negative impact (although a weak one) on the protein content of the larvae that survived. That the protein reduction was just low is not surprising, as bees try to produce a rather constant quality of brood (Imdorf et al. 1998). In our experiments, the surviving larvae were fed well enough to pass the quality check of the adult bees that seal their cells at the end of their larval development, but the bad pollen supply did not allow optimal feeding for the survivors.

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