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CANNIBALISM AND BROOD-REARING EFFICIENCY IN THE HONEYBEE *

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Summary

During 34 continuous observations of hive entrances averaging 7 hours a day, 3% of brood disappeared from 5539 cells recorded. No brood or parts of brood could be found in the hive, and none were seen being carried out of it. It is therefore concluded that the brood that disappeared was eaten by the workers.

Records of 6606 eggs and the individuals arising from them showed that the youngest brood was most likely, and the oldest least likely, to be eaten. There were significant differences between spring, summer and autumn. Brood survived to emergence of the adult at 75—80% in spring, 80—90% in summer, and 50—75% in autumn. Significantly more drone brood than worker brood was eaten. Similar survival rates were found (for worker and for drone brood) in queenright and queenless colonies in spring and summer, but in autumn, significantly more of both survived in queenless (75%) than in queenright (50—65%) colonies. Thus, by dequeening a colony in autumn, its efficiency in drone rearing could be raised to that in spring and summer. Survival rate of brood, resulting from the action of sex alleles, should be tested on very young brood.

Introduction

To get maximum production from honeybee colonies (*Apis mellifera*), the beekeeper manages them so that they have the highest population of workers during the main honey flow. Queens that lay many eggs are preferred. But adults do not develop from all eggs deposited by a queen; the population of workers may be lower from one queen that lays many eggs than from another queen that lays fewer eggs but whose progeny have a higher survival rate. The efficiency of brood rearing may depend on genetic as well as environmental conditions, which may themselves markedly affect the genetic results, and the conclusions to be drawn.

The yearly cycle of brood production of *Apis mellifera* has been investigated by Brünnich (1922), Nolan (1925), Bodenheimer (1937), Moeller (1958), Adlakha (1972), Bornus et al. (1974), and Gerig and Wille (1975). The daily egg production of queens was calculated from the measured amount of brood. Drone brood production was investigated by Allen (1958, 1965), Weiss (1962), Louveaux, Mesquida and Fresnaye (1972), and Free and Williams (1975). But in 1924 Merill had found a marked discrepancy between the number of eggs deposited and the amount of sealed brood resulting from them. This was later confirmed under different conditions by Montagner (1962), Fukuda and Sakagami (1968), Free and Williams (1975), Woyke (1976*a*, 1977) and Garófalo (1977).

According to Sturtevant (1920) and Woodrow (1941), brood killed by disease, or 'unwanted' drone brood (Weiss, 1962), is carried out of the hive by the workers. But several authors have pointed out that when brood is infected (Schulz-Langner, 1956) or when colony conditions are abnormal (Myser, 1952; Naulleau, 1960; Newton & Michl, 1974), larvae are eaten by the worker bees. This also happens with diploid drone larvae (Woyke, 1963).

The present invertigation was carried out to see whether workers eat brood in a normal colony, whether there is a seasonal variation in this, and whether the beekeeper can alter brood-rearing efficiency of a colony by simple operations. If so, it should be possible to increase the efficiency of rearing valuable bee material, and to prolong the bee breeding

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season by rearing drones in the autumn. Knowledge of the efficiency of rearing brood in different development stages should also enable us to choose the right method for testing the survival rate of brood that is determined by sex alleles.

Materials and Methods

Altogether more than 8500 cells with brood were individually investigated several times in this study, which was divided into two main parts.

1. The first part investigated whether cannibalism occurs in normal honeybee colonies. Known numbers of worker and drone cells containing sealed and unsealed brood were marked with the aid of special stencil plate. After the comb was returned to the colony, a black plastic sheet was placed on the hive floor, and the entrance was observed continuously for several hours, to observe whether the bees removed any larvae out of the hive. The remaining brood was then counted and the plastic sheet examined.
2. The second part of the study investigated the number of larvae of each sex that were eaten in different rearing conditions in three seasons of the year.

First, an empty comb was inserted in the centre of a brood nest, in which a naturally mated queen laid eggs. Next day, the comb was taken out of the colony, and the workers brushed off without shaking the comb. An area about 140 cm^2 was marked in the central part of the comb, where 200-250 eggs were recorded. The queen was restricted on another comb with a queen-excluder cover for the next 3 days, until the eggs hatched. The comb under observation was kept in the brood nest from which it was taken, being removed for counting when the eggs were 3 days old, when the larvae were 1, 3 and 6 days old (at sealing time), 10 days old, and at the pupal stage 16 and 21 days after the eggs were deposited. The number of surviving brood at each age was recorded twice: in the morning and 12 h later. The following were calculated: (*a*) percentage of larvae of each known age that disappeared during these 12 hours; (*b*) percentage of eggs initially recorded that gave rise to brood surviving to the age in question. To prevent drying of larvae and larval food, the comb with eggs and unsealed brood was wrapped in a moist towel during each series of counts, leaving only a few cells uncovered at a time.

A similar investigation was conducted with drone brood, but using fewer eggs, usually about 150.

The investigations on both worker and drone brood were repeated in 6 colonies, at intervals of a few days. Three of the colonies were queenright and three were dequeened shortly beforehand. The whole experiment with 6 colonies was carried out three times: in spring (20 April—20 May), summer (1 June—5 July) and autumn (10 August—15 September).

Fisher's analysis of variance (split-plot design) was applied, and Student's t-test was used to find significant differences between the means. Since the percentage of brood that disappeared did not have a normal distribution, the Bliss transformation was applied to the data before an analysis of variance was made.

Results

Do worker bees eat the brood?

At first, records on unsealed and sealed brood were conducted without determining the exact age of the brood. Between 28 April and 3 June worker brood was recorded and the hive entrance observed during 11 observations lasting from 3 to 6 hours each (Table 1A). The hive entrance was watched altogether for 36 hours. From 1177 cells containing unsealed brood, 63 individuals (5·4%) disappeared, and from 295 sealed cells 5 (1·7%)

Between 5 August and 12 September, drone brood was recorded and the hive entrance watched (Table 1A). From 336 cells containing unsealed brood, 36 individuals (10·7%) disappeared; out of 124 sealed brood 1 (0·8%) disappeared.

TABLE 1. Brood disappearing during periods of continuous observation of hive entrances.

Brood stage	*Age of brood*	*Observations* *No.*	*Duration (h)*	*Total no. brood cells observed*	*Brood disappearing* *No.*	*%*
A. Worker and drone brood (age not known)						
Worker		11	3-6			
unsealed	—			1177	63	5·4
sealed	—			295	5	1·7
Drone		5	5			
unsealed	—			336	36	10·7
sealed	—			124	1	0·8
Total		16	61	1932	105	5·4%
B. Worker brood of known age						
Eggs	2-3	3	10	651	27	4·1
Larvae (1 day)	4	3	10	610	22	3·6
Larvae (3 days)	6	3	10	582	16	2·7
Larvae (6 days)	9	3	10	599	9	1·5
Larvae (10 days)	13	2	10	363	2	0·5
Pupae	16	2	10	395	0	0
Pupae	21	2	10	407	0	0
Total		18	180	3607	76	2·1%

Next, worker brood of known age was recorded, and the hive entrance was watched for 18 10-hour periods. Table 1B shows that 0—4·1% of brood of different ages disappeared during the observation periods. A total of 76 (2·1%) eggs and larvae disappeared out of the 3607 recorded. Thus, with the records in Table 1A, brood disappeared from 181 cells out of 5539 (3·3%). The recorded brood represented only a very small part of the total brood present in the colonies observed.

While the entrance of the hive was being watched, bees were seen to carry out particles of debris, cappings of cells, lumps of pollen, and parts of adult bees like antennae and legs, but no larva or part of a larva was seen being carried during the 241 hours. Neither did examination of the plastic sheet after each observation period reveal any larva or part of one.

It was therefore deduced that the disappearing brood was eaten by the workers, and in the rest of the paper it is assumed that this was so.

TABLE 2. Percentage of brood eaten by bees during a 12-hour observation period. Average for 3 colonies calculated in relation to the number present at each morning examination.

Rearing conditions: Brood	Rearing conditions: Colony	No. eggs	Eggs 3 days	Larvae 1 day	Larvae 3 days	Larvae 6 days	Pre-pupae	Pupae	Pupae	Means	Means
			Age of brood (days from oviposition)								
			3	4	6	9	13	16	21	3-16	
Spring											
Worker	with queen	739	4·8	3·2	2·9	1·9	0·1	0·0	0·0	2·2	2·25e
Worker	queenless	518	3·0	2·6	1·9	1·1	0·0	0·4	0·0	1·5	
Drone	with queen	467	4·8	3·7	3·5	1·6	1·1	0·5	0·0	2·5	
Drone	queenless	397	4·2	4·0	3·8	2·2	0·9	1·3	0·0	2·8	
Summer											
Worker	with queen	734	2·4	1·1	1·5	0·5	0·0	0·1	0·0	0·9	1·34f
Worker	queenless	737	2·1	1·3	1·5	0·7	0·4	0·0	0·0	1·0	
Drone	with queen	639	2·6	1·6	1·7	0·7	0·7	0·6	0·0	1·3	
Drone	queenless	399	3·5	2·9	1·9	1·1	1·2	1·3	0·0	2·0	
Autumn											
Worker	with queen	583	6·5	5·4	5·1	3·3	0·7	0·8	0·0	3·7	3·51g
Worker	queenless	533	4·3	4·6	3·2	2·5	0·7	0·0	0·0	2·5	
Drone	with queen	402	11·1	5·9	5·2	4·4	4·0	2·2	0·0	5·5	
Drone	queenless	458	3·7	2·7	3·1	1·6	1·3	1·1	0·0	2·2	
Total and mean for each age		6606	4·4a*	3·3b	2·9b	1·8c	0·9d	0·7d	0·0		
Mean for sex				worker brood 1·98h			drone brood 2·75i				
Mean for presence of queen				queenright 2·69j			queenless 2·05k				

* Different letters indicate significant differences between overall means (after Bliss transformation, $P < 0{\cdot}05$).

Efficiency of brood rearing in three seasons in different conditions

Percentages of brood eaten in the 12 hours between morning and evening counts are presented in Table 2. Brood of all ages except the oldest (pupa), were eaten within each 12-hour observation period. Therefore analysis of variance was applied to data for larvae and pupae 3–16 days old. Table 3 shows that the value of F calculated for age was much higher than the tabulated value. This means that the relation between the disappearance rate and the age of the brood was very highly significant, the youngest brood being eaten most and the oldest brood least. Statistically significant differences were found between the mean percentages of brood eaten at different ages, but not between larvae 1 day old and 3 days old, or between sealed brood 13 days and 16 days after egg deposition. No interaction was found between age and season or combinations. Therefore, in all the conditions studied, the youngest brood was eaten in the highest percentage and the oldest in the lowest percentage.

Table 3 shows also a very highly significant effect of season on the rate at which brood was eaten. Table 2 shows that the brood was eaten least in summer (1·34%) and most in autumn (3·51%). (After the Bliss transformation, 7·22 for spring, 5·48 for the summer, 9·57 for autumn, $lsd_{0\cdot01} = 1\cdot46$.) The differences between all the seasons were highly significant.

Very highly significant relationships were found between the rate of disappearance and the four combinations of factors (Table 3): worker and drone brood in queenright and queenless colonies (Table 2). Grouping the data on the basis of the sex of brood (Table 2) showed that more drone brood than worker brood was eaten within a 12-hour period (after transformation, 6·61 worker and 8·24 drone brood, $lsd_{0\cdot001} = 1\cdot61$); $P < 0\cdot001$.

TABLE 3. Analysis of variance for data in Table 2, after Bliss transformation.

Source of variation	*Degrees of freedom*	*Sum of squares*	*Mean square*	*F calc.*	*F tab.* 0·05x	*F tab.* 0·005xxx
Seasons	2	604·23	302·12	30·30xxx	3·40	6·66
Combinations	3	180·68	60·23	6·04xxx	3·01	5·52
Season × Combination	6	279·02	46·50	4·66xxx	2·51	4·20
Error (a)	24	239·20	9·97			
Subtotal	35	1303·13				
Age	5	2419·75	483·95	66·84xxx	2·29	3·55
Age × season	10	124·71	12·47	1·72	1·91	
Age × combination	15	172·42	11·49	1·59	1·75	
Age × season × combination	30	274·98	9·77	1·35	1·55	
Error (b)	120	869·02	7·24			
Total	215	5164·01				

TABLE 4. Percentages of brood reared to different stages, by bees in different rearing conditions in different seasons, calculated in relation to the number of eggs.

Rearing conditions		*No. eggs*	*Eggs 3 days*	*Larvae 1 day*	*Larvae 3 days*	*Larvae 6 days*	*Pre-pupae*	*Pupae*	
Brood	*Colony*		*Age of brood (days from oviposition)*						
			3	4	6	9	13	16	21
Spring									
Worker	with queen	739	95·2	90·5	86·3	81·8	81·0	81·0	81·0
Worker	queenless	518	97·0	91·8	87·6	84·3	83·5	82·8	82·8
Drone	with queen	467	95·2	88·4	82·0	77·5	75·6	74·9	74·9
Drone	queenless	397	95·8	88·9	82·6	78·0	76·0	75·0	75·0
Summer									
Worker	with queen	734	97·4	95·3	92·2	90·0	89·4	89·4	89·4
Worker	queenless	737	97·9	95·2	92·5	90·0	88·3	88·3	88·3
Drone	with queen	639	97·4	93·2	89·5	88·2	87·3	87·0	87·0
Drone	queenless	399	96·5	92·7	89·7	85·7	83·2	82·2	82·2
Autumn									
Worker	with queen	583	93·5	83·8	75·9	73·2	67·9	67·4	67·0
Worker	queenless	533	95·7	87·6	82·5	77·8	76·1	76·0	76·0
Drone	with queen	402	88·9	79·1	71·1	63·9	58·7	54·9	53·4
Drone	queenless	458	96·3	91·7	86·4	82·7	80·1	77·7	75·9

Table 3 shows a very highly significant interaction between seasons and certain combinations. The progress of the efficiency of brood rearing in the different combinations in the three seasons is presented in Table 4. In early spring (April in Poland) a lower percentage of drone brood (75%) than of worker brood (81-83%) was reared to emergence, but almost identical percentages in queenright and in queenless colonies.

In summer, both worker and drone brood were reared in very similar percentages in queenright and in queenless colonies (82-89%).

The survival rate of brood in autumn was very different in the four combinations. Brood survival in queenright colonies (worker 67%, drone 53%) was lower than in queenless colonies (worker 76%, drone 76%). It appears that brood survival in autumn could be significantly increased in a colony by dequeening it.

Comparing the seasons, the percentage of brood eaten was:

1. significantly lower for worker brood in summer than for drone brood in spring;
2. significantly higher for almost any brood in queenright colonies in autumn than for any brood in spring;
3. similar for any brood in queenless colonies in autumn to any brood in spring;
4. mostly, significantly higher in autumn than for any brood in any conditions in summer;
5. but similar for drone brood in queenless colonies in autumn, to those reared in any conditions in summer (no significant difference).

Thus by dequeening colonies in autumn, drone rearing can be made as efficient as in spring or summer.

The smallest variations between the four combinations occurred in summer, and the highest in autumn. Survival of brood in individual colonies in the two seasons is presented in Fig. 1 and Fig. 2. Fig. 1 shows that survival of brood in the three colonies was very similar in summer, although some variations occurred. The greatest differences were for drone brood in queenless colonies. The survival rates of brood in individual colonies in spring (not presented here) were similar to those in summer. Fig. 2 shows greater differences between the three colonies in autumn than in summer, and most in the rearing of drone brood by queenright colonies. Although individual colony differences in brood-rearing efficiency were found, they were not high between similar colonies investigated at the same time.

Discussion

Not all brood is reared to the adult stage, and the daily rate of egg deposition of a queen cannot be assessed by estimating all the brood, or sealed brood only, as has commonly been done; these estimations are useful in giving a general picture of the brood-rearing activity of a colony in a particular period and conditions. Due to appreciable losses during larval development, survival rate of brood depending upon sex alleles must be judged at an early larval stage, unless the pollen and nectar flows are just right for maximal efficiency of brood rearing.

Why does all the brood not survive in a colony? This is a complex question. Doubtless some of the larvae disappear from the action of the homozygous sex alleles (Mackensen, 1951), but these are eaten within 6 hours after hatching (Woyke, 1962). Montagner (1962) found that after the comb with eggs was replaced, the percentage of brood reared depended on the presence of sealed brood and the distance of the larvae from the queen. Fukuda and Sakagami (1968) suggested that brood mortality is mainly attributable to physiologically conditioned weaknesses; normally this would kill only a fraction of the brood. Garófalo (1977) supposed that brood mortality is caused by genetic factors similar to the homozygosity of X alleles.

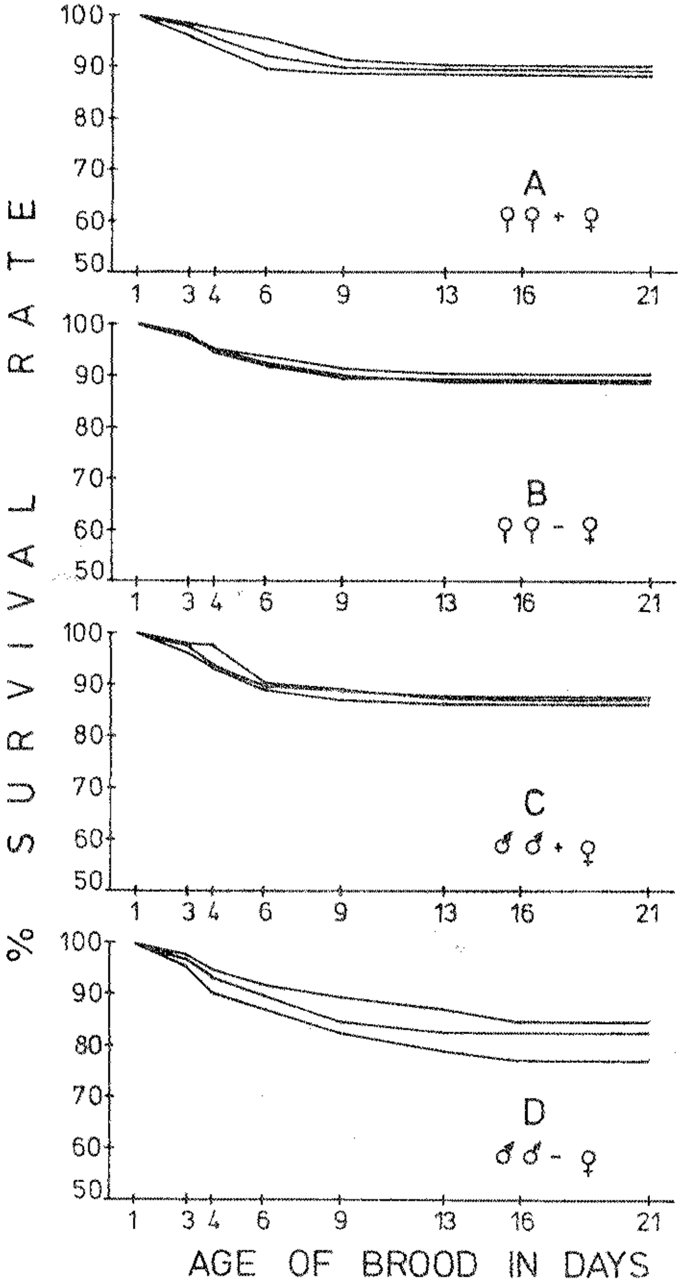

FIG. 1. Survival of normal brood in different colonies in summer (three repetitions).
A, worker brood in queenright colonies
B, worker brood in queenless colonies
C, drone brood in queenright colonies
D, drone brood in queenless colonies

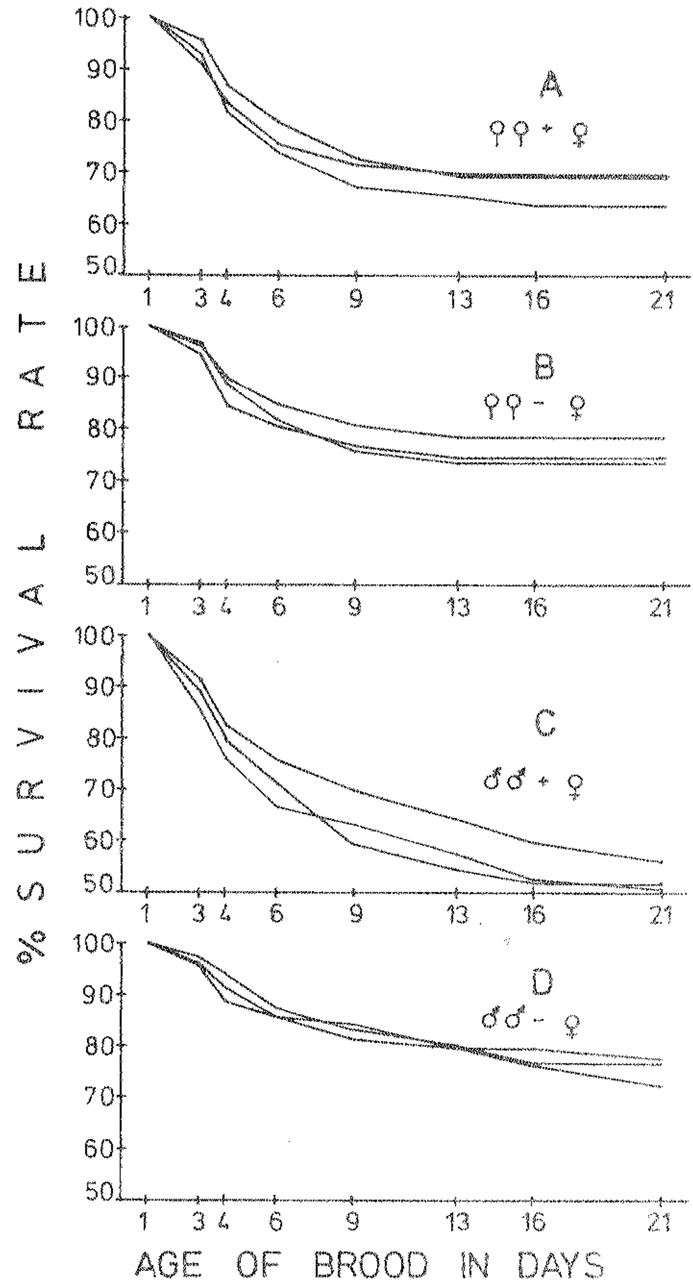

FIG. 2. Survival rate of normal brood in different colonies in autumn (three repetitions).
A, worker brood in queenright colonies
B, worker brood in queenless colonies
C, drone brood in queenright colonies
D, drone brood in queenless colonies

What happens to the brood that disappears from the cells? According to some authors, remains of brood killed by European (Sturtevant, 1920), or American foul brood (Woodrow, 1941) drop to the hive floor and are carried out of the hive by workers. Weiss (1962) observed this with drone pupae in the middle of July. But Schulz-Langner (1956) suggested that infected as well as starved larvae are eaten by the workers, even before they die. Rothenbuhler (1964) found a striking difference between resistant and susceptible lines of honeybees in removing disease-killed brood. Some authors have shown that, in unusual conditions, brood is eaten by the workers. Myser (1952), using an observation hive, observed ingestion of eggs in cells of a comb under a queen-excluder cage, where the queen was forced to lay eggs. Similar observations were made by Sakagami (1968) on eggs laid at the periphery of the brood area in an observation hive. Nauleau (1960) and Newton and Michl (1974) saw sealed brood being eaten after the cells were manually uncapped. Nauleau suggested that worker bees might transport larvae to other cells. Woyke (1963) reported that workers ate live diploid drone larvae, and also that in an observation hive workers with a normal queen ate eggs and live larvae.

The present investigation shows that brood disappears—and is eaten—in the centre of the brood nest in normal colonies throughout the season. Thorough observations made by the author on thousands of unsealed brood sometimes revealed dead larvae in cells taken from normal colonies, and many of these larvae had a supply of food. Partly eaten larvae were also encountered, and these were not dead when eating commenced, because peristaltic and respiratory movements were still visible. Little is needed to induce workers to eat larvae: altering the position of a brood comb in the hive may be so. In the Indian bee (*Apis cerana indica*), merely inspecting a drone comb and replacing it can lead to some or all the brood in it being eaten.

It is thus concluded that, of the disappearing brood, a high proportion at least is eaten alive. Races—and colonies—are likely to have different genetic predispositions to eat live brood. In *Apis cerana indica*, well grown larvae were eaten in the highest proportion (Woyke, 1976), whereas in the present study on *Apis mellifera*, larvae were most commonly eaten at 1-3 days old. The variations linked with seasons and other conditions show that such predisposition is not solely genetic; for instance brood mortality was higher in queenright than in queenless colonies. Suppression of cannibalism seems to depend more upon the ability of the workers to rear the brood. This is not determined by the total worker population of a colony, but by the population of workers capable of rearing brood in relation to the population of brood to be reared (survival was higher in queenless colonies). This is supported also by the reduction of survival rate in *Apis cerana indica* after an artificial increase in the amount of brood in the colony. Woyke, 1977).

There are more workers (and more nurse bees) in relation to the amount of brood to be reared in autumn than in summer; yet relatively more larvae were eaten in autumn than in summer.

The higher survival rate of brood when the pollen supply was good, and in colonies to which pollen combs were added (Woyke, 1977), suggests that shortage of pollen releases cannibalism in the honeybees. Doull (1974) and Taber (1973) showed that the workers eat mostly pollen that is close to the brood area (within 3-4 cm), and do not respond to pollen farther than 7 cm away.

Pollen may be available in one comb, and not in another, or even in another part of the same comb. So the bees with no pollen nearby, eat brood instead, and are thus able to produce food for the queen and for larvae. With the decreasing day length in autumn, pollen and nectar flows drop off; the bees' fat-body builds up, and less bee milk is produced. These processes are linked with an increase in cannibalism. We still do not know whether the bees eat larvae that are in the centre of the brood nest because they are weak (due to insufficient or improper food), or by chance, because these larvae are the most accessible protein food; perhaps both factors operate.

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