

BROOD-REARING EFFICIENCY AND ABSCONDING IN INDIAN HONEYBEES*

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Summary

The population of colonies, and their honey production, depend very much upon the efficiency of brood production. Brood of *Apis cerana indica* in India was very scattered. An irregular pattern of egg laying by the queens was a contributory factor, but the main cause of the scattered brood was that the number of eggs laid gave rise to more larvae than the bees could rear. During the main period of nectar flow about 95% of larvae were sealed. During a moderate intake of nectar and pollen the bees reared about 70% of larvae to 4 days, but only 50% were sealed. During a dearth of nectar and pollen the queens continued to lay, but the worker bees ate all the larvae, and no brood was reared. Absconding colonies left viable eggs in the combs.

Because of these low and variable levels of brood-rearing efficiency, it is impossible to calculate the daily oviposition rate of a queen from the amount of brood present in a colony.

Observations in brood rearing in *Apis florea* and *Apis dorsata* are included.

Introduction

The efficiency of brood production in a honeybee colony has a direct influence on the worker population, and because of this it also affects honey production and queen and drone rearing, as well as further brood production. The author inspected many colonies of *Apis cerana indica* during his stay in India in 1974. He found that the brood was very scattered and that the number of unsealed brood cells was surprisingly low in relation to numbers of eggs and sealed brood cells. In some colonies only sealed brood and eggs were found, and in others there were only eggs. Colonies without brood were most likely to abscond, and this is a serious problem in Indian apiculture. It is therefore important to understand the mechanisms which govern the production of brood and absconding in *A. c. indica*.

Evidence of European foul brood was found in very few colonies. American foul brood was not encountered, and no evidence of any other known brood disease was noticed. There were thus three possible reasons for the scattered brood :

1. the queen deposited the eggs irregularly;
2. a high degree of inbreeding occurred; this causes homozygosis of the sex locus (Mackensen, 1951; Woyke, 1962);
3. the brood was not reared to the adult stage for some reason.

Brood rearing of *Apis mellifera* has been studied by Brännich (1922), Nolan (1925), Merrill (1924a) and others, and by Adlakha (1972) in India. Brood rearing of the plains variety of *Apis cerana indica* was investigated by Kapil (1957) and Bisht and Pant (1968), and that of the hill variety by Sharma (1958) and Saraf and Wali (1972). They calculated the number of eggs laid daily from the amount of brood in the colony. But Merrill (1924b) had earlier found a marked discrepancy between the number of eggs deposited and the amount of sealed brood resulting. Montagner (1962) showed that the bees did not rear brood placed far away from the queen. Fukuda and Sakagami (1968) presented the following figures of survival in different developmental stages : 100 eggs, 94 larvae, 86 sealed brood and 85 adults. They did not study the causes of scattered brood nor the

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question of absconding. Absconding in Indian bees was discussed by Singh and Sharma (1943) and in *A. m. adansonii* by Fletcher (1975/76).

Materials and Methods

The plains variety of *A. c. indica* was studied, in apiaries at the Apicultural Institute in Mahableshwar hill station (altitude 1370 m) and in the Central Bee Research Institute in Poona (altitude 573 m), Maharashtra State, India, in April-September 1974.

To investigate the regularity of egg deposition, virgin combs were inserted in the middle of the brood nest, between two brood combs. After the queen laid eggs in these combs, cells containing eggs were recorded. The combs were checked 2 days later, to see whether the queen had laid more eggs in cells omitted earlier.

To investigate the efficiency of brood rearing, the colonies were prepared as follows. In the first period, starting on 6 April, the colonies were divided by a vertical queen excluder, and the test comb with brood was placed in the queenless part in the centre of the brood nest. Four days later the queen excluder was removed. In the second experiment, starting on 10 June, the colony was prepared in the same way, but queen excluders were not used: the experimental brood comb was placed in the centre of the brood nest.

The efficiency of brood rearing was calculated from the survival rate of larvae. The number of eggs laid in a comb by a queen was recorded, and then the number of survivors was checked on succeeding days. This procedure was carried out in detail as follows. A selected comb with scattered brood, containing eggs of different ages as well as other stages of developing brood, was fitted with a strip of plastic 1 cm wide between the top and bottom bars of the frame (Fig. 1). Row numbers of cells were written on the strip, and individual cells containing eggs were recorded before returning the comb to the colony. Further procedure depended upon the purpose of the investigation.

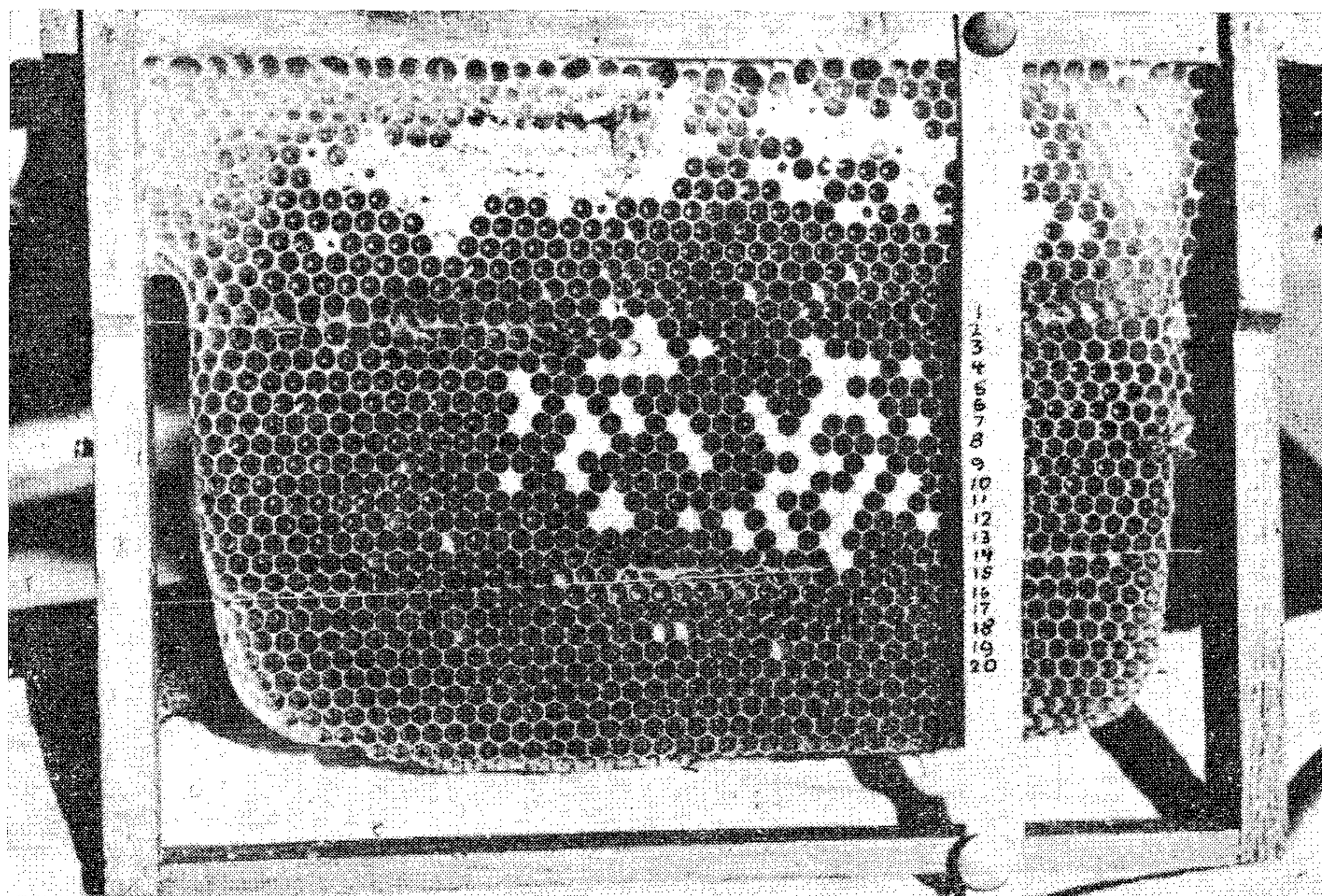


FIG. 1. Scattered brood of *Apis cerana indica* at the end of April in Mahableshwar. Plastic strip on right used to identify cells (see text).

In the first experiment the comb was removed from the colony 4 days after the egg count, and the number of larvae which had hatched from these eggs was recorded. The larvae were at this time 1-3 days old. The same comb was removed from the colony 5-6 days later, when the brood was sealed, and the number of cells containing brood again recorded.

In the second investigation the exact age at which brood disappeared was determined by recording the number of surviving larvae each day. Daily examination of each cell made it possible to detect any new egg which might have been laid in a cell from which recorded brood had been removed. This was true even if a recorded egg was removed and a new one laid, because then an egg would be found in the cell on 4 or more days.

Altogether, 2500 eggs were recorded, and 10 000 individual counts were made.

Brood rearing was also investigated in five colonies of *Apis dorsata*. The colonies with their combs were transferred to special hives without a front wall (Thakar, 1973). The colonies could then be examined easily, and the observer needed no veil or other protection, provided he did not breathe on the bees. After the "curtain" of *A. dorsata* workers was pushed apart, the contents of cells could be examined with the help of a magnifying glass.

Brood in several colonies of *Apis florea* was also examined at different periods of the year.

Results

Regularity of egg deposition

Since the brood was very scattered, all developmental stages of brood occurred in the same comb, side by side, and it was not possible to detect the cause of this phenomenon. After a virgin comb was inserted in the middle of the brood nest, the queen deposited eggs in cells as shown in Table 1. It can be concluded that both the queens laid the eggs quite irregularly. Two days later eggs were found in almost all the cells in the centre of the combs, indicating that the queens returned to these combs and laid eggs in cells earlier left empty. Although the egg deposition now appeared to be regular, the differences of 2-3 days in oviposition could subsequently cause considerable irregularity in appearance, especially after several generations. Thus irregular oviposition could be at least partly responsible for the scattered appearance of the brood.

TABLE 1. Patterns of egg deposition of *A. cerana indica* queens in new combs

Queen no. 490, Mahableshwar, 30 April 1975
Both sides of one comb

Row no.	Cell no. containing eggs															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	<i>side 1</i>															
1		x			x	x	x	x								
2			x		x	x					x					
3		x			x	x	x	x				x				
4					x	x	x	x	x							
5																x
	<i>side 2</i>															
1		x		x			x									x
2	x	x	x		x				x		x		x			
3	x				x							x	x			x
4							x		x			x	x			

Queen no. 1/195, Poona, 18 May 1975
One side of a comb

Row no.	Cell no. containing eggs																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
3		x		x			x							x	x					
4			x		x															
5				x		x	x	x			x	x	x	x	x					
6				x	x	x	x		x	x	x	x	x	x	x					
7			x			x	x	x	x	x	x			x	x	x				
8		x	x		x	x	x	x	x		x	x		x		x	x	x	x	x
9			x	x	x	x		x	x	x		x			x		x		x	x
10	x	x		x		x		x		x		x			x		x		x	x
11		x									x	x	x	x	x		x			
12						x	x	x			x			x						

Efficiency of brood rearing

The main honey flow in Mahableshwar was finished in April. Some nectar was still available, but pollen income was very low, and the brood was very scattered (Fig. 1). Table 2 shows that at the beginning of April only 19-46% of larvae 1-3 days old were left from eggs recorded 4 days earlier. No larvae were sealed subsequently.

TABLE 2. Survival rate of *Apis cerana indica* brood

Date	Colony no.	No. eggs counted	Larvae surviving 4 days after egg count (%)	Brood sealed (%)
Apiary in Mahableshwar				
6.4	133	76	46	0
9.4	382	186	19	0
Apiary at Institute in Poona town				
23.5	85	111	87	52
Apiary by Mulla river in Poona, before monsoon				
5.6	106	100	92	8
5.6	63	127	98	85
5.6	77	136	95	62
5.6	1	94	93	77
8.6	13	187	96	0
Apiary by Mulla river in Poona, after monsoon				
31.8	96	216	99	95
Colony imported to Poland, brood comb next to pollen				
9.6	10	237	96	93

In the apiary near the Institute in Poona town, some nectar and pollen were available from gulmohar (*Delonix regia*) at the end of May. Here 87% of larvae were reared to 1-3 days, and 52% were sealed (Fig. 2).

A better flow appeared in June by the Mulla river, from different agricultural plants and *Acacia*. Therefore further investigation was conducted there. Table 2 shows that 92-98% of larvae were reared to 1-3 days, more than in Poona town, and at least twice

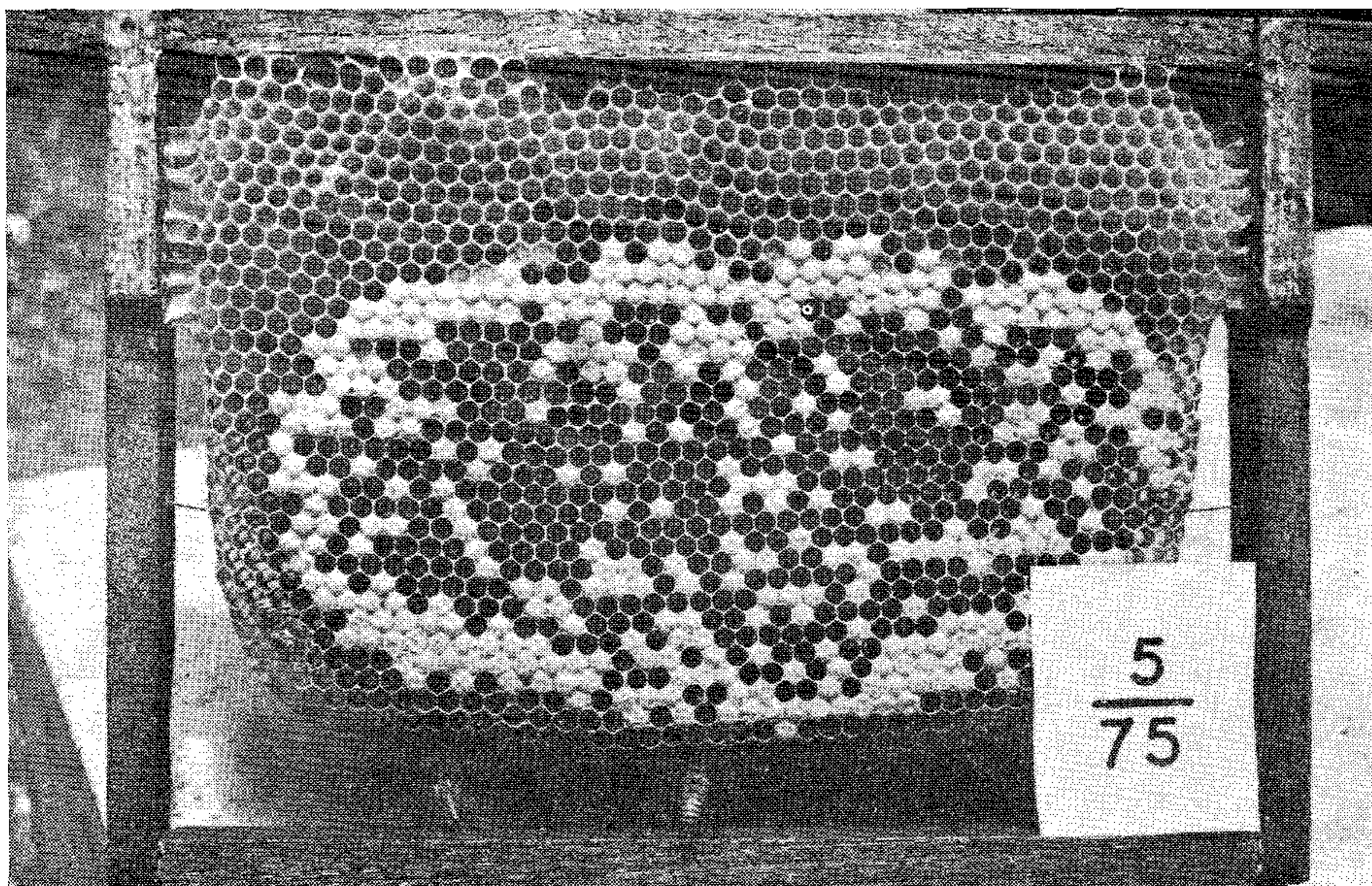


FIG. 2. Scattered brood of *Apis cerana indica* in May in Poona.

as high a proportion as in Mahableshwar. Of the eggs counted in colonies by the Mulla river, 0-85% of larvae were sealed: there was a surprisingly wide range between individual colonies working on the same pollen and nectar flows; even more surprising, the least efficient brood rearing did not occur in the weakest colony. Colony no. 106, in which only 8% of brood was sealed, was the strongest colony in the apiary. This colony was so overpopulated that a big cluster of workers was hanging beneath the high roof of the hive. Colony no. 13 which had no sealed larvae in June (Table 2) absconded in September (Table 4), and it is not clear whether the two phenomena were related, since 3 months elapsed between them, and some brood was reared and sealed in this period.

In August after the monsoon was over, and when many plants were in blossom (including sunflowers in the apiary), the bees reared 99% of larvae to 1-3 days, and 95% of brood was sealed. A similar survival rate was found in an *A. c. indica* colony imported to Poland and placed in an area with quite good nectar and pollen flows.

Thus it can be concluded that scattered brood of *A. cerana indica* is to a great extent caused by the fact that many larvae are not reared to the sealing stage. This is determined mainly by the interaction between pollen availability and unknown internal colony factors, which would account for the great variations between individual colonies.

To what age is brood reared ?

Daily examination of brood made it possible to determine the exact age at which the brood disappeared, which had not been possible in the first investigation.

TABLE 3. Survival rate of *Apis cerana indica* and *Apis mellifera* brood to different ages.

Date of egg count	Colony no.	No. eggs counted	Percentage of surviving larvae (days after hatching)					
			1	2	3	4	5	sealed
Apiary in Mahableshwar								
29.4	41	107	84	49	6	—	—	—
30.4	341	75	79	52	13	7	—	—
30.4	158	141	55	25	4	—	—	—
30.4	494	78	94	85	76	44	1	1
Apiary at Institute in Poona town								
22.5	5/75	105	88	70	67	67	65	64
23.5	4/75	243	98	96	89	72	34	26
23.5	85	111	98	91	87	70	59	52
Apiary by Mulla river in Poona, before monsoon								
10.6	2/17	132	85	54	17	—	—	—
10.6	96	111	84	44	9	—	—	—
Colony supplied with pollen combs								
10.6	85	141	95	89	85	84	79	38
Apiary by Mulla river in Poona, after monsoon								
2.9	1/260	135	87	74	67	64	56	55
6.9	96	128	96	96	95	95	95	94
7.9	3/341	181	99	96	95	94	94	94
<i>Apis mellifera</i> in Poland								
8.7	95	292	98	97	97	97	96	94
8.7	79	238	97	96	95	95	93	93

Table 3 shows that in Mahableshwar, with a scarcity of pollen, a high percentage of larvae disappeared after the first day. Colony no. 158 reared only 55% of larvae to 1 day, but the other colonies 80% or more. Most of the larvae disappeared before day 3, but only the best colony (no. 494) reared the larvae up to day 4. Only one larva was sealed out of the 401 recorded in Mahableshwar.

More brood was reared in colonies located near the Institute in Poona, where quite a good pollen flow occurred in May. Table 3 shows that about 90-98% of larvae were reared to 1 day here. During the following days the amount of brood reared gradually decreased to about 70% on day 4. The greatest decrease was recorded in two out of the three colonies between day 4 of larval life and the time of sealing, and altogether only 26-64% of brood was sealed.

Pollen flows in India are characterized by rapid changes over short periods. One day many foragers would be seen returning to hives with large pollen loads, and a few days later almost no foragers carried pollen. This change was due either to weather conditions or to other factors which influenced pollen production in plants.

One such sudden pollen dearth occurred by the Mulla river in June. Table 2 shows that larvae hatched from eggs recorded on 5 June were reared quite well, while those in colony no. 13 investigated 3 days later did not reach the sealing stage. A few days later the pollen flow stopped almost completely. As can be seen from Table 3, no larva were reared beyond day 3 from eggs recorded on 10 June in colonies no. 2/17 and no. 96. Lack of pollen was noticed in most of the colonies, and colony no. 85 was chosen as having the largest amount of pollen in the combs. In addition, a comb full of pollen was placed next to the test comb. This resulted in better rearing of brood but, nevertheless, without

pollen income only 38% of brood was sealed (Table 3). The highest loss occurred in colony no. 85 just before sealing ; the greatest loss usually occurred at late larval stages.

During the monsoon period (mid-June to end-August) almost no open brood except eggs could be found in the colonies.

After the end of the monsoon the pollen and nectar flows increased, and the colonies reared more brood. Out of 3 colonies investigated at the beginning of September, two were headed by inbred queens (1/260, 3/341), but the brood investigated in these colonies was transferred to them from other colonies headed by naturally mated queens. Colony no. 1/260 was weak, and did not collect much pollen, as the author's records show. As a result, the amount of brood declined gradually on successive days, until only 55% was sealed. The two other colonies collected a lot of pollen. Colony no. 96 even built queen cups under the swarming impulse, and the queen laid eggs in them. As a result of good flow conditions 96-99% of larvae survived day 1. Very few larvae disappeared on the following days, and 94% of larvae were sealed (Table 3). This is very similar to the results

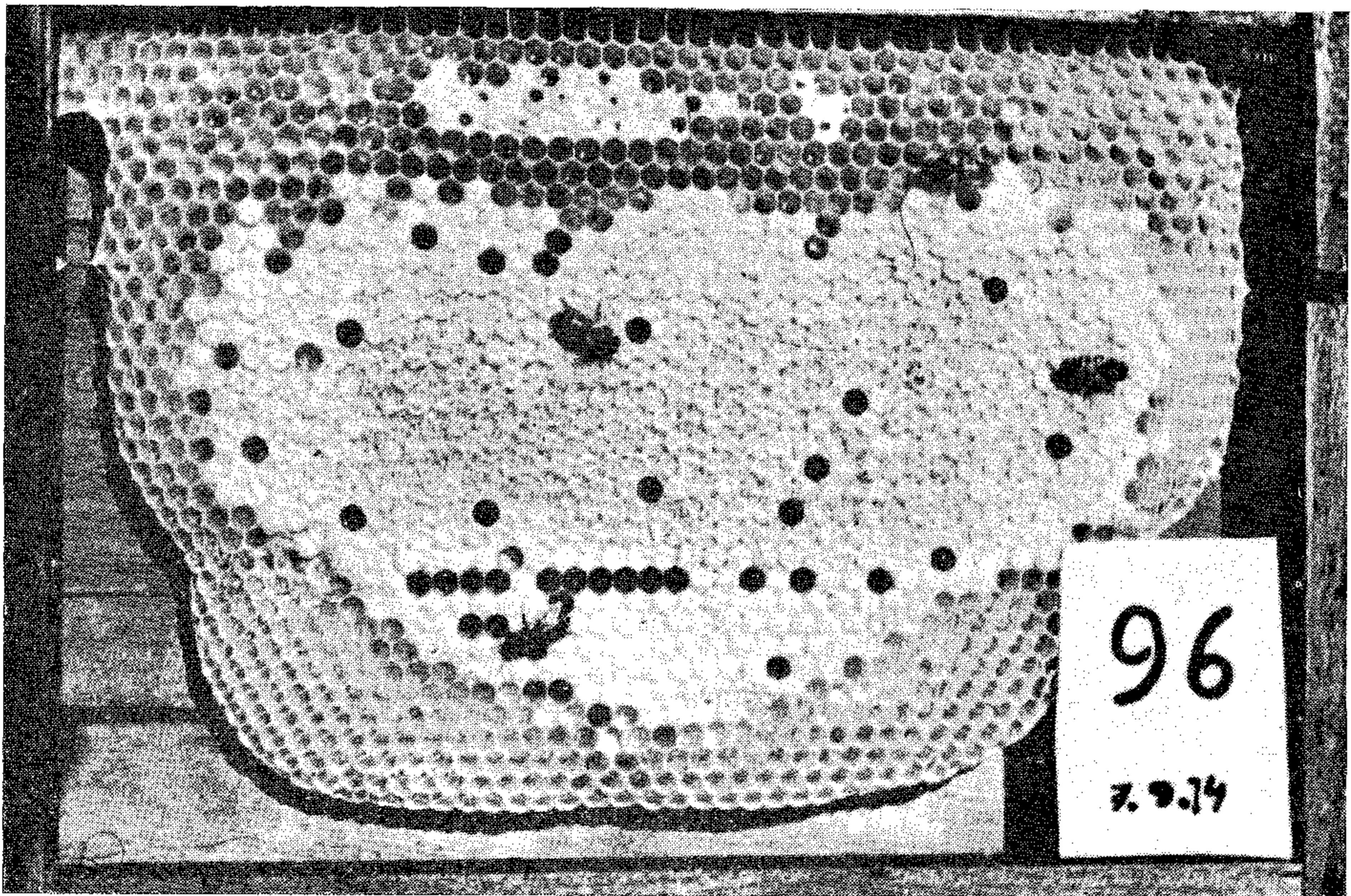


FIG. 3. Compact brood of *Apis cerana indica* during a heavy pollen flow in September, after the end of the monsoon.

presented in Table 2 for colony no. 96 investigated one week earlier, at the end of the monsoon. At this time, when good pollen and nectar flows occurred, the brood was compact in many colonies (Fig. 3).

Table 3 shows that an *A. mellifera* colony in Poland in July sealed 93-94% of brood; this is similar to the brood-rearing efficiency in favourable conditions in India.

It can be concluded that in most colonies more than 80% of larvae were reared to day 1 by *A. cerana indica* under any conditions. In dearth periods the percentage was sometimes less, and larvae were rarely reared beyond day 3. In moderate pollen and nectar flows more than 95% of larvae were reared to day 1, and usually 70% or more reached the age of 4 days. Then there was a rapid loss, and only about 50% or even less

brood was sealed. During good pollen and nectar flows more than 90% of brood was sealed.

The fate of disappearing larvae

No larvae were found on the bottom of the hive, or being carried out of it. But several times workers were seen to eat larvae, and partly eaten larvae were found. These partly eaten larvae were seen to move : they had not starved to death, but were eaten alive. The only exceptions were the dead young larvae in colonies ready to abscond, or larvae left in combs in hives from which colonies had ascended.

It can be concluded from the data presented in Tables 2 and 3 that the larvae were eaten because there was a lack of pollen. The great need for pollen was shown when a pollen comb was given to colony no. 1/260 on 14 June; it was all eaten by the next day. Colony no. 3/341 consumed almost all the pollen from 2 combs added on 16 June in 2 days.

The speed with which the pollen flow influenced brood rearing could be seen when colony no. 2/260 was transferred from the apiary by the Mulla river (where there was some pollen flow) to the Institute, where no pollen flow was observed :

3 July : colony transferred, all stages of brood present;

5 July : larvae 4-5 days old partly eaten, larvae 3-4 days old poorly fed;

7 July : larvae 1 day old without food, larvae 2-5 days old eaten, sealed brood present.

It was found that nurse bees reared brood only when pollen was located on the same comb as the larvae. The workers often ate larvae from one comb although pollen was still available in a comb farther away.

A colony of *A. cerana indica* imported from Poona to Poland did not collect much pollen, and in the beginning did not rear brood. It reared brood only after it was given a comb of pollen taken from *A. mellifera*, and only in the comb next to the pollen comb.

Egg laying in periods of dearth and before absconding

Results presented earlier would suggest that after nurse bees have eaten the larvae in a period of dearth, no more brood would be reared, but this was not so. After all larvae in the experimental colonies in Mahableshwar had been eaten, new eggs and young larvae (1-3 days old) were found again and again. Except for these, only a few scattered cells of sealed brood were present. From 7 May only eggs and sealed brood were found, and colony no. 333 had only eggs for the next two weeks.

Several dozen colonies in the apiaries located in the jungle around the Institute were also checked. Here again mostly eggs, young larvae and scattered sealed brood were found, but a few older unsealed larvae (3-4 days old) were present in some colonies.

A similar pattern of brood rearing was also found in Poona. After the larvae were eaten, the queen repeatedly laid eggs in empty cells. She did not stop laying even in the dearth period during the monsoon. Table 4 shows that when colony no. 2/260 was transferred to an area with a poor pollen flow, the workers ate all older unsealed larvae and stopped feeding the young ones, but at the same time 693 eggs were found in the colony : the queen had laid on average 231 eggs a day in the dearth period.

When the period of dearth was prolonged the sealed brood matured and adults emerged before it ended. Thus almost no larvae or sealed brood could be seen at that time in some colonies, although new eggs were encountered in them all the time. Colonies in such a condition were ready to abscond.

TABLE 4. Number of cells containing brood at different developmental stages in 4 colonies in the dearth period.

Type of brood	Brood in normal colony		Brood left by absconding colonies	
	7 July no. 2/260	22 July no. 5/75	4 Sept. no. 13	5 Sept. no. 80*
Eggs	693	274	316	648
Larvae 1 day old with food	27	16	1	43
Larvae 1 day old without food	132	27	51	125
Larvae 2-3 days old	0	0	0	295
Larvae 3-5 days old	0	0	0	13
Sealed brood	331	4	110 (+97)	265 (+12)

* diseased

+ figures in brackets refer to partly eaten larvae and pupae in cells that had been uncapped.

Brood in colonies that had absconded

Nests left by several colonies which absconded were examined. Eggs were found mostly on 2-3 combs. Detailed counts of brood left by three colonies were presented in Table 4. Colony no. 5/75, which absconded during the monsoon period, left only 4 sealed brood cells, a few larvae 1 day old and about 270 eggs, together with some honey but no pollen.

Colonies no. 13 and 80 absconded at the beginning of September, when the monsoon was almost over, and other colonies had started to collect pollen and to rear brood. Table 4 shows that young larvae in colony no. 13 were not fed, older larvae were missing (eaten), and half the 200 sealed cells were opened and the pupae partly eaten; but 300 eggs were left. Colony no. 80 was very strong, but European foul brood occurred suddenly and the colony absconded, leaving brood at various stages (including 650 eggs) and some honey and a little pollen.

Immediately after the colonies absconded, 50 eggs were collected from several combs of colony no. 13, and 130 eggs from colony no. 80. The eggs were fixed and their developmental stage determined. None were younger than 24 h, which may indicate that the queens stopped laying on the day before absconding. If all the eggs had been laid in 2 days, the laying rate by queens shown in Table 4 would be higher, 137-324 eggs per day before absconding. More investigations are needed on this point. It is certain that *A. c. indica* queens may lay eggs until the last day before absconding, and yet be able to fly. On several occasions the laying queens of colonies containing a large amount of brood flew off while a colony was being inspected. The queens usually returned to the colonies, but some were lost that returned to their hive after this was closed: it is common practice in India to cover the flight entrance with queen excluder to prevent absconding.

It can be concluded from the data presented that although the worker bees reduced amount of brood reared, and ate almost all the larvae in a dearth period, the queens usually laid eggs up to the time when the colonies absconded.

Determination of absconding

Indian beekeepers keep a queen excluder on the hive entrance all the time, to prevent the queen leaving, and so prevent the colony absconding. The workers still abscond, but

without the queen they return to the hive. After they have repeated this several times, they leave the queen in the hive and do not return. A few newly emerged worker bees also remain, but most of them leave it, and the young bees which cannot fly crawl on the ground. The number remaining was relatively small, and it seems that *A. c. indica* workers can fly at an earlier age than *A. mellifera* workers.

Examination of several colonies showed that the bees were ready to abscond after most of the adults had emerged, and little or no sealed brood was left. Some of the colonies which were preparing to abscond did not collect pollen, and did not rear brood, even if the winter and flow conditions improved meanwhile.

In August when the monsoon was almost over in Poona, many colonies collected pollen and reared brood. But foragers of colony no. 1/195 did not collect pollen, and the workers absconded; because the queen excluder prevented the queen leaving the hive, the workers returned. The colony was then given two combs with brood of different ages, and a pollen cake was placed on the top of the combs. During the following 2 days the bees ate all the unsealed brood from the additional combs and did not collect pollen. It was only after the colony received 2 more combs, containing all stages of brood, that the workers started to collect pollen and to rear the brood. It seems difficult to prevent colonies absconding once the impulse to abscond is firmly established—as with swarming.

The pollen flow started and stopped several times during the season. A definite cycle of pollen collection and brood rearing was evident, although the cycles differed in different colonies of the same apiary. Some colonies collected a lot of pollen as soon as it was available, and reached a peak of development early; others collected less pollen and developed more slowly. After the flow started to diminish some colonies reacted very quickly, reducing brood rearing and preparing to abscond, while others still collected some pollen and reared brood.

Thus there are significant differences in the reactions of different colonies to pollen and nectar flows.

Brood rearing in *Apis dorsata* and *Apis florea* colonies before they abscond

Five *Apis dorsata* colonies hived in different periods of the year collected pollen and nectar, but the workers did not rear the unsealed brood and the queens did not lay eggs. The colonies absconded when most of the adults had emerged. No honey was left, but some cells containing pollen were found.

The author was told that, in natural conditions, *Apis dorsata* queens usually cease to lay several weeks before absconding; such behaviour is different from that of *A. c. indica* queens.

Five well developed nests of *Apis florea* were investigated in different periods of the year. Brood in all stages of development was found (a piece was cut out from the centre of one brood comb to investigate this). After 3 weeks very little honey was present in that nest; to help the colony, a piece of *A. c. indica* honey comb was offered, but the colony absconded. Some eggs were found but no larvae or sealed brood. Although these *Apis florea* workers did not rear brood before absconding, it is not clear whether the queens continued to lay, or whether they stopped laying and then restarted because the weather and floral conditions improved.

Discussions and Conclusions

The main cause of scattered brood in *A. c. indica* colonies is as follows. During poor pollen flows the eggs laid by the queen produce more larvae than the nurse bees can feed.

The workers eat the older larvae and thus produce bee milk, which is fed to the queen and to young larvae (1-2 days).

The daily rate of egg laying by a queen cannot be calculated from the amount of brood present in a colony; the total amount of brood does, however, indicate the developmental stage of the colony. From the data the daily average brood-rearing ability of a colony can be calculated for a specific period.

In the plains variety of *A. c. indica*, changes in pollen flow are reflected very quickly in brood-rearing efficiency. This suggests that the fat-body of *A. c. indica* is less developed than that of *A. mellifera*, in which brood-rearing efficiency does not change so suddenly. This difference between the two species may be connected with their respective abilities to survive unfavourable conditions. It would be interesting to investigate the same characteristic in the hill variety of *A. c. indica* and in other *A. cerana* subspecies living in localities which have a winter period, and also in the tropical races of *A. mellifera*. Fletcher (1975) reported that *A. m. adansonii* destroyed all its brood before absconding.

There is some evidence that the pattern of egg laying and brood rearing which is characteristic of *A. c. indica* does not occur in *Apis dorsata*.

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