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NEST ARCHITECTURE AND BROOD DEVELOPMENT IN A NEOTROPICAL BUMBLEBEE, *BOMBUS ATRATUS* (1)

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Recently the biology of bumblebees has been greatly clarified by the successive appearance of many excellent contributions. But our knowledge on this interesting group depends nearly entirely on the observations made in temperate species. Information upon the species inhabiting other climates, especially those in the tropics is still very scanty. In the revision of the Brazilian bumblebees, one of us (S.F.S.) summarized and reviewed biological accounts so far obtained in South American lowlands (MOURE and SAKAGAMI, 1962. In this work the observations made by MEYERS (1935), on *B. transversalis* (Olivier), cited as *B. incarum,* is omitted from citation). But until the appearance of two papers by DIAS (1958, 1960) only fragmentary and careless observations have been carried out, and among them only the old paper by v. IHERING (1903) has been repeatedly cited by Northern Hemisphere specialists, as suggesting probable difference of life cycle and social organization from the well known haplometrotic and annual colony life in temperate areas.

In 1963-1965 we succeeded in rearing one colony of *B. (Fervido-*

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bombus) atratus Franklin in an observation hive and obtained some interesting results concerning behaviour and social organization. Observations on the behaviour during winter season was published elsewhere (SAKAGAMI and ZUCCHI, 1965). As a second report, the present paper deals with observations upon the nest architecture and brood development made during winter season. The results are themselves a byproduct of continuous observations on the behaviour within the nest by S.F.S. and R.Z. For his histological work, one of us (Y. A.) needed to have continuous series of immature stages of known ages. For this purpose, newly constructed egg cells were marked daily and their subsequent development was mapped daily, until the necessary number of cells of known ages were produced. Through this procedure, we also obtained some information about the duration, and body weight in each stage. Further, by the daily mapping some detailed accounts on the development of each brood batch and related nest elements were also observed.

I. — MATERIAL AND METHODS

On June 4, 1963, one medium-sized colony of *B. atratus,* containing 64 workers, ranging from completely black to distinctly yellow banded (*cf.* MOURE and SAKAGAMI, 1962), one queen alive and one queen that had recently died, was taken at the margin of Hôrto Floresta, the reserve forest of Rio Claro, State of São Paulo. The bees were, as is the rule for this species, so aggressive that transfer of the colony to the laboratory was possible only by anesthetizing them with carbon dioxyde. The colony was tentatively put in a flat, double walled wooden observation hive with glass lid and electric heater, deviced for stingless bees (*cf.* SAKAGAMI, 1966), again after anesthetization. The dimension of the inner case was kept at 30 × 20 × 4 cm. during winter (later enlarged). The comb groups of about 7 × 8 sq. cm. were put at one half of the case and a piece of fully deposited honeybee comb was given at the opposite corner.

Only about 30 workers remained alive on June 6, probably as a result of repeated anesthetization. But these surviving bees adapted amazingly well to the new domicile. The queen started to lay on the same day, and the colony expanded steadily. Every day the position and growth of each brood batch was mapped precisely. During and also after this daily mapping the temperature within the inner case was kept about 27-29° C. On July 11, one day after the first emergence of adults from batches of known eggs, all batches were removed and the contents (all workers) were counted, weighed and fixed. The observations on the nest architecture were made before as well as after the extraction of material. The results given below deal only with those obtained up to July 23, the date of the departure of S.F.S. from Brazil, that is, during the winter season under local climate.

II. — NEST ARCHITECTURE

B. atratus is a typical pocket making species, as already mentioned by v. IHERING (1903) (1). After the hatching out of larvae, the waxen pocket is constructed at one side of the cell, through which the pollen is progressively supplied to the larvae. The subsequent development of each batch does not differ essentially from that observed in Northern Hemisphere species.

1º ***Nesting site.*** — The observed nest was found on the ground, lined and covered with vegetable matter. No precise observation was made upon this outer cover, due to the terrible aggressiveness of the bees even when treated with carbon dyoxide, which is very contrasting to the mild temperament of most Northern species. Up to the present, all bumblebees nests found in South American lowlands are epigaeic, with the single exception of a semi-subterranean nest of *B. (Fervidobombus) brasiliensis* Lepeletier (*cf.* MOURE and SAKAGAMI). But it is still premature to give any definite conclusion. DIAS (1960) found an aerial nest of *B. atratus* (recorded as *B. medius*) from the State of São Paulo, which suggests its plasticity in nesting site preference. Also MICHENER and LA BERGE (1954) found a large subterranean nest of *B. (F.) medius* Cresson, a species close to *B. atratus,* from Mexico.

2º ***Location of brood cells.*** — As in temperate species, the egg cells are constructed solely by the queen, except for those made by laying workers. The behaviour in cell building and egg laying was described elsewhere (SAKAGAMI and ZUCCHI, 1965). In our colony, the egg cells were, under normal conditions, in most cases made on older brood cells, the ages and stages of which are presented in Table I.

From a glance at the table, it is obvious that the queen has a definite preference for the cells containing post-feeding larvae to make egg cells upon. When the cells containing young pupae were chosen, the waxen cover of such cells was usually still not completely removed. The result agrees with that by BRIAN (1951) in *B. (Agrobombus) agrorum* Fabricius. WEYRAUCH (1934) also writes that egg cells are always constructed on pupae or cocoon spinning larvae, never on growing larvae. Brian further noticed that the number of eggs laid in each batch was proportional to the number of pupae present in the cell on which each egg cell was constructed. This relation was not detected in our colony because the number of eggs in each batch did not vary much during winter as referred to later.

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(1) He cited *B. cayennensis* and *B. carbonarius.* The former is apparently the yellow banded form of *B. atratus* (not *B. transversalis* of Amazonic Basins) and the latter corresponds to either *B. (F.) morio* (Swedrius) or the melanic form of *B. atratus.*

TABLE I. — LOCATION OF EGG CELLS

STAGE \ AGE SINCE OVIPOSITION (IN DAYS)	NUMBER OF EGG CELLS CONSTRUCTED ON BROOD CELLS OF VARIOUS AGES AND STAGES																			TOTAL
	9	-	11	-	12	13	14	15	16	17	18	19	-	21	22	23	---	30	unknown	
Still with pocket						1														1
Still with pocket but the latter probably already without function	1		1			4	6	2		1									1	16
Pocket disappeared. Outer waxen cover still nearly intact..			1			2	2	3				1		1	1	1			5	17
Outer waxen cover more or less removed								2	2	1	2	1			1				10	19
Outer waxen cover nearly completely removed												1			1	2		1	3	8
TOTAL	1		2			7	8	7	2	2	2	3		1	3	3		1	19	61

After the removal of all brood cells on July 11, egg production was not disturbed, but the queen lost the favorable substratum. Under these conditions, all egg cells were constructed at the side of empty pollen pots, and the latter were transformed to the feeding pockets when the larvae hatched out. About two weeks after, the preference for older brood as laying substratum recovered, corresponding with the appearance of adequate larval cells. As an abnormal instance, the construction of one egg cell upon another was once observed as cited also by WEYRAUCH. Further, one small egg cell, probably of laying worker origin, was once found isolated on the hive floor, about 6 cm. apart from the bulk of combs, in spite of the presence of adequate old larvae. It is plausible that the laying worker prefered such a place after interference by the queen.

3° Arrangement of combs. — The development of combs is largely determined by the location of egg cells. In subsequent development, WAGNER (1907) distinguished several different types in some European species. This distinction was later developed by WEYRAUCH, complemented by his own observations, as follows : 1° Planloses Durcheinander der Einzelteile : *B. (Bombus) terrestris* (Linné) and *B. (B.) lucorum* (Linné), 2° Schichtenförmiges Nebeneinander der Wabenregionen gleicher Entwicklungsstufe ohne bestimmten Bauplan : *B. (Lapidariobombus) lapidarius* (Linné), 3° Gekreuzten länglichen Wabenplatten : *B. (Agrobombus) ruderarius* (Müller) (cited *B. derhamellus*), *B. (A.) humilis* Illiger (cited *B. variabilis*), 4° Vogelnestartige Rosette : *B. (A.) sylvarum* (Linné), *B. (A.) equestris* Fabricius, 5° Kranzförmige um das Nestzentrum angeordneter Einzelrosetten : *B. agrorum*.

Probably these patterns are not so fixed among species as such distinction of pocket-makers versus pollen-storers (SLADEN, 1912). Yet it is plausible that different bumblebee species exhibit different tendencies in comb arrangement and types other than those designated by WEYRAUCH might be discovered. In our colony, the upward development of combs was limited by the height of the observation hive, so that the resulting arrangement cannot be said to represent the pattern natural to this species. But the arrangement was not entirely irregular.

FIG. 1.

Comb arrangement on June 25, 1963. Numerals indicate days after oviposition (21+ means more than 21 days). Cells of 1-7 days old still without pocket, of 8-12 days old with pocket, of 12-17 days old already without pocket but waxen wall still not completely removed, of 17-21+ days old with cocoons exposed by removal of waxen cover. *C :* Old cocoons; *P :* Honeypots made from wax; *P′ :* Honeypot modified from empty cocoons; *Pp :* Pollen pot later changed to feeding pocket.

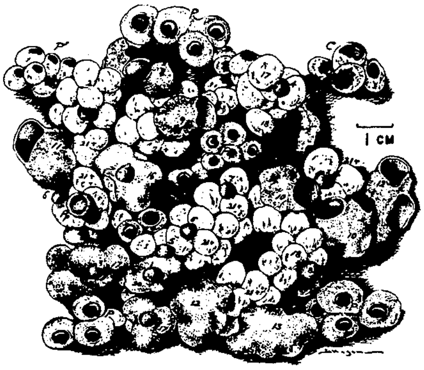

Figure 1 shows the arrangement on June 25, 1963, in which brood cells of diverse stages are shown by the numerals indicating age since construction. The formation of new cells are seen everywhere, but a closer inspection shows that comb development is more active at the periphery than the centre of the nest. Later this tendency becomes clearer. Figure 2 presents schematically the development of combs until July 11. The numerals give the order of construction. Although the cells are constructed everywhere, the peripheral areas are characterized by the

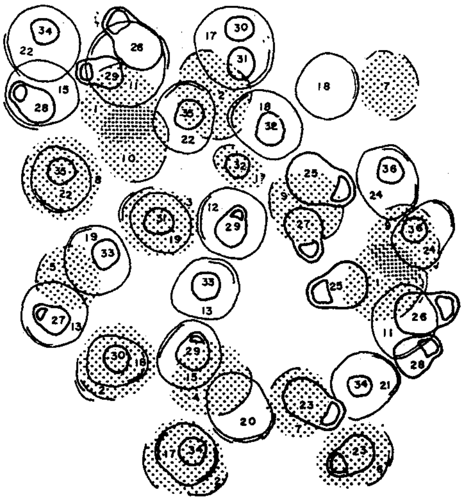

FIG. 2.

Schematic presentation of comb arrangment on July 11. Numerals indicate order of oviposition in days (two yougest batches, marked 36, were laid on July 10, night). Old batches (1-10) are shown with dots, intermediate batches already without pocket with thin solid lines, while young ones with pocket or still without pocket with heavy solid lines. In old and intermediate ones, the position of the pockets and if it occurred, their gradual change is given with thin lines.

occurrence of many stories up to 4 as seen on the righthand (1, 9, 24, 36). On the other hand, the central area is relatively free from cells, resulting in an irregular ring arrangement. This pattern is closest to type 4, *Vogelnestartige Rosette* by WEYRAUCH. It is also plausible that the nest could develop to type 5 of WEYRAUCH, or, both these types could be linked by the intermediate ones.

It must be mentioned, however, that such comb arrangement, even if classified in several types, could be traced definitely only in relatively young nests. In older nests, increased inhabitants and decreased available space obscures the pattern if it occurs. This must be kept in mind when the nests of Neotropical lowland species are examined, because they can develop enormous nests (DIAS, 1958).

4º Development of brood cells. — All observers agree on the fact that construction of cell and oviposition are performed solely by the queen. The queens of all bumblebee species so far observed seem to « lay their first batch of eggs on top of a bed of pollen. Of some species those egg cells which are built subsequently are also primed with pollen » (FREE and BUTLER). SLADEN (1912) calls these species pollen-primers, all of them are, according to him, underground pocket makers. There are known at least two other non-pocket making species with the same habit : *B. (Pyrobombus) impatiens* Cresson and *B. (P.) pratorum* (Linné). In our colony, all examined egg cells did not contain pollen and in all cells, where laying was directly observed, no deposition of pollen in any ways was seen either before or after laying.

The eggs are laid horizontally piled up one another (fig. 4, 3 b). This orientation seems to be prevalent in bumblebees. WAGNER recorded this as a rule except for *B. terrestris,* the orientation of eggs in this species is, according to him, quite irregular. WEYRAUCH presented a figure illustrating a cell with vertically deposited eggs (his Abb. 4), but the famous illustration by SLADEN (his fig. 10) shows the horizontal orientation. Cells are about 5-7 mm in diameter and 4-6 mm in height. WEYRAUCH distinguished two types of egg cells, one is flat and constructed on the niche between older broods, the other is flat-cylindrical and made on the flat surface. According to this distinction, all egg cells of *B. atratus* clearly belong to the second type (figs. 1, 4-3 b). Usually within one day or a little more after hatching out of larvae, one or two, rarely three feeding pockets are made at the sides of the cell, and pollen food is supplied through these pockets, though direct feeding by perforating the cell wall was also observed. Subsequent development of batches does not essentially differ from that recorded in temperate species, which will best be explained by particular examples.

Two egg cells, A and B, were successively constructed on June 8 and 9 on an old cell containing spinning larvae (X), the waxen cover of which was still not completely removed. Figure 3 presents the daily change of these two cells (initial size and position given in dots). The numerals in the figure correspond to dates (1 = June 8). On June 8, there was already another egg cell on X (*cf.* 1), the development of which was omitted from the illustration for simplicity. Before hatching out, all but one egg of cell A were extracted and devoured by workers, so that the cell diminished in size (*cf.* 1-10). This was one of the oophagy cases being relatively rare in our colony compared to the results of BRIAN (1951). Simultaneously, during 3.-7. day, two cells were externally connected by a waxen bridge as seen in the figure. 9 days after oviposition, one pocket appeared in cell B, the younger one (*cf.* 9). One the next day, cell A also received one pocket, while cell B another one (10). Thereafter, the feeding took place to day 14 and the cells enlarged rapidly (compare with the initial size and position given in dots). Correspondingly to the growth of larvae, the waxen cell wall became thinner and individual positions of larvae became easily recognizable as bulges in wall. On day 15, the pockets still remained but without function. Another new cell was constructed on cell B (20 B in 15, *cf.* also table IV). The pockets completely disappeared on day 16 and individual positions of larvae were demarcated by cocoon spinning activity. On day 20, cell B received another egg cell (15 B in 20 and table IV). Thereafter cell B became gradually invisible covered by the growth of cells 20 B and 15 B (day 22-30, again cômpare with the initial size and extent given in dots). On day 30, cell 15 B received two egg cells (7 A and 7 B in 30 and table IV). On day 31 cell A received one egg cell (5 A in 31 and table IV). On 32 day the first adult worker emerged from cell B. On day 34 cell 20 B received one further egg cell (2 in 34 and table IV). 35 days after the construction of cell A, all adults from cell B and the unique adult from cell A emerged.

FIG. 3.

Growth of particular batches. Growth of batches A and B is fully given, while of 15 B and 20 B only partly. Numerals mean the days since oviposition of batch A (June 8 =1). Dotted areas indicate initial size and position of batches A and B (during 9-19 days) and of 15 B and 20 B (during 23-35 days).

Figure 4 illustrates cross-sections of cells of representative stages, all examined on July 11. From the figure, it is seen that the waxen wall is the thickest at the egg stage, gradually becoming thinner. When the larvae begin to spin cocoons, the waxen wall is removed so that each cocoon is clearly recognized (15 c). In this stage, however the cocoons are still homogenously pale brown. The removal of wax proceeds further when the larvae take up on erect position in the cocoons, which become yellowish (19 a) and finally the waxen cover is nearly completely removed except for bases (27).

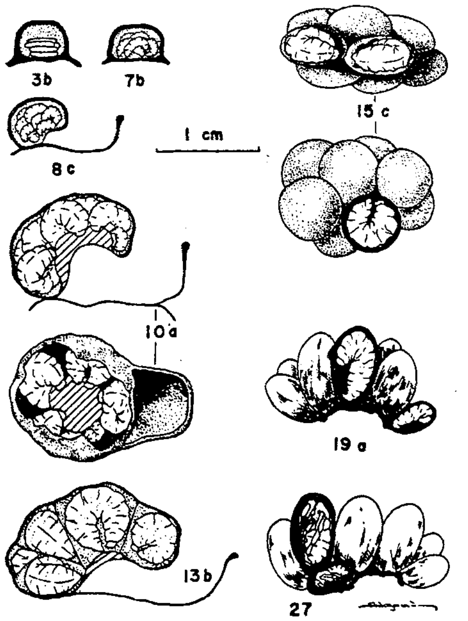

FIG. 4.

Structure of cells in representative stages. Numerals show the age since oviposition and correspond to that given in Table IV.

3 b : Egg cell; *7 b :* Larvae still without pocket; *8 c :* Larvae with pocket; *10 a :* Ditto, but with older larvae. Diagonal hatching shows the pollen deposition; *13 b :* Pocket still present, larvae making partitions; *15 c :* Separation completed, but larvae still in horizontal, coiled position; *19 a :* Erect post-defecation larvae; *27 :* Pupae (shown as white pupae, but truly already black. *Cf.* Table IV). In *10 a* and *15 c*, both dorsal and lateral views are given.

In 10 a, one larva is shown, which is remarkably smaller than her sisters. Such individuals were noticed in many older batches. When the larvae finished the spinning of cocoons, such dwarf individuals were always found at the base of cocoon cluster, orienting horizontally in contrast to others which lie vertically (fig. 4, 19 *a* and 27). CUMBER (1949) also noticed in *B. agrorum* that « the small cocoons of a single group are invariably peripheral ». He suggested probable competition among larvae of the same batch around the diet supplied through the pocket. He considered that, after larvae formed partitions and separating themselves one another by spinning partitions and thus fixing their positions within the cell, peripheral larvae would be less advantageous than the central ones, and that this would result in the marked difference in body size. But the size difference already appears before such separation and local fixation (compare 10 a and 13 b in fig. 4), so that it may depend, as he commented by himself, « rather in a combination of factors than in a single factor ».

5º ***Translocation of cells.*** — Although the social organization of bumblebees seldom reaches the level attained by other advanced groups such as honeybees, ants and termites, they have certainly developed some interesting features from the standpoint of social evolution. The rearing of several larvae within a common cell may be regarded as such, being a trait relatively rare among insects, and they are unique in the invention of flexible cells capable of expanding in dimension according to the growth of larvae.

In addition to such flexibility, we confirmed that brood cells could change their location even if gradually. Such translocation is achieved in most cases indirectly by the displacement of the older brood cells used as substrata, but occasionally directly by the gradual elaboration of a cell wall.

The indirect translocation was frequently observed. After pupation and removal of the waxen wall, the batch losses its firm attachment to the neighbouring nest elements. It was often observed that so far erected pupal batches were nearly rectangularly inclined, invariably toward the periphery of the nest. When one or more younger cells were found on such older cells, they change their positions passively together with the substrata. During the feeding period, the cell expands rapidly. As this expansion mostly directed to the nest periphery, the centre of each cell gradually translocates. Rarely a complete translocation is resulted in. Because of these two causes, direct and indirect translocations, the exact change of location is often difficult to trace, unless setting some reference points.

Figure 5 A shows some examples of such gradual translocation. It corresponds to a part of the left section in figure 1, the nest centre lies to the righthand. The initial size and position of seven cells are shown with thick outlined circles, subsequent expansion by thin contours (pockets with thick lines) and directions with arrows. In cell A, B, and G, gradual and centrifugal expansion is obvious but translocation is practically absent, the initial position being always within the later contour of the cell. On the other hand, the other four cells encircled by A, B, and G made conspicuous translocation. Cell D did not move directly but it was turned rectangularly two days after the disappearance of the pocket. Three other cells (C, E, F,), all laid on D moved from the initial position before the turning of cell D, the substratum. As seen in the figure, the translocation shows the topographical accomodation of initially closely located cells, through which collision among them is avoided. This would be the reason why cell E made the rather rare centripedal expansion.

A more conspicuous instance is given in figure 5, B, which shows the daily positions of cell 28 *a* (cf. table IV) by double projections (The positions on the preceding days with dotted lines). In this case both direct and indirect causes affected the cell in combination. On day 8 the cell in the figure appears to have contact with the substratum cell, but this is caused by the vertical projection. Actually the two cells

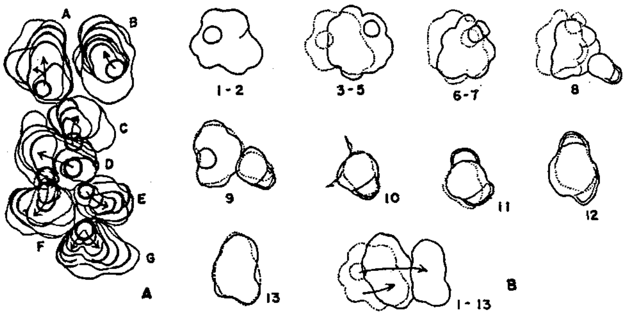

FIG. 5. — *A*. Expansion and translocation of seven peripheral cells. *B*. Translocation of one cell (28 *a* in Table IV, laid on June 14). Numerals show days since oviposition. In *B*, the cell position on each day (solid line) is given together with that on the preceding day (dotted line). The last figure, 1-13, shows the total extent of translocation.

were on that day separated by a narrow interspace, though they after again had contact due to a further expansion. That last figure, 1-13, shows the translocation between the first and last days.

6º Observations on pockets. — The pockets are probably constructed in most cases one day after the hatching out of larvae. At first they appear as two waxen streaks issuing in parallel from the cell side (fig. 6, A), which rapidly fuse together, forming a ring and increasing in height. The margin of the pocket is, as noted by WEYRAUCH, always distinctly thickened. On the other hand, the bottom often seems to be not specially elaborated. In a few cases, in which egg cells were made on relatively older cells, the waxen cover of which was quite removed, the yellow cocoon was often visible at the bottom of pockets. WAGNER records that the orifice of pockets is sometimes directed laterally. This was not confirmed in our colony, in which the orifice was always directed upward. Another, more important dis-

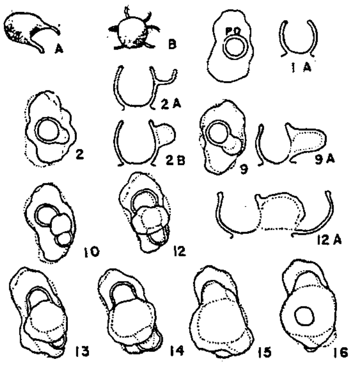

FIG. 6.

Formation of pocket. *A*. Beginning of pocket construction, seen laterally. *B*. Ditto. Three pockets at the same time. 1-16. Transformation of pollen pot to pocket. Numerals correspond to the day since construction of pot (1 = June 23). (Some lateral views are also given with alphabetical suffices. Dotted lines in dorsal views show the contour in preceding days).

crepancy occurs between WEYRAUCH and other students. He wrote that pockets persisted only one day or two, then were incorporated in the cell and again newly formed. This has so far never been recorded by other writers. In our colony, too, the pocket persisted during the feeding period, except sometimes when there was more than one pocket. It is not plausible that a keen observer such as WEYRAUCH made erroneous records, especially when he himself asserted the discrepancy between his own observations and those of Sladen. WEYRAUCH observed *B. agrorum* and *B. ruderarius* (= *derhamellus* in his paper), but both species are also observed by SLADEN and by other writers, too. It is open to further work to determine whether or not such differences appear within the same species. After the pockets have finished their function, they still persist one or two days. Thereafter they are simply destroyed or transformed to other nest elements, mostly to storage pots in our colony.

It is reported that only rarely are two pockets formed in one and the same cell. In our colony, the formation of two pockets was not rare, it occurred in 12 out of 57 accurately observed cells. Even three pockets were sometimes constructed (3/57). These cases are divided in several types with respect to the appearance and disappearance of each pocket : two throughout the feeding period (3 cases); first one, then two (5); first two, then one (3) and further the following cases : 3→2→1, 1→2→4, 1→3→2, 1→2→1→2. Figure 2, 3 and 5 show some instances of such sequence.

The opposite case, a pocket common to two cells is seen in figure 3. In this case, cell B had three pockets (fig. 3, 10). One of them was later used for cell A, too. On two days, the pocket was common to both cells (fig. 3, 10-11), then used exclusively for cell A.

Corresponding to the expansion of the larval cell, the pocket is also continuously elaborated and increased, in some degree, its size. Table II shows the gradual increase of both cell and pocket measured by the maximum transverse widths (When more than one pocket occurred in the same cell, each was regarded independently). As seen in the table, both pocket and cell expand gradually. But the expansion of pockets ceases on about to third day after construction, whereas the cells develop greatly on day 2-4 and the expansion continues more or less to day 8, resulting in a clear difference between them (*cf.* also fig. 1-5). Naturally a considerable variability exists in the development of pockets, viz., in dates of appearance and disappearance, in duration of persistence and relative and absolute sizes of cell and pockets. When two or more pockets occur, there is no decrease in size of either, as is readily understood from the manner of construction and utilization. Table III presents several individual records of representative cases.

WEYRAUCH points out that pockets are always constructed at the peripheral side of the cell in relation to the whole nest arrangement. As already mentioned, he observed the incorporation of pockets into

TABLE II. — GRADUAL INCREASE OF CELL AND POCKET SIZES GIVEN BY THEIR MAXIMUM TRANSVERSE WIDTHS (in mm)

WIDTH OF CELL (C) AND POCKET (P) (in mm)	DAYS SINCE APPEARANCE OF POCKET															
	1		2		3		4		5		6		7		8	
	C	P	C	P	C	P	C	P	C	P	C	P	C	P	C	P
	NUMBER OF CASES															
4	7	*14*		*1*												
5	7	*14*		*2*												
6	6	*2*		*4*								*2*	2	*1*		
7	4	*5*	3	*11*		*4*		*11*		*1*						
8	1	*2*	9	*6*	1	*18*		*20*		*17*		*11*		*5*		*1*
9			2					*1*		*2*		*4*				
10			4	*1*	5	*2*	1	*4*		*5*		*3*		*1*		
11					5											
12			2		6		7		3				1			
13					1				3		4					
14					2		5		1		2		2			
15					1		3		3		1					
16							1		3		1					
17									4		2		1			
18													1			
19									1		1				1	
20											2					
21											1		1			
22											1		1			
MEAN-WIDTH (in mm)	5.9	*5.7*	8.8	*6.9*	10.9	*8.0*	13.2	*8.3*	14.9	*8.4*	14.5	*8.3*	17.0	*8.0*	19.0	8.0

the cells one or two days after appearance. In this way, according to him, the pocket induces the outward expansion of cells, consequently, to accomodate the nest arrangement, inhibiting collisions between expanding cells.

Although the pockets in our colony persisted throughout the feeding period, the construction of pockets on the peripheral side of cells in relation to the whole nest arrangement was confirmed in most cases. Based upon figure 2, in which the position of pocket is given in each cell, the cells were arbitrarily divided into peripheral and central ones. And the position of pockets in each cell was divided into three groups : peripheral (P), intermediate (I) and central (C). The frequency distribution of these groups in all cells examined was as follows :

TYPE OF POCKET	P	I	C
Peripheral cells	24	3	1
Central cells	7	2	3

The preference for peripheral position is apparently predominant both in peripheral and central cells, though the distinction of position is a little arbitrary in the latter case. Further it is seen from figure 5,

TABLE III. — EXPANSION OF CELL AND POCKET IN SOME REPRESENTATIVE CASES, GIVEN BY TRANSVERSE WIDTHS OF CELL/POCKET (in mm) (× : without functional pocket).

CASE No.	DAYS SINCE OVIPOSITION										REMARKS
	7	8	9	10	11	12	13	14	15	16	
1				5/3	7/5,4	10/8,8	10/8,8,8	15/8,8,8	15/8,8,8	×	Later appearance of pocket. Pocket first 1, then 2, finally 3. Pocket at first very small.
2			5/6	5/6	6/9	6/9	10/9	10/9	×		Only one larva (= cell A in figure 3).
3		5/6	8/6,6	15/7,7	17/8,7	17/8,7	×				First, pocket larger than cell. At first 1, then 2.
4	5/4	6/5	10/8	14/8	17/9	20/9	×				Early appearance of pocket.
5		5/5	8/7	11/10	14/10	×					Short persistence of pocket.
6		5/5	10/7	14/8	16/8	16/10	20/10	×			Standard case.
7		6/5,5	10/7,7	13/8,7	14/8,8	17/8,8	17/8,8	×			Two pockets throughout.

that cells expand in the direction of pockets. The daily change of the position of pockets is given in figure 2. In most cases the change was rather gradual, but more conspicuous in some cases (these cases are excluded from the above mentioned distribution) : In two peripheral cells, pockets changed C→P and P→C respectively and in two central cells, C→I and P→C →I respectively.

When more than one pocket is constructed, the relationship becomes complicated as follows (all represented by a single case, unless parenthetically mentioned) :

Central cells : 2 (P, C) → 1 (P, —) (= at first two pockets, one peripheral and the other central. Later the latter disappeared), 2 (I, C) → 1 (—, C), 3 (P, P, I) → 2 (P, P, —) → 1 (P, —, —).

Peripheral cells : 2 (P, P) (= throughout the feeding period, two cases), 1 (P, —) → 2 (P, P), 2 (P, I) → 2 (P, C) → 1 (P, —), 2 (P, P) → 2 (P, I) → 2 (P, C), 1 (I, —) → 2 (I, P) (two cases), 1 (P, —, —) → 2 (P, I, —) → 3 (P, I, P), 1 (—, P, —) → 2 (—, P, P) → 1 (—, P, —) → 2 (C, P, —).

Besides the construction of pockets in the ordinary way, two abnormal cases were observed :

On the first one or two days after the introduction of the colony to the observation hive, several larvae succumbed and were taken away from the cell. The resulting orifices were usually closed immediately. But in one instance, such an orifice was modified to a pocket and used throughout the feeding period, although the cell already had its proper pocket.

The other instance is more noteworthy. It was previously mentioned that for about two weeks after all brood cells were taken on July 11, the egg cells were constructed at the sides of empty pollen pots (= true pots, not those secondarily modified from empty cocoons) and the pots were later transformed into pockets. This is obviously an outcome of the lack of appropriate substrata (post-feeding larvae and young pupae). But such secondary transformation of pots was once observed under normal situation, in spite of the occurrence of adequate old broods. The observations are presented in figure 6, 1-16.

On July 23, one pot was constructed on an old brood cell by workers. (This is already rather an unusual event) (fig. 6, 1 and 1A). On the next day, one egg cell was constructed by the queen at one side of the pot, without contact to the substratum cell (fig. 6, 2, 2A, and 2B, *cf.* also fig. 1, Pp). The cell and pot remained with no change until July 1, on that day the pot was modified to a pocket (fig. 6, 9 and 9A) and on the next day another pocket was made at the opposite side of the cell (fig. 6, 10). Both were used on subsequent days until July 6 (fig. 6, 14). In some European bumblebees HAAS (1962) mentioned the behavioural changes elicited by the small changes in nest structure and suggested their phylogenetic significance in nest building behaviour. It is possible that the secondary transformation of a pot to a pocket relates to such phenomenon. But we are still not in the position to give any definite conclusions from limited data cited above.

It has been said that in pocket-making species both males and queens were provisioned directly, not through pockets (FREE and BUTLER, 1959 (1), MICHENER and MICHENER, 1951). One of us (R. Z.) observed later the provisioning to queens and males in the same colony. This will be described elsewhere, so that here it is only mentioned that : 1° All three castes are fed through pockets, 2° In queens, the feeding continues during 3-5 days after the disappearance of pockets by means of a permanent orifice through which abundant food is frequently given by regurgitation.

7° ***Miscellaneous notes on other nest elements.*** — Storage pots were either constructed entirely from wax or made by using empty cocoons (P and P′ in fig. 1). In the latter case, a thick waxen margin was added ringwise to the orifice as is well known in temperate species. This application of a waxen margin was often quite rapid. For instance, one cocoon had a thick waxen margin and about 1/3 of nectar deposition 6 h and 5 min. after the emergence of an adult from it. No deposition of pollen to such cocoon-derived pots was seen. The waxen pots were of variable size as seen in figure 1, ranging from 1.3 to 0.5 mm in diameter, and mostly situated at the nest periphery, though sometimes at the centre. Most of these pots were used for nectar deposition, while only a few were for pollen, which was mainly deposited directly into the pockets. PLATH (1934) cited different opinions upon the sealing of pot filled with honey : HOFFER denied this while SLADEN and PLATH observed such sealing. In our colony, too, some fully deposited pots were sealed with wax.

When the colony was taken from the original nesting site, no waxen envelope was found as is recorded in many temperate species, especially in subterranean nests (WAGNER, SLADEN, WEYRAUCH, FREE and BUTLER). In this case, too, we cannot conclude that *B. atratus* does not make such envelope, for WEYRAUCH showed circumstancially that some species, which were usually devoid of such an envelope in their nests, sometimes constructed one. But it is probable that *B. atratus* makes such an envelope rarely if at all, because such an envelope has so far not been recorded in South American species. Further, some epigaeic species, so-called carder bees (SLADEN, 1912), are known to be disinclined to make such a cover. After being introduced into the observation hive, our colony made some fragmentary pieces of waxen lamellae (*cf.* fig. 1, above righthand), but never an entire cover. Two days after the introduction into the hive, the glass lid of the hive was continuously exposed to indoor daylight. Under these conditions some

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(1) FREE and BUTLER write « Plath (1934) noted that in the American pocket making species, *B. impatiens*, those larval groups whose members all become queens are fed solely by food *regurgitated* by the workers tending them, and no pollen pockets are formed. » We failed to discover this comment in PLATH. At any rate, *B. impatiens* is a non-pocket making species as PLATH himself classified it in his *Amarsipopea* (= non-pocket makers).

involucrum-making stingless bees kept in the same room immediately began to make a waxen cover. Probably *B. atratus* is a species that find it difficult to make a waxen cover. Such specific difference is, even if not rigidly fixed, known among European species. For instance many European observers record that *B. lapidarius* as a species which makes a waxen cover immediatley and intensively (WAGNER, SLADEN, WEYRAUCH).

Besides fragmentary waxen lamellae, they made a few pillars connecting the tops of some brood cells to the glass lid. Further some particular individuals smeared brownish wax upon the surface of the honeybee comb placed in another corner of the hive, approximately 10 cm away from the nest mass, being comparable to the sealing of their own honeypots. On the other hand, some other workers continuously transported the honey from the comb to their own honey pots. This indicates different evaluations of the honeybee comb among nest members. Some regarded it as being a part of the nest area, while others did not : the topographical evaluation of the nest area (HAAS, 1962) seems to be different among individuals, though obviously within a definite limit.

III. — BROOD DEVELOPMENT

As already mentioned, all immature stages of exactly known age were removed on July 11 from the colony and weighed. This removal was primarily made in order to obtain the material for histological work by one of us (Y. A.), but some comments about the brood development are given here, because, except for the work by BRIAN (1951) on *B. agrorum*, we have still no precise knowledge on the post-embryonic development of bumblebees.

Table IV presents the results of our observations and measurements. Each batch is arranged in the descending order of day-age. As the queen made 1-3, usually 2 egg cells and laid in them on each day, the corresponding number of the same-aged batches were obtained. They are distinguished by using alphabetical suffices (The younger batch, i. d., that containing younger stages precedes). The castes of eggs and larvae in batches 1 *a*-18 *b* are unknown but all are indubitably workers. During the winter season, the colony produced no reproductive castes.

The table shows the fairly constant number of individuals per batch. In Nos. 5 *b* and 14 *b*, the queen's oviposition was artificially disturbed (SAKAGAMI and ZUCCHI, 1965). Excluding these, the individual number per cell varied as follows : 6 (2 cases), 7 (11), 8 (20), 9 (17), 10 (2), with the mean 8. 11. BRIAN (1951) recorded quite high mortality during immature stages in two colonies, 64 and 69 % respectively. Obviously such high mortality was not seen in our colony. The individual number per batch does not decrease in the course of development. A dozen times the queen's oviposition was directly observed, the number of

TABLE IV. — INDIVIDUAL NUMBER AND BODY WEIGHT (in mg) OF BROOD IN EACH BATCH (measured on July 11, 1963).

AGE IN DAYS (1)	No. INDIVIDUALS	BODY WEIGHT		REMARKS
		MEAN	SD	
1 *a*	8	2.07		All eggs.
1 *b*	9	2.10		All eggs.
2 *a*	8	2.16		All eggs.
2 *b*	9	2.22		All eggs.
3 *a*	10	2.21		All eggs.
3 *b*	7	1.34		All eggs.
3 *c*	8	1.90		All eggs.
4 *a*	7	1.84		All eggs.
4 *b*	8	2.07		All eggs.
5 *a*	8	2.06		All eggs.
5 *b*	4	2.10		All eggs. Oviposition artificially interrupted.
6 *a*	10	1.75		All eggs.
6 *b*	8	1.94		All eggs.
7 *a*	8	1.70		All larvae, immediately after hatching out.
7 *b*	7	1.46	0.10	All larvae, immediately after hatching out.
8 *a*	9	3.80	0.39	Feeding larvae, cell with pocket.
8 *b*	8	7.67	1.10	Feeding larvae, cell with pocket.
8 *c*	8	8.08	0.82	Feeding larvae, cell with pocket.
9 *a*	9	8.41	0.72	Feeding larvae, cell with pocket.
9 *b*	9	20 50	2.14	Feeding larvae, cell with pocket.
10 *a* (2)	8	25.64	9.60	Feeding larvae, cell with pocket.
10 *b*	9	30.67	7.71	Feeding larvae, cell with pocket.
11 *a*	8	54.69	16.70	Feeding larvae, cell with pocket.
11 *b*	9	48.67	9.71	Feeding larvae, cell with pocket.
12 *a*	7	84.36	12.11	Feeding larvae, cell with pocket.
12 *b*	7	152.50	47.72	Feeding larvae, cell with pocket.
13 *a*	8	102.19	15.15	Appearance of silken partitions between larvae.
13 *b*	7	157.21	31.86	Appearance of silken partitions between larvae.
14 *a*	9	167.05	44.58	Appearance of cocoons outwardly, pocket still present but nearly without function.
14 *b*	5	157.00	15.13	Ditto. Oviposition artificially interrupted.
15 *a* (2)	8	248.25	66.12	Waxen wall gradually removed. Pocket disappeared.
15 *b*	7	238.21	84.19	Waxen wall gradually removed. Pocket disappeared.
15 *c*	8	299.75	71.33	Waxen wall gradually removed. Pocket disappeared.
16	7	297.56	33.73	Removal of wax advanced, but cocoons still brownish.
17	8	279.25	38.25	Removal of wax advanced, but cocoons still brownish.
18 *a*	9	260.44	60.83	Removal of wax advanced, but cocoons still brownish.

(1) Alphabetical suffices in same-aged batches are given approximately in the ascending order of mean body weight, serving also as individual batch marks.

(2) Body weight of each individual in two batches, which showed a marked variation, is given as follows :

Batch 10 *a* : 7.5, 16, 25.5, 27.5, 28, 29.6, 34, 37.
Batch 15 *a* : 141.5, 160, 225, 225, 248, 268, 400.

TABLE IV *(suite)*.

AGE IN DAYS (1)	No. INDIVIDUALS	BODY WEIGHT		REMARKS
		MEAN	SD	
18 *b*	8	202.44	83.05	Cocoons becoming yellowish. 3 predefecation larvae and 5 postdefecation larvae.
19 *a*	7	197.71	52.67	All postdefecation larvae.
19 *b*	9	253.00	40.23	One prepupa, others postdefecation larvae.
20 *a*	9	200.11	51.12	Two prepupae, others postdefecation larvae.
20 *b*	9	232.33	57.77	Four prepupae and 5 white eyed pupae.
21 *a*	8	209.12	51.32	One pink eyed pupa, others white eyed pupae.
21 *b*	9	227.33	45.69	One white eyed pupa, others pink eyed pupae.
22 *a*	9	252.00	46.08	One violet eyed, 2 pink eyed, others white eyed.
22 *b*	7	184.36	45.85	Two pink eyed, others violet eyed.
23	8	310.75	72.10	One black eyed, 2 pink eyed, others violet eyed.
24 *a*	6	282.75	85.08	One pink eyed, others violet eyed.
24 *b*	9	281.11	60 96	One body pigmented, 2 violet eyed, others black eyed.
25	9	267.22	56.46	Five body pigmented, 4 black eyed.
26 *a*	6	312.17	36.49	One body pigmented, others black eyed.
26 *b*	8	190.50	51.34	Two adults, 2 black eyed, others preimagines.
27	8	226.31	70.27	Three body pigmented, others black pupae.
28 *a*	7	157.86	42.77	One black eyed, 2 body pigmented, others black pupae.
28 *b*	9	307.33	94.32	Five body pigmented, 4 black pupae.
29	5	334.00	50.30	One body pigmented, others black pupae, someones already emerged.
31	3	403.33	63.51	One body pigmented, 2 black pupae, someones already emerged.
32	4	228.25	75.39	Two adults, 2 preimagines, some ones already emerged.
33	5	297.60	52.10	Two adults, 3 preimagines, someones already emerged.

(1) Alphabetical suffices in same-aged batches are given approximately in the ascending order of mean body weight, serving also as individual batch marks.

eggs per cell was always 7-9, and the removal of immature stages from the cells by adults bees was observed only exceptionally.

The table shows also a great variability in individual size within the same batch. The individual weights in each batch were converted to the percentage deviations from the mean bach weight and their fluctuation was shown in figure 7. Most individuals fall within ±20 % of

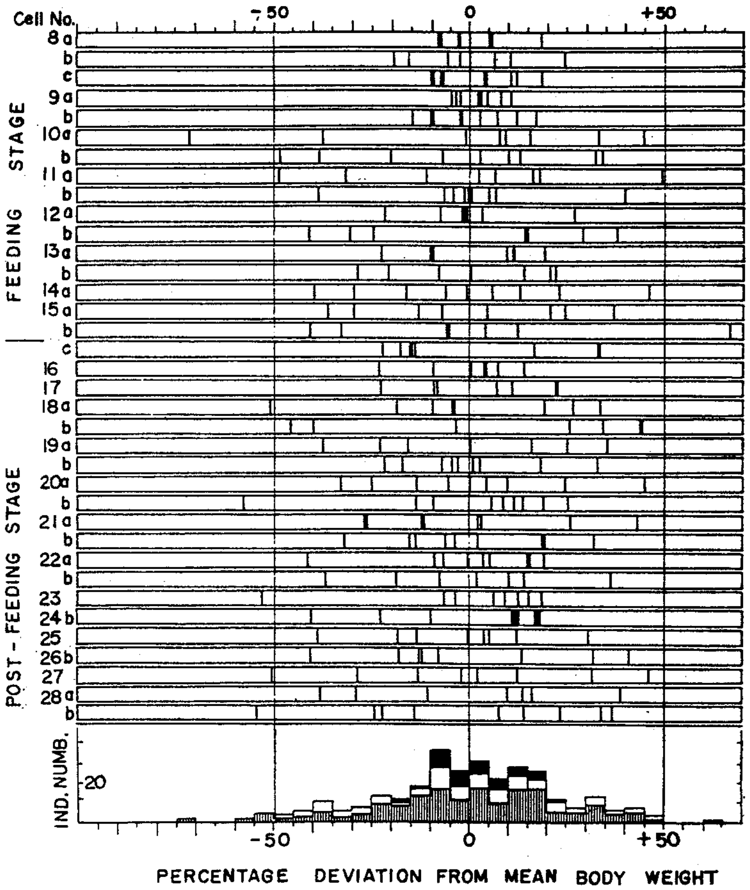

FIG. 7. — Fluctuation of relative body size within each batch. The batches containing less than 7 individuals were excluded. Abscissa shows % deviation of the weight of each individual to the mean batch weight. Occurrence of more than one individual of the same weight is given by thick vertical lines. Frequency distribution of total individuals is given at bottom, in which young larvae, old larvae and post-feeding stage are shown separately by black, white and striated areas.

the mean weight, but there are many exceptions, reaching +67.7 % and —70 % at the extremes. It is interesting that the variation is not so great in younger larvae (Nos. 8 *a*-9 *b*), while already conspicuous in older larvae (Nos. 10 *a*-15 *b*). This indicates, that, at least in our colony, the difference in body size has begun by the middle of the feeding stage and thereafter the variation not much increased. Also it suggests that the size differences were not accelerated by the position of larvae after their spinning of cocoons as assumed by CUMBER (1948). The instar of each larva could not be determined, but until the defecation, no marked difference was observed in developmental stages within each batch. Thereafter, the difference becomes apparent, especially in late pupal stages. In some batches (Nos. 26 *b*, 24 *a*, etc.), the advanced stages were seen in smaller individuals, but the tendency was not constant among other batches.

In our colony, the day to day inspection by opening brood cells was not undertaken, so that the exact duration of each stage was unknown. But the approximate estimation is given, together with previous information, as follows (in days) :

	Egg	Larva	Pupa	Total
B. atratus	6	12-13 feeding 7, post-feeding 5-6).	8-12	ca. 28
B. lapidarius (Sladen, 1912)	4	7	11	22-23
B. agrorum (Brian, 1951) :				
1947	4-6 (5.1)	10-19 (14.4)	10-18 (12.5)	32.0
1948	4-7 (5.3)	7-15 (14.0)	10-20 (14.8)	34.1

Comparing the data, the length of the egg stage is in *B. atratus* distinctly longer than in the others (Plath, 1934, also gives 3-4 days without giving reference to the species observed). Otherwise our data are approximately intermediate between those by Sladen and Brian.

It is concluded, that the immature stages of the bumblebee are longer than those of the honeybee, *Apis mellifera* Linné under any, not too extreme, circumstances.

The growth rate is given in figure 8 in comparison to that of the honeybee. The abscissa shows the relative age (28 days = 100 %) and the ordinate the logarithm of the ratio of mean percentage weight in each day-age to the mean weight at the end of the larval stage (16. days). Similarly, the growth rate in the honeybee was shown by using data by Melampy and Willis (1939) and, as to the change in the egg stage, those by v. Rhein (1933) (21 days = 100 %). The relative weight was given as the ratio to the weight at the end of larval stage, 5.-6. days. Further, the relative lengths of successive immature stages were compared between *B. atratus* and *A. mellifera* (after Wedemore, 1932, in figure 8, above, and Hassanein and Banby, 1956, in figure 8 below, both taken from Jay, 1963).

The figure indicates that : 1° The increase in weight during the egg stage is observed in the honeybee but not in *B. atratus*... In our data, weights of eggs in No. 3 *b* are remarkably small (*cf.* table IV), but otherwise there is no sign of gradual increase. The cause of this difference is unknown. 2° The egg stage is *relatively* longer in *B. atratus*, but there is no marked difference in the relative length of other stages. The difference in the egg stage could no be regarded as a general rule, because the length is shorter in other data (*cf.* above). 3° The

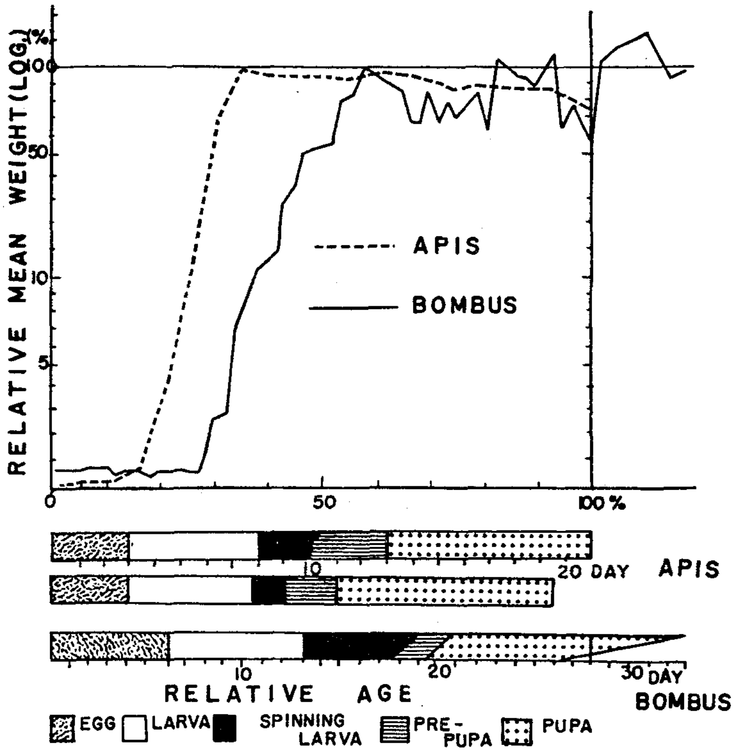

FIG. 8. — Comparison of growth rate and lenghts of each immature stage between *Bombus atratus* and *Apis mellifera*. Explanations in text.

growth rate during larval stage is more or less similar between both species, though slightly slower in *B. atratus*. 4° Both species show the decrease of the body weight after attaining the maximum at the end of the larval stage. The marked irregularity in *B. atratus* is caused by the greater individual difference already mentioned. In general, there is no marked difference in the growth pattern between two species.

IV. — CONCLUDING REMARKS

The results given in the present work show the similarity rather than the difference of *B. atratus* to the temperate bumblebee species, as far as nest architecture and brood development are concerned. It was proven on these aspects, and in general traits of behaviour (SAKAGAMI and ZUCCHI, 1965), the bumblebees behaved at about 125 km north of the Tropic of Capricorn like their Northern Hemisphere congeners. But it must be mentioned that this similarity was obtained in winter under the coldest season in local climate. Both cell building activity and brood development continued with little sign of disintegration during the season, though under artificial heating. This is not expected in the temperate species and suggests the different life cycle in South America as described elsewhere.

However, despite the general similarity of habits with the temperate species, closer observation shows some aspects so far relatively ignored. As to the absence of outer nest envelope, development and displacement of feeding pockets, translocation of cells, lengths of immature stages, especially of egg stage, and size differences in larval stage, we need further comparative information. Because the mode of life is more or less similar among different bumblebee species, the previous descriptions have often been given without citing the species name in each item of observations, especially when several species were used together in the same study. To avoid the discrepancy of results due to the specific difference, however it would be small, we think it is necessary to cite the species name accurately in each item of observation.

Finally, one point, though already well known, is stressed as a particular habit aquired by the bumblebees in the course of their social evolution : The rearing of several larvae together within the same cell, which is capable of expanding and even translocating according to the development of larvae. On this point, the bumblebees took a unique way in bee evolution, an interesting departure from the widely adopted unit-cell system, even if the way chosen was less efficient than the highest development in the latter, shown in the comb system of honeybees and stingless bees.

SUMMARY

1. Nest architecture and brood development of a Neotropical bumblebee, *Bombus (Fervidobombus) atratus* Franklin, were observed during the winter season, in Rio Claro, State of São Paulo, Brazil.

2. The egg cells are mostly constructed on the older brood cells, the larvae of which had already finished the feeding and began the cocoon spinning.

3. The development of comb was, though under spatial limitation, active at the periphery, resulting in the type similar to « Vogelnestartige Rosette » by WEYRAUCH.

4. The daily change of individual cells was precisely traced in some representative cases. The cells often change their original position, indirectly by the displacement of substrate cells. This change is often adjustive in the sense that it avoids the collision between neighbouring cells.

5. The feeding pockets are made soon after the hatching of the larvae in the cell, usually at the sides of the cells in the direction of the periphery of the whole nest mass, and persist during the feeding period as

reported by the other authors except WEYRAUCH. The size of the pocket increases slightly in the earlier half of the feeding period. One cell can have two or rarely three pockets, while two cells occasionally share the common pocket. In one instance, the egg cell was made at side wall of a pollen pot, and the latter was later modified to the pocket.

6. Besides cells and pots, some waxen pillars and lamellae were made but no envelope was constructed, nevertheless the colony was daily exposed to the indoor light.

7. The contents of accurately age-known cells were counted and weighed. The egg stage lasted 6 days, the larval and pupal stages each 12-13 and 8-12 days, and the total lenght of immature stage about 28 days.

8. The individuals in the same cell show great variation as to body weight and, in later stages, as to the development. The size difference begins already by the middle of the feeding stage.

9. The general growth curve is approximately similar to that in the honeybee, except, for the absence of the increase of weight in egg stage.

ZUSAMMENFASSUNG

1. Nestarchitektur und Brutentwicklung einer neotropischen Hummel, *Bombus (Fervidobombus) atratus* Franklin, wurden während Wintermonate in Rio Claro, Staat von São Paulo, Brasilien, beobachtet.

2. Die Eierzellen sind meistenfalls auf der älteren Brutzellen gebildet, deren Larven schon die Futtereinnahme beendet und das Kokonspinnen begonnen haben.

3. Die Wabenentwicklung war, trotz der räumlichen Beschränkung, aktiver an der Peripherie als dem Nestzentrum, somit eine dem von WEYRAUCH « Vogelnestartige Rosette » genannten Typ ähnliche Einordnung zeigend.

4. Die tägliche Veränderung einzelner Zellen wurde in einigen repräsentativen Fällen genau verfolgt. Die Zelle ändert häufig ihre Originalposition durch die Verschiebung der Substratzelle. Solche Transposition ist oft anpassungsmässig, weil der Zusammenstoss zwischen benachbarten, sich ausbreitenden Zellen dadurch vermeidet wird. Auch wurde die direkte Transposition der Zelle selten beobachtet.

5. Die Futtertasche wird sofort nach Ausbrüten der Larven, meistenfalls an der in bezug auf die Nestmasse peripherischen Seite der Zellwand gebildet, und bleibt während der Fütterungsperiode ständig, wie, ausgenommen von WEYRAUCH, von der anderen Autoren berichtet ist. Die Futtertasche nimmt ihre Grösse während der ersten Hälfte der Fütterungsperiode ein wenig. Eine Zelle kann zwei, selten sogar drei Taschen haben. Andererseits besitzen zwei Zellen gelegentlich eine Tasche gemeinsam. In einem Fall wurde die Eierzelle an der Seitenwand eines Pollentopfes gebaut und der letztere wurde später in die Tasche umgeformt.

6. Ausser der Brutzellen und Vorratstöpfen wurden einige Wachspfeilen und-lamellen, aber keine Aussenhülle gebildet, obwohl die Kolonie täglich dem Zimmerlicht ausgesetzt war.

7. Die Inhalte einer Zellenserie sofort nach Eiablage bis zu Ausschlüpfen, deren Tagesalter genau protokolliert wurde, gerechnet und gewogen. Das Eistadium dauerte 6 Tage, das Larven- und Puppenstadien je 12-13 und 8-12 Tage und die Gesamtentwicklungsstadien zirka 28 Tage.

8. Die Individuen in ein und derselben Zelle zeigen eine erhebliche Variation hinsichtlich des Körpergewichtes an späteren Stadien der Entwicklungsphasen. Die Differenz der Körpergrösse beginn schon in der Mitte der Fütterungsperiode.

9. Die Entwicklungskurve von *B. atratus* verläuft im allgemeinen derjenigen bei der Honigbiene ähnlich, ausgenommen von der Abwesenheit der Gewichtszunahme während Eistadiums.

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