Improvement of Bodenheimer's Method for Estimating Individual Number in Honeybee Colonies[1)2)3)]

By

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(*With 2 Text-figures and 2 Tables*)

In the study of insect populations, social insects present a set of particular problems. In contrast to other insects, the unit of their life is the colony and not the individual. Consequently the population problems in social insects must be studied at two different levels, the unit of which is respectively the number of colonies in a given area and the number of individuals in a given colony. In the European honeybee, *Apis mellifera* L., now reared all over the world for apiculture, however, the estimation of the number of colonies in a given area evokes a complicated problem. The colonies are artificially divided, fused and transported from one place to another. Thus the population dynamics at colony level is governed not only by natural conditions such as climate and flower abundance, but also by intricate processes devised by man.

With respect to the second problem (the individual number within each colony) the honeybee stands at a remote place from other insects. Up to the present, numerous methods have been devised to estimate the population size in various insects (reviewed by Southwood, 1966). One of the main problems in these studies is the accurate estimation of individual numbers at a given time. In honeybee colonies, however, this is not a serious difficulty, because of their concentration within a compact space and the absence of dispersal except for the occasion of swarming. On the other hand, the honeybee possesses numerous peculiarities, which are not seen in other insects, especially: 1) oviposition is made only by a single queen, 2) oviposition occurs continuously throughout a long period and the daily rate of oviposition varies considerably from 0 to 2,000, 3)

1) Contribution No. 867 from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan.

2) Contribution from JIBP-PT No. 75. This study was in part supported by a grant in aid from the Ministry of Education for the special project research, "Studies on the dynamic status of biosphere".

3) Population and bioeconomic studies on the honeybee colonies IV.

mortality in pre-imaginal stages is very low, resulting from care by adult members of the colony against external factors.

The estimation of the individual number of immature and adult bees in honeybee colonies is important from both theoretical and practical points of view. Up to the present, several procedures such as weighing, photographing, etc., have been planned for this purpose. Bodenheimer (1937) devised a method for calculating the individual numbers in each developmental stage on each day, based upon the periodical measurement of the number of sealed brood cells. The results obtained by this method are often cited in standard books of ecology (Allee *et al*, 1949; Odum, 1959), but they are relatively ignored in apicultural research. The method is excellent in principle but, as already pointed out by Uchida and Sakagami (1955), involves certain defects, which produce errros of the following three kinds:

1) Errors produced during measurement.

2) Errors produced in the course of calculation, especially the appearance of negative numbers and false cyclicity.

3) Errors produced by the oversimplified premises with respect to the duration and mortality of each stage.

The removal of these defects is necessary if accurate estimations of population flucutation, age structure and the total annual production of individuals in honeybee colonies are to be made by Bodenheimer's method.

The first kind of error is mainly produced when the number of sealed brood cells is estimated indirectly. For instance, Bodenheimer used Polteff's method, in which the sealed brood area in each comb was regarded as an ellipse and the number of cells was estimated from the extent of the area, measuring its long and short axes. This method gives a fairly precise estimate when all cells within the area are occupied by sealed brood, but the accuracy decreases when numerous cells within the area are either empty or occupied by eggs, feeding larvae or are used for food storage. However, this error can be almost completely removed by counting the number of sealed brood cells, based upon photographs of the sealed brood area as described by Nolan (1925) or by measurement with a brood grid such as that described by Jeffree (1955).

The third kind of error can be largely removed by the preparation of life tables for workers and drones, produced in different seasons under a given climate, such as those made by Sakagami and Fukuda (1968) for worker bees kept in Sapporo, Northern Japan. The present paper deals mainly with the second kind of error produced in the course of calculation. For this purpose, Bodenheimer's method is first described and some of its defects are criticized, and then a modified method is proposed, followed by a comparison of the two methods using a model population.

Before going further, the author expresses his sincere thanks to Prof. Mayumi Yamada and Dr. Shoichi F. Sakagami for their guidance and valuable suggestions during the present work and Dr. E. Crane who read through the manuscript.

Outline of Bodenheimer's method

This method is based upon three premises as follows:

1) The duration of each developmental stage is regarded as constant: Egg (3 days), Unsealed brood (=feeding larva, 6 days), Sealed brood (=post-feeding larva+pupa, 12 days), Nurse bee (10 days), House bee (10 days), Field bee (22 days).

2) The mortality in each developmental stage is postulated as zero, and each worker is assumed to die 42 days after emergence.

3) The fertility of the queen is assumed to deviate very little from day to day, changing only gradually.

Under these premises, the calculation is made in the following manner (*cf.* Table 1).

1) The actual number of sealed brood cells is periodically measured and is

Table 1. Summary of calculation of Bodenheimer's method (modified from Uchida and Sakagami, 1955)

I	II	III	IV	V	VI	VII
Date	Number of sealed brood present on each day (*a*)	Difference from the previous day (*b*)	Daily increase of adult bees (*c*)	Actual daily increase of sealed brood (*d*)	Daily increase of eggs (*e*)	Daily increase of larvae (*f*)
t_{-8}					$e_{-8}(=d_1)$	
t_{-7}					$e_{-7}(=d_2)$	
t_{-6}					$e_{-6}(=d_3)$	
t_{-5}					$e_{-5}(=d_4)$	$f_{-5}(=d_1)$
t_{-4}					$e_{-4}(=d_5)$	$f_{-4}(=d_2)$
t_{-3}					$e_{-3}(=d_6)$	$f_{-3}(=d_3)$
t_{-2}					$e_{-2}(=d_7)$	$f_{-2}(=d_4)$
t_{-1}					$e_{-1}(=d_8)$	$f_{-1}(=d_5)$
t_0					$e_0\ (=d_9)$	$f_0\ (=d_6)$
t_1	a_1	$b_1(=a_1-0)$		$d_1(=b_1)$	$e_1\ (=d_{10})$	$f_1\ (=d_7)$
t_2	a_2	$b_2(=a_2-a_1)$		$d_2(=b_2)$	$e_2\ (=d_{11})$	$f_2\ (=d_8)$
t_3	a_3	$b_3(=a_3-a_2)$		$d_3(=b_3)$	$e_3\ (=d_{12})$	$f_3\ (=d_9)$
•	•	•		•	•	•
•	•	•		•	•	•
•	•	•		•	•	•
t_{12}	a_{12}	$b_{12}(=a_{12}-a_{11})$		$d_{12}(=b_{12})$	$e_{12}(=d_{21})$	$f_{12}(=d_{18})$
t_{13}	a_{13}	$b_{13}(=a_{13}-a_{12})$	$c_{13}(=d_1)$	$d_{13}(=b_{13}+c_{13})$	$e_{13}(=d_{22})$	$f_{13}(=d_{19})$
t_{14}	a_{14}	$b_{14}(=a_{14}-a_{13})$	$c_{14}(=d_2)$	$d_{14}(=b_{14}+c_{14})$	$e_{14}(=d_{23})$	$f_{14}(=d_{20})$
•	•	•	•	•	•	•
•	•	•	•	•	•	•
•	•	•	•	•	•	•
t_{20}	a_{20}	$b_{20}(=a_{20}-a_{13})$	$c_{20}(=d_8)$	$d_{20}(=b_{20}+c_{20})$	$e_{20}(=d_{29})$	$f_{20}(=d_{26})$

plotted graphically and the number present on any given day is then read from the graph (a, Table 1, II).

2) The daily change (b) in the number of sealed brood cells is given by the difference between a_i and a_{i-1} (Table 1, III), but this difference is less than the actual number of sealed brood cells produced because adults emerge from the oldest cells every day.

3) The number of new adults on each day (c) is the same as the actual number of sealed brood cells produced 12 days before (Table 1, IV).

4) The actual daily addition of sealed brood (d) is therefore given by the sum of b_i+c_i (Table 1, V). Thus c and d are reciprocally calculated with an interval of twelve days.

5) The daily production of eggs (e), larvae (f) and nurse bees (c) is obtained, respectively, by shifting d along the time table, that is $e_i=d_{i+9}$, $f_i=d_{i+6}$, and $c_i=d_{i-12}$ (Table 1, IV, VI, VII).

6) Finally the total number of each stage on day t_i is calculated as follows:

$$\text{Total eggs} = \sum_{n=i-2}^{i} e_n \qquad \text{Total sealed brood} = \sum_{n=i-11}^{i} d_n$$

$$\text{Total unsealed brood} = \sum_{n=i-5}^{i} f_n \qquad \text{Total nurse bees} = \sum_{n=i-9}^{i} c_n$$

The total number of house and field bees are calculated in the same manner.

Improvement of Bodenheimer's method

Bodenheimer's method is excellent in theory because it enable estimates to be given for individual numbers of every developmental stage on each day, based upon the periodical measurement of the number of sealed brood cells.

As previously mentioned, the present paper deals with the removal of the second kind of error in Bodenheimer's method, which is produced in the course of calculation. His procedure indicates the daily population fluctuations accurately, if actual numbers of sealed brood cells are counted every day. But by using the linear interpolation between two actual measurement his method postulates a constant daily rate of addition of sealed brood between two observation times, whereas the actual rate obviously fluctuates from day to day, so that a considerable deviation is produced between actual and estimated numbers from very nature of his method, these errors affect each successive cycle of 12 days, because 1) the estimated number of changes into sealed brood (which involves some measuring error on day t_{i-12}) is regarded as the number emerging 12 days later (t_i), and 2) the difference between this number (on day t_i) and that on the previous day is estimated as the number of individuals newly changed into sealed brood on day t_i. In this way, the original measuring is transferred to the number estimated 12 days late, and subsequently two errors are transferred to the next estimation of sealed brood cells. Generally the population curve obtained by Bodenheimer's method shows negative numbers when the sealed brood cells is decreasing in amount, and the duplication of errors causes the appearance of a false cyclicity in the late half of the curve (Fig. 2).

In order to remove these errors it is proposed that the interval between measurements should be 12 days, since Fukuda and Sakagami (1968) confirmed that the duration of the sealed brood stage was remarkably constant, that is, 12 days in 92.6% of total number of individuals observed (Incidentally, the mortality during this stage was only 1.5%). Therefore, any individuals of this stage observed on a given day, t_x, have disappearred from the sealed brood area by emergence when the next observation is made on t_{x+12}, while those entering into the sealed brood stage after t_x still remain in the same stage on t_{x+12}; thus duplicate counting is almost entirely avoided. For example, some representative cases from photogarphs taken at 12 day interval of three combs occupied with brood cells through the most part of active period are shown in Fig. 1. Unfortunately, photographs at beginning on June 2 could not be shown, because of unsatisfactory exposure, though the count of sealed brood cells was possible. The colony used was reared in the apiary in the campus of Hokkaido University from May to wintering in 1970, and the days photographed are as follows: 1: June 15, 2: June 27, 3: July 9, 4: July 21, 5: August 2, 6: August 14, 7: August 26, 8: September 7, 9: September 19, 10: October 1.

When the number of sealed brood cells is counted every 12 days in a temperate climate from their first appearance in spring, that is on t_0, t_{12}, t_{24}, t_{36} (or, $t_{0\cdot 12}$, $t_{1\cdot 12}$, $t_{2\cdot 12}$, $t_{3\cdot 12}$), ..., $t_{i\cdot 12}$, until their autumn disappearance on $t_{n\cdot 12}$, the total number produced throughout the year measured n times is given by $\sum_{i=0}^{n} a_{i\cdot 12}$ where a_i is the number of sealed brood cells obtained on day $t_{i\cdot 12}$. Thus the present method can give an accurate estimate of the total annual production of sealed brood.

Bodenheimer adopted, like many other authors, durations of 3, 6 and 12 days as the durations of the egg, unsealed and sealed brood stages, but this combination appeared in only 3.7% of the individuals observed by Fukuda and Sakagami (1968). They found that the durations of egg, unsealed and sealed brood stages are respectively 3, 5 and 12 days in 80.9% the individuals observed; Using the figures of Fukuda and Sakagami and assuming 0% mortality in these three stages,[1] the oldest individuals among the sealed brood observed on day $t_{i\cdot 12}$ were produced from eggs, laid 19 days before and the youngest ones from eggs laid 8 days before. The average number of eggs laid per day in the period between 19 and 8 days earlier is therefore estimated as $a_i/12$. Because the number of eggs laid on $t_{i\cdot 12}$ corresponds to that of newly hatched larvae on $t_{i\cdot 12-3}$, and of newly sealed brood on $t_{i\cdot 12-8}$, the number of the three stages on a given day is calculated as in Bodenheimer's original method. By the adoption of an average daily number of eggs laid during

1) The correction based upon the actual mortality is easy from the life tables prepared by Sakagami and Fukuda (1968).

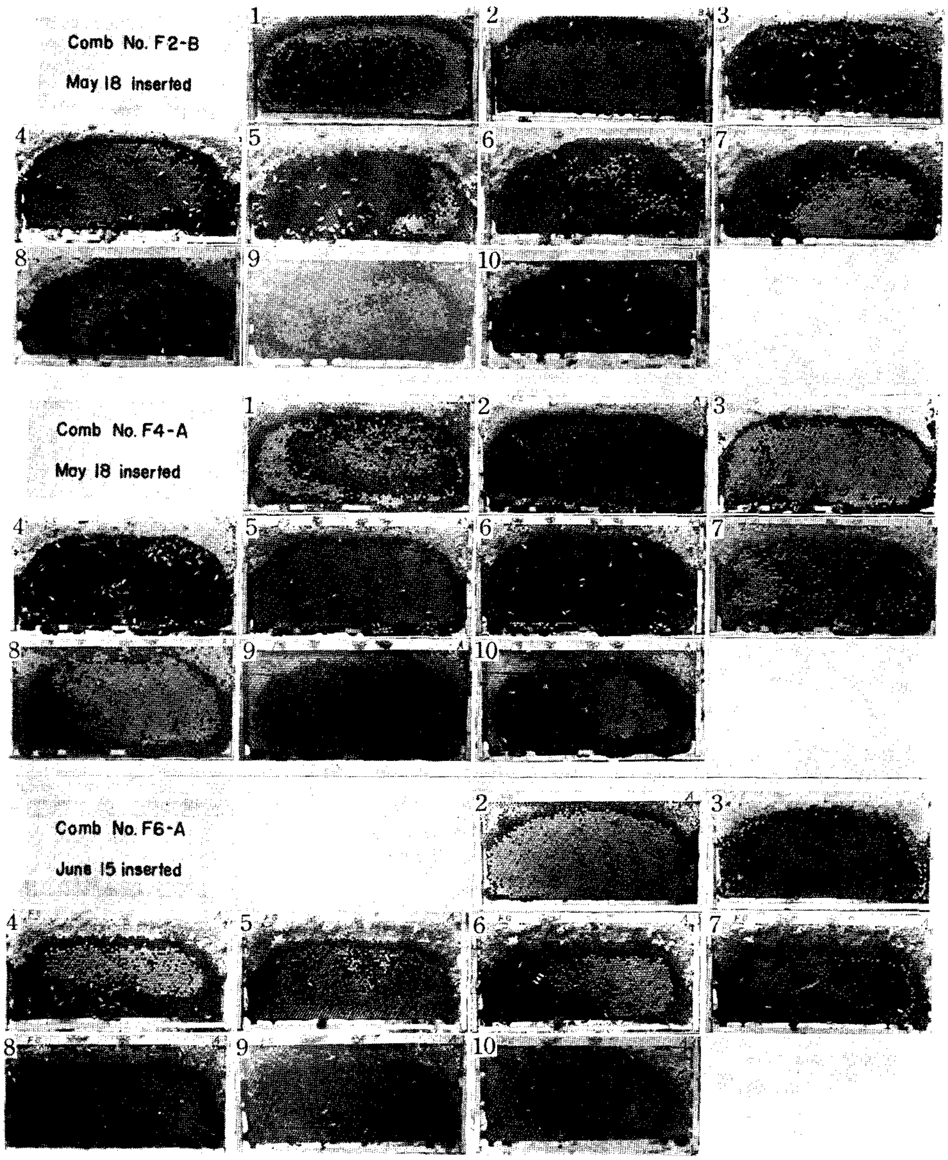

Fig. 1. Photographs taken at 12 days interval of three combs (see text)

12 days, the influence of the errors is cleared within each 12 day period, and does not affect the later results.

Where difficulties arise in practical colony management in keeping to the measuring interval of 12 days, the problem can be solved in the following way. If regular measurements on days t_0, t_{12}, $t_{24}, \ldots$ are impossible and the second measurement is made on day t_n (where $n=12\pm a$), the third measurement must be done on t_{24}, and not on t_{n+12}. The number of sealed brood cells present on t_{12} is found by the linear interpolation between t_0 and t_n (when $n>12$), or t_n and t_{24} (when $n<12$). In this case, a deviation from the actual number may occur but it does not later cause the appearance of negative numbers and false cyclicity. This procedure is also applied when using previous records not made with 12 day interval. The original data are graphically plotted and the numbers of sealed brood on days t_0, t_{12}, $t_{24}, \ldots, t_{i.12} \ldots$ are estimated by linear interpolation, and the subsequent calculation is made with these estimated numbers by using the procedure described.

Correction necessary when combs are removed or inserted or measurements started in the middle of bee season

There are some additional advantages in the inproved procedure. One of them is that it allows for the exchange of combs between colonies during the course of the observations, whereas Bodenheimer's original method cannot be applied when combs are removed or inserted during the observations. Although these are important routines in bee colony management, abrupt increases or decreases of numbers are brought by these operations. In the procedure developed in the present paper, the problem is solved by estimating the average numbers of eggs laid daily and of newly emerged bees in the comb to be removed or inserted. In this case, it is recommended that both removal and insertion should be done, as far as possible, on days of regular measurement ($t_{i \cdot 12}$).

At the removal of a comb on a given day, the number of eggs, unsealed brood in the comb (e_i, f_i, d_i) are counted by one of the techniques mentioned earlier, and are regards as originating from eggs laid, respectively, 2 days before, 3 to 7 days before and 8 to 19 days before, as mentioned previously. The number of eggs laid daily in the comb is obtained by dividing the numbers recorded by the duration of each stage (*i.e.* 3, 5 or 12 days). Daily numbers of each stage obtained are added to uncorrected number for the period of 19 days prior to the removal. For instance (Table 2, day 0), if the comb removed contained 300 eggs, 1,000 unsealed brood cells and 3,600 sealed brood cells, a previous 20 days, respectively, the numbers being, 100 for 3 days, 200 for 5 days and 300 for 12 days. Table 2 shows the value of the correction.

At insertion of a comb, the number of sealed brood cells present in the comb is measured (a_i) and divided by 12. This number, a_i, is subsequently added to the number of newly emerged adults for every 12 days after insertion. No correction is

Table 2. Corrections to be made after the removal or insertion of a Model comb (see text)

Day	Daily population of comb at removal				Daily population of comb at insertion		
	No. eggs per day	No. to be added			No. eggs per day	No. to be subtracted	
		Eggs	Unsealed brood	Sealed brood		Eggs	Unsealed brood
−19	300	300					
−18	300	600					
−17	300	900					
−16	300	900	300				
−15	300	900	600				
−14	300	900	900				
−13	300	900	1, 200				
−12	300	900	1, 500				
−11	300	900	1. 500	300			
−10	300	900	1, 500	600			
− 9	300	900	1, 500	900			
− 8	300	900	1, 500	1, 200			
− 7	200	800	1, 500	1, 500	100	100	
− 6	200	700	1, 500	1, 800	100	200	
− 5	200	600	1, 500	2, 100	100	300	
− 4	200	600	1, 400	2, 400	100	300	100
− 3	200	600	1, 300	2, 700	100	300	200
− 2	100	500	1, 200	3, 000	150	350	300
− 1	100	400	1, 100	3, 300	150	400	400
0	100	300	1, 000	3, 600	150	450	500

necessary for eggs and unsealed brood in the comb to be inserted, because they remain as sealed brood on the next regular measurement made 12 days later. But their numbers must be subtracted from the numbers of eggs and unsealed brood in the colony receiving the comb for 8 days prior to insertion, after dividing the numbers by durations of each stage. For instance (Table 2, right), if there were 450 eggs and 500 unsealed brood cells in the comb at insertion, daily subtraction of 150 for 3 days and 100 for 5 days from laying numbers are required.

When the insertion or removal is made on days between regular measurements, the correction, which is less accurate than the treatment mentioned above, is made as follows.

At insertion n days before the next regular measurement, the number of bees daily emerging from the comb, which is the number to be added to the result obtained for n days in the next measurement, is estimated as $d_x/12$, where d_x is the number of sealed brood in the comb at insertion. Further, the correction for immature stages is made by subtracting from the numbers of the three stages before insertion for 20 days, divided by the respective durations of each stage as before.

At removal, the daily population of the immature stages is corrected as in the case of insertion, by adding the number of each of the three stages present at removal (divided respectively by 3, 5, 12) to the uncorrected number for 20 days. Finally, the correction for emerging bees is calculated, based upon the number of bees which emerged from the comb during the period between last measurement and the removal made n days later, given by $n \times d_x/12$, where d_x is the number of sealed brood cells at the last measurement. If the difference is a negative value due to the adoption of an average instead of an actual number, the number of eggs laid during the corresponding period must be regarded as zero.

The application of the procedure in the middle of season still now be discussed. For this purpose, another defect involved in Bodenheimer's original method must be pointed out. Because the measurement is based upon the number of sealed brood cells, his method ignores the number of adults found at the first measuement. These adult bees, gradually dying in the coruse of successive observations, must be counted and incorporated into the result. For this purpose, we need their number and age structure. The number could be estimated by weighing, etc., but the age structure must be ascertained by other means. When the periodical measurement is started in spring after the first appearance of sealed brood, the estimation of adults is achieved relatively easily, because all post-hibernating workers can be regarded as physiologically of the same age (*cf.* Sakagami and Fukuda, 1968). But the situation is different when measurement is started in the middle of the season, for the colony has a more complicated age structure. Therefore, two items of information are a pre-requisite for starting the estimation at this time: 1) a series of life table, as one prepared by Sakagami and Fukuda in Sapporo, at least of spring, summer and autumn bees, prepared in similar climate,[1] 2) at least one sequence of population trend obtained by 12 days periodical measurement from spring onwards made under similar climatic conditions.

Once these data are available, the start of periodic measurement at any time in the middle of seasonal cycle is possible by applying the following two procedures synchronously.

1. Measurement of adult population by weighing, etc.
2. Measurement of sealed brood described above.

Both can be started on any day, but the later measurements must be continued periodically at 12 day interval. In this case, the procedure could be regarded as a modification of the comb insertion discussed above, or even of insertion of many combs into a hive without comb.

As to the adult population, it is theoretically only necessary to make one measurement synchronously with the first measurement of sealed brood. The later decreases by gradual deaths can be estimated by using two items of information mentioned above. But, to have more precise estimations, it may be better to continue

1) This also necessary to give an accurate estimation of the population trend using either Bodenheimer's original method or the improved one given above.

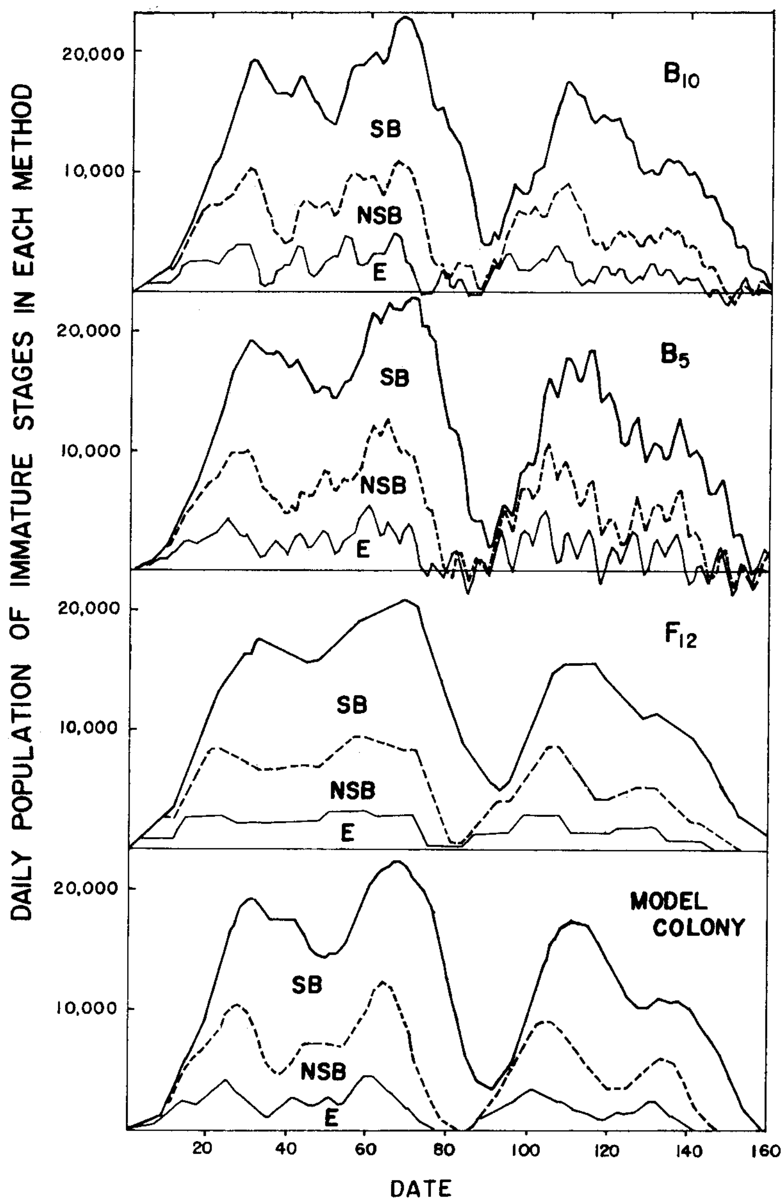

Fig. 2. Hypothetical numbers of eggs (E), unsealed brood (NSB) and sealed brood (SB) in a Model colony, and the numbers of each of these stages calculated from numbers of sealed brood cells on every 5th day (B_5), 10th day (B_{10}) and 12th day (F_{12}).

the same procedure 2–4 times successively at the same time as the measurement of sealed brood. Of course, the synchronous execution of both procedures throughout the season may bring a valuable contribution to the more accurate estimation of population trend. Furthermore, the procedure could be applied with a slight modification to the case of swarming. In this case, too, the adult population size of departing and remaining groups and their age structure must be known. The population size could be estimated by weighing, etc. The age structure is difficult to know accurately, but the age distribution given by Meyer (1956) could be used tentatively.

Comparison of the two methods by using a model population

To compare the deviations produced by the two methods from an actual population trend, a hypothetical model colony, given in Appendix by the number of eggs laid daily, was designed under the following premises.

1) Immature individuals are observed during 160 days.

2) Population trend is interfered with by a supersedure (natural requeening), causing the cessation of oviposition for 10 days.

3) Number of eggs daily laid varies gradually.

4) Duration of egg stage, and of unsealed and sealed brood stages are those adopted by Bodenheimer, that is 3, 6, 12 days, respectively (not 3, 5, 12 days as would be more correct).

5) Mortality in each pre-imaginal stage is assumed to be zero.

These premises are, except 4) and 5), fairly reasonable for a bee colony kept under normal condition in Sapporo.

Fig. 2 shows the actual (hypothetical) populations in a Model colony, and the calculated various using Bodenheimer's original method with a five day interval (B_5), a ten day interval (B_{10}) and the improved method with 12 day interval (F_{12}). The population trends in B_5 and B_{10} follow the actual trends in the Model colony well, but produce negative numbers and false cyclicity for the season and more in B_5 than B_{10}, because of a higher successive accumulation of the errors. The population trend shown in F_{12} produces neither negative numbers nor false cyclicity. On the other hand, the population trend is smoothed out by the adoption of the average number at each 12 day interval, rather than precisely following that of the Model as in Bodenheimer's method. This is a problem of the method to be improved in the future.

Summary

The method devised by Bodenheimer (1937) for estimating individual number of bees in honeybee colonies is criticized and partly improved. His method, though excellent in principle, produces certain errors in the process of calculation caused by linear interpolation of observed values. These errors successively affect the

population curve, resulting in the appearance of negative numbers and false cyclicity. To remove these defects, the estimation of the number of sealed brood cells every twelve days (*i.e.* the duration of sealed brood stage) is proposed. From the mean daily values, a more accurate estimate can be obtained of the number of eggs laid each day, and of the numbers of unsealed and sealed brood cells, as well as, and of the total annual brood production. On the other hand, this procedure is still incomplete as regards the reproduction of the actual population fluctuations, which less precise than in Bodenheimer's original procedure.

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Postscript:

After the preparation of the manuscript, the following paper was noticed from Apicultural Abstract, Vol. 20: page 24, 1969.

Cherednikov, A. V.: Method of determining the number of bees colony (in Ukrainian). Bdzhil'nitstvo (1): 43–67 (1964).

From its abstract cited, the method employed seems to be similar, especially in the use of 12 days interval, to that of the author.

Appendix. Daily population

Date	Number of oviposition	Total number of egg	Total number of larvae	Total number of sealed brood	Date	Number of oviposition	Total number of egg
1	100	100			56	1, 200	2, 800
2	100	200			57	1, 200	3, 200
3	100	300			58	1, 500	3, 900
4	100	300	100		59	1, 500	4, 200
5	100	300	200		60	1, 500	4, 500
6	200	400	300		61	1, 500	4, 500
7	200	500	400		62	1, 500	4, 500
8	200	600	500		63	1, 200	4, 200
9	500	900	700		64	1, 200	3, 900
10	500	1, 200	800	100	65	1, 000	3, 400
11	500	1, 500	900	200	66	1, 000	3, 200
12	800	1, 800	1, 300	300	67	1, 000	3, 000
13	800	2. 100	1, 700	400	68	600	2, 600
14	800	2, 400	2, 100	500	69	600	2, 200
15	800	2, 400	2, 700	700	70	600	1, 800
16	600	2, 200	3, 300	900	71	600	1, 800
17	600	2, 000	3, 900	1, 100	72	200	1, 400
18	800	2, 000	4, 200	1, 600	73	200	1, 000
19	800	2, 200	4, 300	2, 100	74	200	600
20	1, 000	2, 600	4, 400	2, 600	75	200	600
21	1, 000	2, 800	4, 400	3, 400	76	0	400
22	1, 200	3, 200	4, 400	4, 100	77	0	200
23	1, 200	3, 400	4, 600	4, 800	78	0	0
24	1, 500	3, 900	4, 800	5, 500	79	0	0
25	1, 500	4, 200	5, 400	6, 000	80	0	0
26	1, 000	4, 000	6, 000	6, 500	81	0	0
27	1, 000	3, 500	6, 700	7, 100	82	0	0
28	1, 000	3, 000	7, 400	7, 700	83	0	0
29	800	2, 800	7, 400	8, 500	84	0	0
30	800	2, 600	7, 400	9, 000	85	0	0
31	600	2, 200	7, 200	9, 700	86	200	200
32	600	2, 000	6, 800	10, 400	87	200	400
33	400	1, 600	6, 100	11, 100	88	400	800
34	300	1, 300	5, 200	11, 800	89	400	1, 000
35	300	1, 000	4, 800	12, 000	90	400	1, 200
36	400	1, 000	4, 200	12, 200	91	400	1, 200
37	600	1, 300	3, 500	12, 600	92	600	1, 400
38	600	1, 600	3, 000	12, 800	93	600	1, 600
39	800	2, 000	2, 600	12, 800	94	600	1, 800
40	800	2, 200	2, 600	12, 600	95	800	2, 000
41	1, 000	2, 600	2, 600	12, 200	96	800	2, 200
42	1, 000	2, 800	3, 000	11, 600	97	800	2, 400
43	800	2, 800	3, 500	10, 700	98	1, 000	2, 600
44	800	2, 600	4, 200	9, 800	99	1, 000	2, 800
45	800	2, 400	4, 800	8, 700	100	1, 000	3, 200

of model colony

Total number of larvae	Total number of sealed brood	Date	Number of oviposition	Total number of egg	Total number of larvae	Total number of sealed brood
4, 800	8, 800	111	600	2, 000	5, 200	10, 000
4, 800	9, 200	112	500	1, 700	5, 000	10, 600
4, 800	9, 400	113	500	1, 600	4, 600	11, 000
5, 000	9, 800	114	500	1, 500	4, 400	11, 200
5, 200	10, 000	115	500	1, 500	4, 100	11, 400
6, 100	9, 800	116	300	1, 300	3, 800	11, 400
7, 000	9, 400	117	300	1, 100	3, 500	11, 400
7, 700	9, 200	118	300	900	3, 200	11, 400
8, 400	9, 200	119	300	900	2, 900	11, 000
8, 700	9. 600	120	300	900	2, 600	10, 600
8, 700	10, 000	121	500	1, 100	2, 400	9, 900
8, 400	10, 900	122	500	1, 300	2, 200	9, 200
7, 900	11, 800	123	500	1, 500	2, 000	8, 700
7, 400	12, 500	124	500	1, 500	2, 000	8, 200
6, 900	13, 200	125	400	1, 400	2, 200	7, 500
6, 000	13, 700	126	600	1, 500	2, 400	7, 000
5, 400	13, 900	127	400	1, 400	2, 600	6, 500
4, 800	14, 500	128	600	1, 600	2, 700	6, 000
4, 400	14, 900	129	800	1, 800	3, 000	5, 500
3, 600	15, 100	130	800	2, 200	2, 900	5, 200
2, 800	15, 300	131	800	2, 400	3, 000	5, 100
2, 400	14, 700	132	800	2, 400	3, 300	5, 000
2, 000	14, 100	133	800	2, 400	3, 600	5, 000
1, 400	13, 200	134	400	2, 000	4, 000	4, 900
800	12, 300	135	400	1, 600	4, 200	5, 000
600	11, 000	136	400	1, 200	4, 600	4, 900
400	9, 700	137	400	1, 200	4, 400	5, 200
200	8, 400	138	200	1, 000	4, 000	5, 700
0	7, 400	139	200	800	3, 600	6, 200
0	6, 200	140		400	3, 200	6, 700
0	5, 200	141		200	2, 600	7, 200
0	4, 200	142			2, 000	7, 500
0	3, 200	143			1, 600	7, 400
200	2, 600	144			1, 200	7, 300
400	2, 000	145			800	7, 200
800	1, 400	146			400	7, 200
1, 200	800	147			200	6, 800
1, 600	600	148				6, 600
2, 000	400	149				6, 000
2, 400	400	150				5, 200
2, 800	400	151				4, 400
3, 000	800	152				3, 600
3, 400	1, 200	153				2, 800
3, 800	1, 600	154				2, 000
4, 200	2, 000	155				1, 600

Apendex

Date	Number of oviposition	Total number of egg	Total number of larvae	Total number of sealed brood	Date	Number of oviposition	Total number of egg
46	600	2, 200	5, 000	7, 800	101	1, 200	3, 400
47	600	2, 000	5, 200	7, 400	102	1, 000	3, 400
48	800	2, 000	5, 200	7, 200	103	1, 000	3, 200
49	800	2, 200	5, 000	7, 000	104	1, 000	3, 000
50	1, 000	2, 600	4, 600	7, 200	105	800	2, 800
51	1, 000	2, 800	4, 400	7, 400	106	800	2, 600
52	600	2, 600	4, 400	7, 600	107	800	2, 400
53	600	2, 200	4, 600	7, 800	108	800	2, 400
54	800	2, 000	4, 800	8, 200	109	800	2, 400
55	800	2, 200	4, 800	8, 500	110	600	2, 200

(Continued)

Total number of larvae	Total number of sealed brood	Date	Number of oviposition	Total number of egg	Total number of larvae	Total number of sealed brood
4, 600	2, 600	156				1. 200
5, 000	3, 200	157				800
5, 600	3, 800	158				400
6, 000	4, 600	159				200
6, 200	5, 400	160				
6, 400	6, 200					
6, 400	7, 000					
6, 200	7, 800					
5, 800	8, 600					
5, 400	9, 400					