Journal of Apicultural Research

ISSN: 0021-8839 (Print) 2078-6913 (Online) Journal homepage: https://www.tandfonline.com/loi/tjar20

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To cite this article: M. Delia Allen (1965) The Production of Queen Cups and Queen Cells in Relation to the General Development of Honeybee Colonies, and its Connection with Swarming and Supersedure, Journal of Apicultural Research, 4:3, 121-141, DOI: 10.1080/00218839.1965.11100115

To link to this article: https://doi.org/10.1080/00218839.1965.11100115

Published online: 24 Mar 2015.

JOURNAL OF APICULTURAL RESEARCH

Vol. 4 | 1965 | No. 3

THE PRODUCTION OF QUEEN CUPS AND QUEEN CELLS IN RELATION TO THE GENERAL DEVELOPMENT OF HONEYBEE COLONIES, AND ITS CONNECTION WITH SWARMING AND SUPERSEDURE

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Manuscript received for publication 17*th March* 1965

SUMMARY

The production of queen cups, queen cells, worker brood and drone brood in a total of 81 colonies was recorded regularly throughout four summers. All these processes are shown to occur in annual cycles whose peaks were approximately synchronized. All colonies produced queen cups at some time during the summer, and the great majority of colonies possessed them by the end of June. The number of queen cups varied considerably in different colonies but tended to fluctuate with the amount of brood during the season. About half the total number of colonies produced occupied queen cells, but queen rearing was abortive in more than half of these colonies. Many queen cells and some virgin queens were destroyed by the bees. Of 25 colonies with sealed queen cells, 19 replaced their queens, 16 superseding and 3 swarming, and there was some evidence that older queens were more likely to be replaced than younger ones. No queen rearing took place in colonies with queens of the current year. No significant relationship was found between queen rearing and amounts of brood, although colonies with larger amounts of brood in May showed indications of an increased tendency to produce queen cells subsequently. Most supersedure was found to occur during the swarming season.

INTRODUCTION

During the summer months, honeybee colonies (*Apis mellifera*) frequently start to rear queens in special queen cells and it is normally assumed that at this time of year the colonies are preparing to swarm. On observing such queen cells, therefore, many beekeepers carry out various manipulations designed to prevent their further development. However, it has been shown by Simpson (1957*a*) and by Gary and Morse (1962) that many potential queens are killed by the bees during the summer. It has also been stated by various authors (e.g. Wedmore, 1946) that bad weather may eventually cause the bees to abandon their attempts to swarm.

Simpson (1958) has reviewed the work already carried out on swarming; he has also (1957*a*) analysed the very extensive records of two commercial beekeepers in order to determine the proportion of colonies making preparations to swarm. He showed that many colonies produced queen cells but did not replace their queens. These records were, however, subject to the disadvantages that queen cells were removed by the beekeeper every 1 – 2 weeks, and that in some cases other measures to prevent swarming were taken. The tendency of the colonies to rear queens was therefore discouraged to some extent at least. The work of Gary and Morse (1962), on the other hand, was designed to disturb the colonies as little as possible, and in consequence it included no record of queen-cell production, but only of queens thrown out of the hive by the bees.

The present observations had the aim of assessing as accurately as possible the extent of queen rearing and swarming if no preventive measures were taken, and at the same time investigating the relationship between the general development of the colony and the events culminating in the production of queens. Some disturbance inevitably resulted from the necessary examinations of the colonies, but care was exercised in order not to damage any queen cells, and it is hoped that the colonies were not affected to any extent. Free and Spencer-Booth (1963) found that a rather smaller degree of disturbance did not appreciably decrease foraging activity.

MATERIALS AND METHODS

The work was carried out during four consecutive summers (1961-64). The number of colonies studied each year ranged between 19 and 22; Table 1 gives details. In 1961 and 1962 all the colonies studied were in the normal size range and had been overwintered in the apiary. The winter of 1962-63, however, was very severe and prolonged, and resulted in high mortality among the experimental colonies. Rather than discontinue the observations in the following summer (1963), it was decided to work with various small colonies purchased in late May and early June, as available; 7 of these were American Caucasian packages, 8 were 4-comb British colonies, and 4 were 8-comb British colonies. Unfortunately this summer was also very unfavourable; the small colonies failed to increase in size as rapidly as expected, and during July stores of honey were severely depleted. It is therefore emphasized that the 1963 results fall in a category of their own and are not closely comparable with those for the other years. In 1964 11 of the colonies had overwintered in the apiary and the remainder were purchased in early May (5 packages) and in early June (5 8-comb colonies).

The ages of queens are given in Table 1*g*; every queen was marked with a numbered foil disc for future identification. All colonies included in the results had the same queen throughout the periods for which results are given, and when any queen was replaced naturally by swarming or supersedure the routine numerical observations on that colony were terminated for the remainder of the season. Such replacements, however, occurred only twice before the third week in July, and the results quoted are therefore little affected, since the majority precede this period.

The colonies were housed in Modified National hives made up of brood boxes each containing 11 British Standard brood frames (35 × 21½ cm.). A further brood box was added at any time when shortage of space appeared likely to develop, because it has been shown that the overcrowding of adult bees is a major factor in inducing swarming (Simpson, 1957*b*; Simpson & Riedel, 1963).

Examinations of the colonies were commenced in mid-April in 1961 and 1962, in mid-June in 1963, and in mid-May in 1964, and were continued regularly until mid-August, being completed by an examination in mid-September. The examinations were made weekly except during April and May, when the period was slightly extended. During each examination the amounts of worker and drone brood were estimated by means of a specially calibrated grid (Jeffree, 1958), and records were made of the number of queen cups and occupied queen cells*. Normally the bees were shaken off each comb before measurements were made, but if any queen cells were present on the comb a brush was used to dislodge the bees, so that developing queens were not damaged.

The amount of drone comb in the colonies in spring was carefully controlled. In the spring of 1961 no comb with more than a very small area of drone cells

TABLE 1. Experimental details

	1961	1962	1963	1964	*Total*
a. No. of colonies	*22*	*19*	*19*	*21*	*81*
b. No. producing queen cells	18	16	1	7	42
(*a*) sealed queen cells	10	10	0	5	25
(*b*) only unsealed queen cells	8	6	1	2	18
c. No. superseding	6	7	0	3	16
d. No. swarming	0	1	0	2	3
e. No. producing one or more sealed queen cells but not superseding or swarming	4	2	0	0	6
f. No. superseding colonies with 2 queens for a period	3	3	0	1	7
g. Ages of queens:					
(*a*) less than 1 year	—	—	15	5	20
(*b*) 1 year	16	8	4	15	43
(*c*) 2 years	6	9	—	1	16
(*d*) 3 years	—	2	—	—	2
h. Ages of queens in colonies superseding or swarming:					
(*a*) less than 1 year	—	—	0	0	0
(*b*) 1 year	3	3	0	4	10
(*c*) 2 years	3	4	—	1	8
(*d*) 3 years	—	1	—	—	1
i. Ages of queens in colonies with queen cells but not superseding or swarming:					
(*a*) less than 1 year	—	—	0	0	0
(*b*) 1 year	9	3	1	2	15
(*c*) 2 years	3	4	—	0	7
(*d*) 3 years	—	1	—	—	1
j. No. producing queen cups	22	19	19	21	81
k. No. producing drone brood	22	19	17	21	79
l. Race of queen:					
Hybrid (British)	22	19	12	13	66
Caucasian (American)	0	0	7	8	15

* In this paper the term 'queen cup' denotes the empty cup-shaped precursor of a queen cell. The term 'queen cell' is used when the cell contained an egg, larva or pupa.

(about 30 sq. cm. maximum) was left in any colony. In 1962 and 1963 the same procedure was adopted except that the colonies were divided into two groups, one group being given one frame of drone foundation per colony whereas the other group received no additional drone foundation; in 1964 half the colonies were given as much drone comb as they required and the rest were limited as before. The results of this treatment in 1962-64 have been recorded elsewhere (Allen, 1963, 1965), but since it had no significant effect on queen-cell production it has been considered justifiable here to combine results for the two groups in each year.

Details of the nectar and pollen sources are given in Appendix I.

A summary of weather conditions abstracted from the Daily Weather Report* for Dyce Weather Station is shown in Fig. 1, which indicates that none of the four summers was particularly favourable for bees in the Aberdeen area. The method of plotting the data is described in Appendix II, where the results are discussed more fully. Honey production is also quoted there, but it can be stated briefly that the honey yields for July (when queen cells were relatively numerous) were moderate in 1962 and 1964, fairly poor in 1961, and exceptionally poor in 1963.

RESULTS

The findings have been divided into various sections for the sake of clarity, beginning with data on the general course of brood rearing in each of the four summers; these provide a background for the subsequent results.

1. *Amounts of brood*

Fig. 2 shows the mean areas of worker and drone brood per colony in the four years. The areas of worker brood proved to be very similar in 1961 and 1962, and the curves bear a considerable resemblance to the curve of total brood (drone and worker) obtained from a large number of colonies kept in this area between 1945 and 1953 (Allen & Jeffree, 1956), but are possibly a little later and attain a rather greater height. In 1964 the brood-rearing cycle gives the impression of being later than normal, but this was almost certainly not so: the summer was not a late one, as judged by the flowering times of various plants. The true explanation seems to be that the colonies were initially rather smaller than average; also there was a second rise in brood rearing at the end of July and the beginning of August. It has previously been suggested (Allen, 1965) that this was due to the prolonged limitation of foraging by high winds, which caused large numbers of adult bees to be available for brood rearing at this time, whereas normally there would have been a marked decline in brood rearing.

It has already been stated that the results for 1963 must be considered separately because of the atypical conditions. The worker brood curve had a very abnormal shape, due almost certainly to the poor foraging conditions on the bell heather in July; these led to a premature reduction in brood rearing. A brief spell

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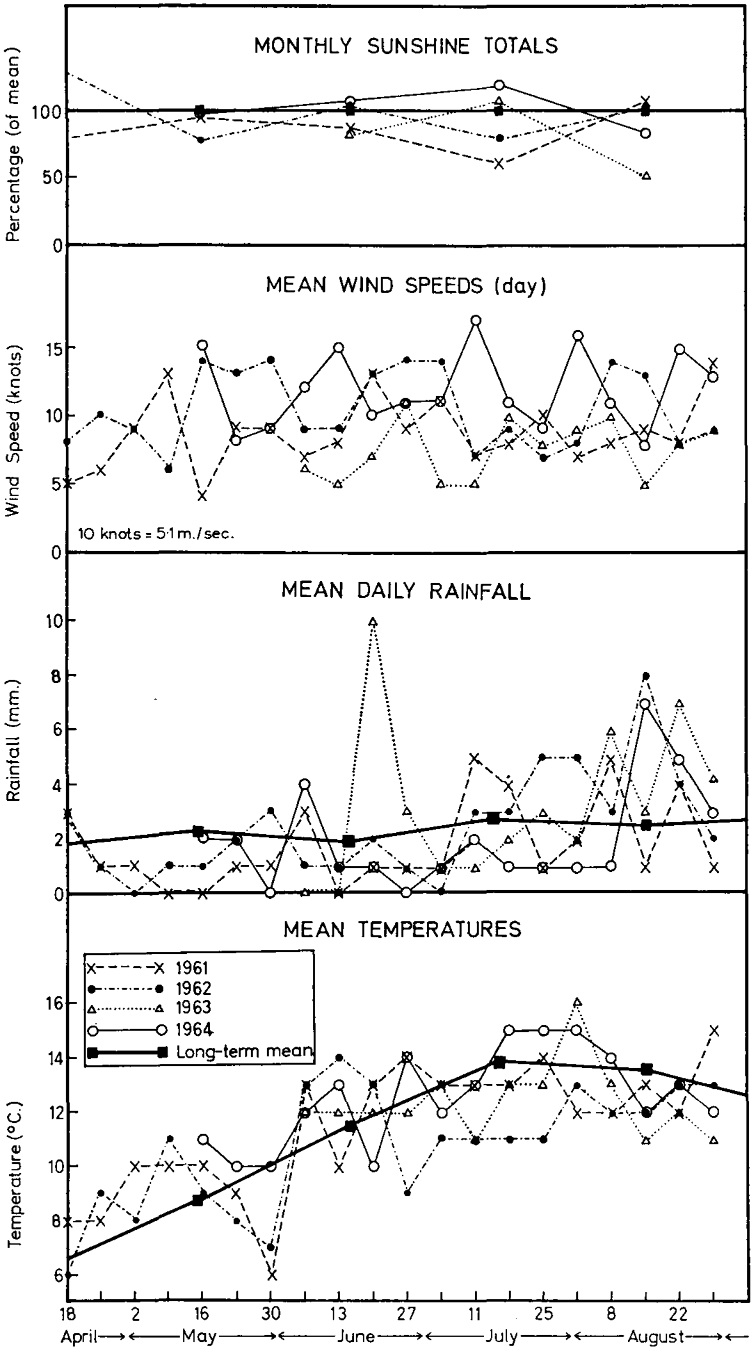

FIG. 1. Meteorological data for Dyce Weather Station, 1961-64 (see text)

of better weather in late July and early August was reflected in increased brood rearing, and a level which was normal for early August was reached, after the previous low values.

Drone brood-rearing cycles in general followed the trends shown by the worker brood of the same year. There was more drone brood in 1962 and 1964 than in 1961; this can be accounted for by the addition of drone comb to half the colonies in 1962 and 1964, as mentioned earlier. In 1963 amounts were much less than in the other three years; this was almost certainly related to the smaller colony size and poor environmental conditions. Two colonies produced no drone brood at all in this year, in contrast with the other three years, when all colonies had some.

2. *Queen-cup and queen-cell formation*

All 81 colonies produced queen cups during the course of the season. It is therefore assumed that this is a virtually universal event in the developmental cycle of the honeybee colony; even the two colonies which had no drone brood in 1963 had two queen cups each. It was confirmed that in the earlier part of the season a colony normally built a very few queen cups and that the number then increased more rapidly. Towards the later part of the active season the workers gradually destroyed the queen cups again.

The annual percentages of colonies with queen cups at each examination are given in Fig. 3, which shows a well defined cycle of production, with a basically similar timing in all four years. (In 1961 and 1962 records were not made in the period when numbers of queen cups were declining.) Fig. 4 shows the mean numbers of queen cups per colony, and a comparison with Fig. 2 demonstrates that the queen-cup curves follow courses which are essentially similar to the corresponding worker brood curves, reaching their peaks at virtually the same time. This was also borne out by data from individual colonies. A particularly evident similarity is seen in 1963 (where both curves had two peaks separated by a dip in the second part of July), and also in 1964, where both showed an unusual extension of the peak area into August.

The number of queen cups per colony was variable. The maximum numbers ranged from 4 to 55 (mean 24) in 1961, from 7 to 62 (mean 22) in 1962, from 1 to 11 (mean 4) in 1963, and from 1 to 48 (mean 14) in 1964. The factors governing the number of queen cups per colony were not well defined, but it seemed that small colonies producing sub-normal amounts of brood tended to have very few queen cups. The numbers produced by larger colonies showed considerable variation.

Queen cups were first converted into queen cells for rearing queens during late May in 1961, and during early June in 1962 and 1964. Both the mean numbers of occupied queen cells and the percentage of colonies with such cells, rose to a peak between the end of June and the end of the third week in July in these three years; in 1963 only one colony had queen cells at one examination (Figs. 3 and 4). Sealed queen cells were present over a shorter period, as also shown in Figs. 3 and 4.

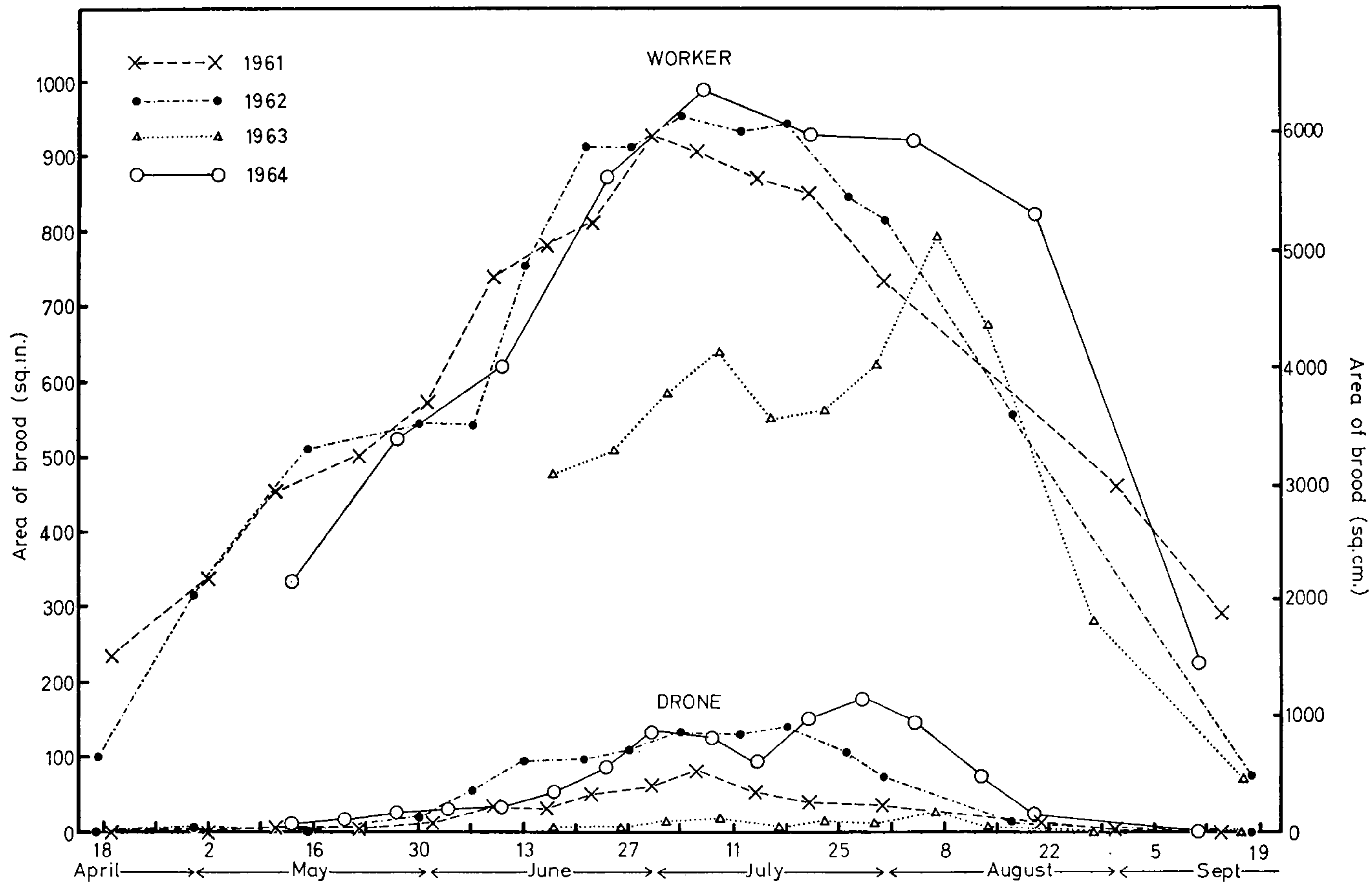

FIG. 2. Mean amounts of worker and drone brood per colony, 1961-64

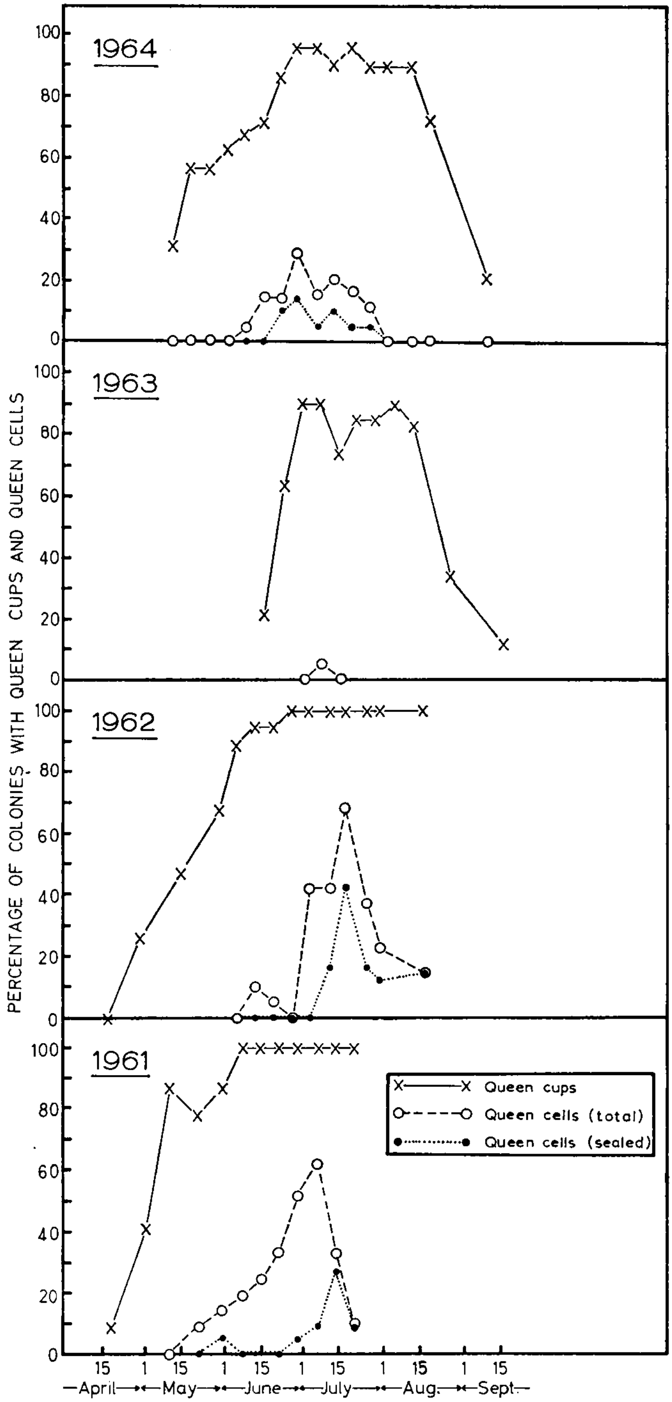

FIG. 3. Percentages of colonies with queen cups and queen cells, 1961-64

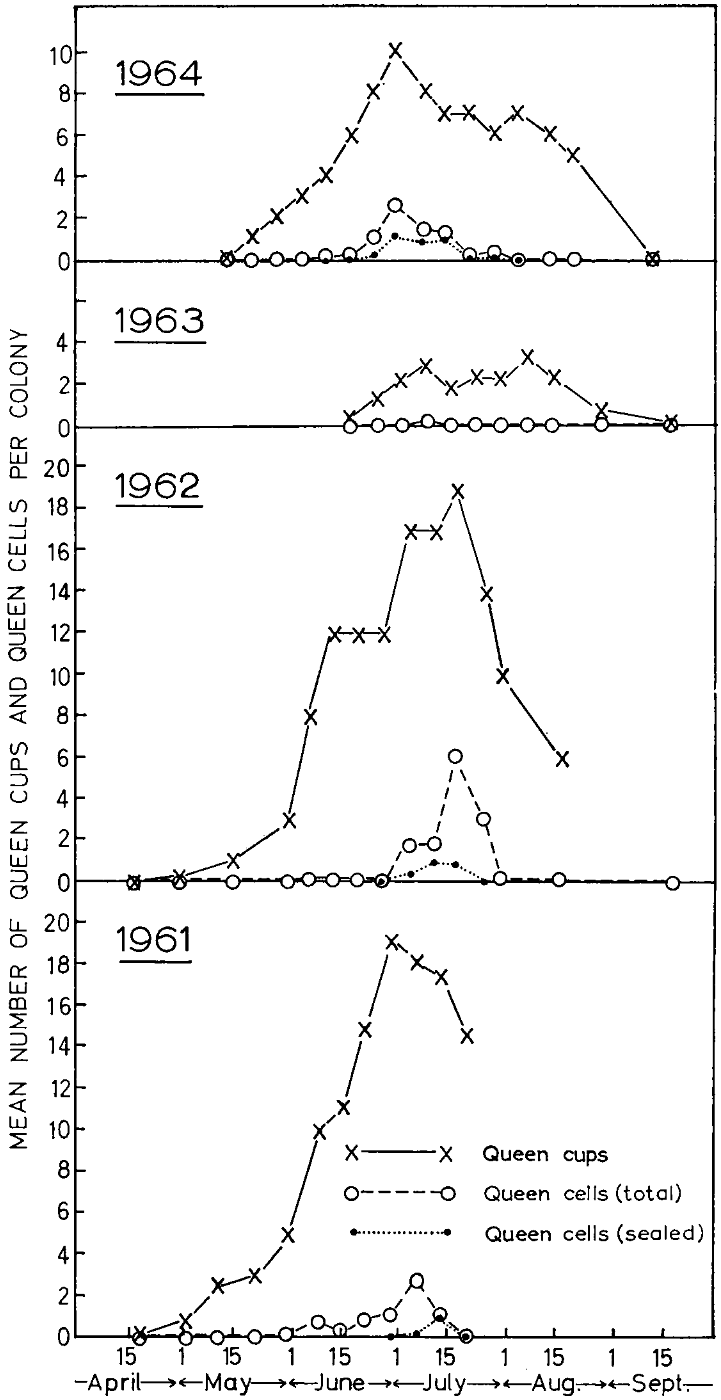

FIG. 4. Mean number of queen cups and queen cells per colony, 1961-64

3. *The extent of swarming and supersedure*

The main object of the investigation was to assess the number of colonies which reared queen cells to maturity, and either swarmed or superseded*. The most noteworthy feature of the results (Table 1) was that although 43 colonies out of a total of 81 produced queen cells, only 19 replaced their queens (16 supersedures, 3 swarms). In other words, queen rearing was abortive in 24 colonies. It should be pointed out, however that only 6 of these 24 colonies had sealed queen cells. It is concluded, therefore, that the presence of unsealed queen cells in a colony does not necessarily indicate that any change of queen will occur (either by swarming or by supersedure); but that where sealed queen cells are present there is a considerable probability of an impending change of queen. In the four years studied, supersedure was far more common than swarming; it may be that this was due to the rather unfavourable weather.

4. *Number of queen cells in swarming and in superseding colonies*

It is commonly thought that if a colony has only a very few queen cells it will supersede its queen, whereas if it has more than perhaps 4 or 5 it will swarm. In the present work the three colonies which reached the swarming condition (Table 2) all had a large number of queen cells (29 – 36) in the week before the first young queen emerged; and this observation supports the popular view that swarming colonies produce many queen cells.

All colonies which superseded their queens in 1961 and 1964 had less than 6 queen cells in the week before the young supersedure queen emerged, but all such colonies in 1962 had more (Table 2). In colony 1 (1962) in particular the number was very high, but there was a slight element of doubt whether the relatively sudden production of queen cells in this colony was linked with the failure of the old queen, since she ceased to lay just after the first queen cells were constructed, and was not seen again. However, apart from the earlier disappearance of the queen, the behaviour of this colony was not unlike that of the three colonies which swarmed, and indeed it is possible that the generally higher numbers of queen cells in the superseding colonies in 1962 was due to a tendency to approach the swarming condition, but that the departure of the swarms was finally prevented by the unfavourable weather.

5. *Time of replacement of original queen*

In none of the three swarming colonies did the swarm depart as early as expected, that is, soon after sealed queen cells were present, or even by the time that the first queen emerged.

Colony 29 in 1962 did not swarm until July 25, although the first of a succession of young queens emerged on July 18; the old queen had ceased to lay (and was presumed dead) on July 20, and the swarm was thus left with a young queen. In 1964, colony 15 was even slower to swarm at a time when weather conditions seemed quite suitable. Here the old marked queen was observed on June 30, when

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* Supersedure is the process in which a young queen is reared in the presence of the old queen, and subsequently replaces her without the emergence of a swarm (see Butler, 1957).

one young queen was just beginning to emerge from her cell. No eggs were laid after July 1, and the old queen was not seen again. For the next 5 days a close watch was kept on the hive (plus an examination of the colony on July 5), but no swarm emerged, although the agitated flying in front of the hive which is often associated with the departure of the swarm was observed. On July 10 the colony was again examined, and still contained 9 sealed queen cells. It did not have the appearance of having swarmed, but it was possible that the emergence of young

TABLE 2. Number of queen cells in colonies in which a young queen emerged during the following week

Colony No.	*Date*	*Total no. queen cells*	*Notes*
27	31.5.61	2	superseded
5	13.7.61	5 (+ 5)*	,,
15	6.7.61	1	,,
16	13.7.61	2	,,
12	14.7.61	1	,,
29	21.7.61	1 (+ 3)*	,,
16	18.7.62	7	,,
19	18.7.62	7	,,
20	18.7.62	17 (+ 2)*	,,
23	18.7.62	11	,,
29	18.7.62	33	swarmed
7	25.7.62	14 (+ 1)*	superseded
1	31.7.62	28 (+ 1)*	,,
4	30.6.64	4	,,
15	30.6.64	36	swarmed
16	8.7.64	29	,,
36	14.7.64	4	superseded
11	*a* 28.7.64	*a* 4	*a* queen failed to mate
	b 3.9.64	*b* 5	*b* superseded

* Numbers added in brackets are of sealed cells cut down by the bees.
Colony 15 in 1962 is omitted from the Table because supersedure occurred after regular examinations ceased.

workers might have disguised the loss of a swarm on one of the three preceding days (when it had not been possible to inspect the hive quite as frequently). The observations were therefore concluded. (This colony was not moved from the original site at Ashtown with the other colonies at the end of June, in order to avoid disturbance at a critical time.) In the other colony (16) which swarmed in 1964 the old queen was seen on July 8, when 29 queen cells were present (18 sealed), and two days later a queen trap of the design described by Gary and Morse (1962) was fitted to the hive entrance. At the next examination on July 14, 2 dead virgin queens were found in the trap and 2 queen cells had hatched. The old queen was not found on this date, nor were any eggs or young larvae present in the colony, and it was deduced that she had been killed by the bees about July 9. Another 2 dead virgin queens were found in the trap on July 17, and the swarm left between then and July 21.

In many of the colonies which superseded, the original queen was apparently killed about the time the replacement queen emerged, but it is known that a mother and daughter queen co-existed for a time in seven colonies. (There seemed

TABLE 3. The production of new queen cells in colonies from mid-May to mid-August

		No. times new queen cells were recorded during routine examinations 1	2	3	4	5	*Totals*
1961	No. of colonies	5	6	2	2	3	18
	New queen cells recorded on	June 15 – July 14	May 22 – July 7	June 15 – July 7	May 31 – July 14	June 8 – July 7	May 22 – July 14
	Total no. new queen cells recorded per colony	1 –10	3 – 6	7 – 13	4 – 20	11 – 18	1 – 20
	Mean	3	5	10	12	15	7
	Notes on colony development	1 supersedure 4 did not replace queen	3 supersedures 3 did not replace queen	1 supersedure 1 did not replace queen	2 did not replace queen	1 supersedure 2 did not replace queen	6 supersedures 12 did not replace queen
1962	No. of colonies	6	1	4	3	1	16*
	New queen cells recorded on	June 27 – August 17	July 26 – July 31	July 4 – July 18	June 13 – August 17	June 13 – July 26	June 13 – August 17
	Total no. new queen cells recorded per colony	1 – 7	28	7 – 47	5 – 32	14	1 – 47
	Mean	3	—	22	16	—	13
	Notes on colony development	6 did not replace queen	1 supersedure	3 supersedures 1 swarm	1 supersedure 2 did not replace queen	1 supersedure	6 supersedures* 1 swarm 8 did not replace queen
1964	No. of colonies	1	1	3	—	1	6†
	New queen cells recorded on	June 30	June 30 – July 28	June 17 – July 21	—	June 10 – July 8	June 10 – July 28
	Total no. new queen cells recorded per colony	2	4	7 – 38	—	10	2 – 38
	Mean	—	—	27	—	—	16
	Notes on colony development	1 did not replace queen	1 did not replace queen	1 supersedure 2 swarms	—	1 supersedure	2 supersedures 2 swarms 2 did not replace queen

* In 1962 Colony 15 is omitted, since supersedure did not occur until late August or early September, although queen cells were produced intermittently from July 4 onwards.

† In 1964 Colony 11 is omitted, since supersedure did not occur until early September, after the disappearance of the first young queen in early August (queen cells from June 30 to September 3).

to be a tendency for the old queen's egg production to fall temporarily at about the time of the young queen's emergence.) Five of the daughter queens emerged during July, and two in late August or September. Sometimes co-existence lasted only until the young queen was mated, but in other colonies it continued after this. In these, and in other colonies noted before these observations, the original queen disappeared from the colony during the winter, and by the spring the daughter was the only queen remaining.

The majority of supersedures took place in July, but the earliest was on June 1 (in 1961), in a very small colony whose original queen had seemed to be laying at the maximum rate possible, in view of the limited number of bees in the colony. The latest supersedure was recorded in September (1964) in Colony 11, which had been fitted with a queen trap at the hive entrance (see earlier) on July 28 when it had 3 unsealed queen cells in addition to another cell which had been sealed for a week. After the trap had been in position for a week it contained no dead queens, and the old queen was still present in the hive; one queen had hatched and the other cells had been cut down by the bees. Egg laying continued, but on September 3 there were 2 unsealed and 3 sealed queen cells. On September 11 the original queen was found dead in the trap, and the new young queen was seen in the colony. There was no evidence of young queens being killed after emergence, and the retention of the old queen saved the colony from queenlessness when the first young queen disappeared, presumably on a mating flight.

The age at which 12 of the young queens started to lay was known fairly accurately; it varied from 15 to 36 days. Eight of these queens began to lay when less than 25 days old.

6. *Production and destruction of queen cells*

Table 2 shows that sealed queen cells which were partially damaged (or 'cut down') by the bees were found in some of the colonies replacing their queens. Unsealed queen cells were found damaged in the same way, with their contents similarly destroyed. In addition, the weekly records included details of the stage of development of each queen cell, and it was possible to deduce the fate of each cell from these, since the duration of each period of the queen's development is known. In many cases, particularly in 1961 and 1962, a picture emerged of 'young' queen cells (containing eggs and young larvae) being destroyed, only to be replaced in the following week by further new queen cells. Sealed cells were also destroyed, but to a lesser extent. Incidentally, the assumption made here is that when the contents of a queen cell are destroyed the cell itself is also at least partly destroyed (see Allen, 1956).

A summary of the results is given in Table 3, which shows the total number of *new* queen cells found at each examination, and also the number of times such new queen cells were recorded in each colony. Since the examinations were not made more than once a week, other queen cells may have been started and destroyed in the intervening days without being observed, so these figures can be regarded as minimal. As might be expected, colonies with queen cells at only one examination produced fewer cells than those with a longer duration of queen rearing; they also tended not to replace their queens. Queen-cell production was generally higher in colonies where the process extended over two or more weeks, but the numbers varied greatly in different colonies. The highest total production of queen cells occurred in the three which swarmed.

7. *Age of queen and probability of replacement*

The number of colonies producing queen cells was considerably greater in 1961 and 1962 than it was in either 1963 or 1964 (Table 1*b*). Many of the colonies were small in 1963 and the weather was not favourable, but in 1964 the colonies developed normally and were strong, so colony size was apparently not the chief limiting factor in queen rearing. However, in both these years, and particularly in 1963, the average age of the queens was lower than in 1961 and 1962 (Table 1 *g*). The number of colonies replacing their queens was not sufficient to allow a very definite conclusion on the effect of the age of the queen, but the proportion of replacements was lower among the queens 1 year old than among those 2 or 3 years old, and no colony with a queen of the current year produced queen cells (Table 1 *g, h, i*).

8. *Influence of the amounts of brood on queen-cell production*

As Simpson (1958) pointed out, several authors have suggested that larger colonies will have a greater tendency to swarm than small ones, and Simpson quotes his own unpublished observations for one year in which the mean size in May of colonies subsequently producing queen cells was significantly greater than that of colonies not producing such cells. In the present work the incidence of queen rearing was examined in relation to the maximum amount of worker brood present in May, since the amount of brood gives a useful indication of colony size (see Allen & Jeffree, 1956).

The number of colonies without any queen cells in 1961 and 1962 was too small to be representative (Table 1 *a, b*), although in both years their mean amount of brood in May was smaller than that in the colonies rearing queens. In 1963 only one colony had queen cells. In 1964 the amount of brood in May in the queen-rearing group just failed to be significantly greater than in the group with no queen cells. The same trend was apparent when the production of *sealed* queen cells was correlated with the May brood amounts in 1961, 1962 and 1964, but it was likewise not statistically significant. It therefore seems that although there may be a greater tendency for colonies with larger amounts of brood in May to produce queen cells, this is by no means the only factor influencing the process. Variability between colonies in both groups was, in fact, considerable.

The mean brood-rearing statistics for the colonies which (1) replaced their queens, and (2) did not replace their queens, during the active seasons of 1961, 1962 and 1964 are compared in Fig. 5. Mean worker brood amounts reached a peak more rapidly in the queen-replacing colonies, but the results for the individual years show that this trend is not a constant feature: it was not apparent in 1961, and was rather more marked in 1964 than in 1962. In 1964 the two swarming colonies contributed considerably to the earlier increase of the queen-rearing group, for they developed very rapidly to a large size. The single colony which swarmed in 1962 also had large amounts of brood fairly early in the season, although it had slightly less than one of the colonies which superseded its queen.

Amounts of drone brood were not appreciably different in the two groups shown in Fig. 5, and only in 1964 was there more drone brood in the queen-

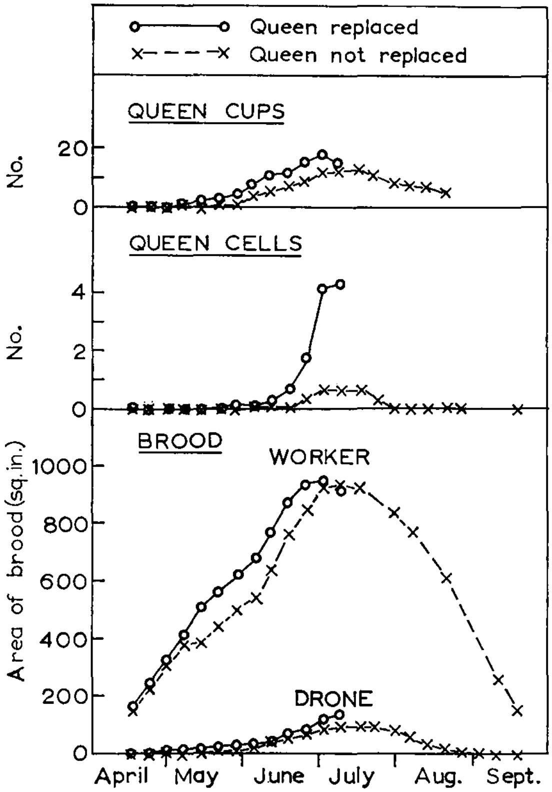

FIG. 5. Mean production of brood, queen cups and queen cells per colony when the queen was replaced, or was not, replaced during the season (1961, 1962, 1964)

replacing colonies; the other two years showed no differences between the groups. Queen-cell numbers reached a considerably higher peak in the queen-replacing group in all years, and queen-cup numbers tended to be higher also.

DISCUSSION

Previous work over a number of years on colonies at the same sites as those in the present investigation showed that the number of bees in colonies, the production of worker and drone brood, and even the amount of pollen stored in the combs, followed annual cycles with peaks normally occurring during late June or July (Jeffree, 1955; Allen & Jeffree, 1956; Jeffree & Allen, 1957; Allen, 1958, 1963). These earlier investigations were made to establish the normal course of events in colonies throughout the year, and to some extent the present work has been an extension of this, although there has been more emphasis on a study of the detailed development of a specific group of colonies, with particular reference to the phenomenon of queen production.

It has been confirmed that the drone brood-rearing cycle is fairly closely related to the worker brood-rearing cycle, but that it is of shorter duration and more liable to sudden variations. It has also been demonstrated that there is a well defined cycle of queen-cup production, with a timing similar to that of the drone brood cycle. The formation of queen cups appears to be a normal part of the colony's development and does not necessarily indicate that any queen cells will be formed subsequently; this is shown by the fact that only half the total number of colonies attempted to rear queens, although all produced some queen cups. Simpson (1959), in a rather similar investigation of queen-cup production, found that 50% of the colonies he studied during one summer had queen cups in early May and nearly all had them during June and July, which corresponds fairly closely with the state of affairs recorded here for 1961 and 1962, and slightly less closely with the results for the earlier parts of 1963 and 1964, although by July the picture for these two years was very similar once again (Fig. 3).

The approximate synchronization of the cycles of worker and drone brood rearing, and of queen-cup production, implies that there is an inherent annual cycle of colony development, whose timing in different years may be to some extent dependent upon weather conditions. Simpson's view (1959) that brood rearing begins to decline in August because of the lack of forage plants at that time cannot apply to the results quoted here, for the main nectar flows of the year for the colonies studied in the present work occurred in July and August, at and after the brood rearing peak. In fact, it is noteworthy that both in the south of England (Simpson, 1959) and in northern Scotland the first major decline in brood rearing normally occurs in August, despite the marked difference in the availability of foraging plants and the lesser difference in climate. Neither can the decline be attributed to shortage of brood-rearing space caused by the accumulation of nectar, since all the colonies in the present observations had ample space.

The timing of queen rearing was less predictable than that of queen-cup production and of brood rearing, and it varied in different colonies. In spite of this, the mean annual curves had peaks which fell within the peak periods of brood rearing. Simpson (1957*a*) gave curves of queen-cell production in colonies which did not replace their queens in the years 1950 – 53, and the timing of their peaks in the different years varied over a very similar period to that found in the present work. Subsequently (1959), apparently commenting on the approximate synchronization of queen rearing and the brood-rearing cycle, he stated that the maximum tendency of swarming colonies to rear queens occurred at about the same time as the maximum brood rearing period in non-swarming colonies, and that more colonies started to rear queens when their brood was increasing than when it was declining.

Prior to the present investigations, routine measures designed to prevent swarming had been used in the Departmental apiary, and it was expected that their absence would result in a considerable incidence of swarming. The results obtained came as a surprise: only 3 colonies swarmed out of a total of 81 in the four years, or 3 out of 62 if 1963 is excluded. Even taking into consideration the 16 colonies which superseded their queens, the number of queen replacements was still very small.

The number of colonies producing queen cells at some time during the summer was more than double the number replacing their queens (Table 1); it is therefore evident that many queen cells were destroyed by the bees, as Simpson (1957*b*) also found. Further evidence of this was revealed by the individual results (Table 3), and the repeated destruction and rebuilding of queen cells is known to have occurred on a number of occasions. There was also evidence from a swarming colony fitted with a trap for dead queens that virgin queens were sometimes killed by the workers, although when such a trap was fitted on a superseding colony no dead virgin queens were recovered. Gary and Morse (1962) demonstrated that the destruction of virgin queens by the workers may occur fairly commonly, since 4 out of the 7 colonies with normal histories studied by them threw out dead virgin queens into their queen traps. One of these four colonies apparently did not replace its original queen; two superseded in May and June respectively, and some virgins were killed before laying queens were found in the traps; the remaining colony swarmed (with a virgin) in June after both a virgin and the laying queen had been killed. In these last three colonies further dead virgins were recovered subsequent to swarming or supersedure, and in one the young laying queen was killed three months later. Both this work and that described in the present paper show that queen replacement is by no means a straightforward process, and may be subject to many delays. Gary and Morse unfortunately did not state if weather unfavourable for the departure of swarms might have contributed to their result, nor did they give the ages of the original queens of their colonies.

It is difficult to judge how important the weather and the age of the queen were in influencing the production of queen cells, and also the subsequent fate of the occupants, but it seems likely that both factors had some effect. Simpson (1957*a*) showed that the proportion of colonies not producing any queen cells can vary with locality and year, and he concluded that the probability that a queen would be replaced increased with her age. A similar indication was given by the present work, for no colony with a queen of the current year produced queen cells, and colonies with queens 1 year old had a lower queen-replacement rate than those with queens 2 and 3 years old (Table 1). Although the poor summer of 1963 undoubtedly affected the colonies, a number of which were bordering on starvation in July, the great lack of queen rearing that year may well have resulted largely from the very high proportion of young queens.

The effect of the weather is not easy to determine, since several factors are involved and it is difficult to judge which is the most important. An attempt has been made in the present work (see Appendix II) to assess the prevailing weather from the meteorological data available, and it is clear that the weather in June and July, when queen-cell production was most common, was not outstandingly good in any of the four years. Apart from 1964, the tendency was for below-average temperatures, and in 1964 there were many days of high winds which must have affected foraging. Honey yields confirmed that July 1963 was very unfavourable for foraging and that none of the other three years was especially favourable. It is unfortunate that none of the summers could be classed as particularly good for honey production.

There is every reason to suppose, however, that the 1961, 1962 and 1964 summers did not prevent the colonies from developing normally; and in 1964 they reached an unusually large size, with brood rearing continuing at a high level in August. From this point of view one might expect queen-cell production to have been at a fairly normal level (or even higher) in 1964, since there seems to be some tendency for increased colony size to encourage queen rearing. However, the level in 1964 was considerably lower than in 1961 or 1962, when the majority of colonies produced queen cells, and one cannot be certain if this was again an effect of the generally lower age of the queens in 1964 or whether it was due to some other factor.

The higher proportion of swarms to supersedures in 1964, as well as the much lower incidence of abortive queen rearing in this year as compared with 1961 and 1962, may well have been related to more favourable weather conditions, although the delay in the departure of both swarms in 1964 suggested that conditions were not highly favourable. If unsuitable weather was the reason why only one swarm departed in the first two years it would not have been surprising if the queen-rearing colonies in these two years had built large numbers of queen cells in preparation for swarming but had finally cut them down, perhaps after superseding the original queen. In 1962 there was some evidence that this was the case, but in 1961 the number of queen cells per colony was small, indicating that supersedure was more likely to take place than swarming. Indeed, it is still not entirely clear why a colony should supersede rather than swarm, or vice versa, particularly since the present results show that supersedure may often occur during the normal swarming season, as well as earlier or later; its incidence is clearly not governed entirely by the time of year.

APPENDIX I

NECTAR AND POLLEN SOURCES

In the earlier part of the year minor nectar flows occurred in the locality of the Departmental apiary (Ashtown), about 10 km. north-west of Aberdeen, but the area did not provide good foraging apart from plentiful supplies of pollen from broom (*Sarothamnus scoparius*) and gorse (*Ulex europaeus*). In 1961, 1962 and 1964 the colonies were moved at the end of June from Ashtown to a heather moor near Dinnet, about 50 km. west of Aberdeen on Deeside, for the flowering period of bell heather (*Erica cinerea*) during July and of ling heather (*Calluna vulgaris*) during August and early September. In 1963 the colonies were moved from Ashtown on June 20 to fields of raspberry (*Rubus idaeus*) about 40 km. south-west of Aberdeen near Fettercairn, Kincardineshire; from there they were moved to Dinnet Moor on July 10, when the bell heather was just beginning to come into bloom in this unusually late summer.

APPENDIX II

WEATHER CONDITIONS

The weather is clearly of considerable importance to bees, both directly and indirectly. Flight activity is favoured by high temperatures and low wind speeds (few bees fly at a wind speed of more than 13 knots [21 km./hr.]—Wedmore, 1946) and also by the absence of long periods of heavy rain. Nectar secretion is also normally increased by high temperatures; on the other hand it may be decreased severely in periods of drought. It is, therefore, not a straightforward matter to correlate weather conditions with the amount of successful foraging carried out, although data on such factors as temperature and rainfall provide useful indications. The 'earliness' or 'lateness' of the spring, as judged by the flowering times of certain plants (see Jeffree, 1960), also affects the development of colonies, perhaps largely because of the differences in the timing of nectar and pollen supplies. Certainly it has been found in this Department (unpublished) that colonies at a good spring foraging site increased in size more rapidly, and tended to produce queen cells earlier, than colonies at a poor spring site only a few miles away. Very poor weather during the summer (as in 1963), with a corresponding shortage of nectar, may prevent the colonies building up to normal strength, and drone brood and queen cells may be destroyed at such times (see Allen, 1956, 1958).

By comparing the yields in the different years of honey from bell heather (July) and ling heather (August – early September) some indication of the relative foraging conditions prevailing at the time can be obtained, although the estimates are necessarily not highly accurate. The mean amount of bell heather honey extracted per colony was 8 kg. in 1961, 16 kg. in 1962, nil in 1963, and 15 kg. in 1964. The corresponding figures for ling heather honey were 8 kg. in 1961, 3 kg. in 1962, nil in 1963, and 7 kg. in 1964. One would deduce from these yields that foraging conditions in July were more favourable in 1962 and 1964 than in 1961 or 1963, and that August and early September were better in 1961 and 1964 than in 1962 or 1963. The poor honey production in 1963 was probably attributable not only to the weather, but also to some extent to the smaller size of the colonies; this has been discussed in the main part of the paper. A subjective comparison, using experience gained at the same site on previous years, suggests that total yields (of bell and ling heather honey) were moderate in 1964 and 1962, that 1961 was a rather poor year, and 1963 exceptionally bad.

In 1964 a thermograph in a Stevenson screen was installed near the colonies throughout the period of the observations, but for a comparison of meteorological conditions in all four summers, and also for records other than temperature, data for Dyce Weather Station (only 3½ km. from Ashtown Apiary) were abstracted from the Daily Weather Report, and are given in Fig. 1 as means for 7-day periods. Mean temperatures were derived from the day maxima and night minima, mean rainfall from the daily totals, mean wind speeds from the records at 12 hr. and 18 hr. each day, and mean monthly sunshine percentages from the Monthly Summaries. It is known that local variations in weather may be considerable, and that these figures do not therefore necessarily give an exact representation of the conditions where the colonies were situated, particularly while they were at Dinnet Moor in July, August and early September; they do, however, give some indication of the type of weather prevailing in the area. The 1964 thermograph records showed, in fact, that the general trends in temperature fluctuations were similar to those at Dyce throughout the season, although actual temperatures recorded were usually lower at the two apiary sites.

Temperatures shown in Fig. 1 for 1961, 1962 and 1963 tended to be rather below average in June, July and August, but in 1964 they were rather above average. Rainfall amounts were mostly below average in the early part of the year (apart from a very wet spell in June 1963), but rose above average in August. In 1964 the wind speeds during the daytime were generally higher than in the other three years, a fact which was very noticeable when making observations on the colonies; 1962 also had fairly high winds, although they dropped somewhat in July. Monthly sunshine totals were only noticeably above average in July 1964, and they were considerably below average at times in 1961, 1962 and 1963. The general conclusion from these figures seems to be that none of the four summers was exceptionally favourable for bees, but that 1964 was the best, although in this year the effects of the low rainfall and high winds were not advantageous. The fact that more honey was not produced in this year was probably related to these two factors. It is surprising that conditions in July 1962 appear to have been worse than in the same month of 1961, since the honey yields point to the opposite conclusion; no explanation can be offered, apart from the possibility of a marked local difference between the climates at Dinnet Moor and Dyce.

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