CROP CONTENT AND POLLEN LOAD STUDIES OF HONEY BEES

A Thesis

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by

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ABSTRACT

A study was done in 1969 - 1970 to determine the effect of several environmental factors on the crop contents and pollen loads of worker honey bees. The following were obtained: weather data, flowering dates of the major sources of pollen and nectar, daily changes in colony weights and pollen income through the use of scales and pollen traps, and records of colony growth throughout the season.

The crop contents of worker bees (grouped according to duties performed) were investigated for weight, sugar concentration and pollen content. Pollen load weights were also obtained.

Certain general trends became evident. The weights of crop contents obtained in 1969 can be expressed as follows: workers on open honey> workers on open brood> nectar foragers entering the colony> pollen foragers entering the colony> foragers leaving for the fields. In 1970, however, the nectar foragers carried more food in their crops than did workers caught on open brood, but less than did those caught on open honey. Pollen foragers in that year carried more food than did workers caught on open brood, in July, only. Consistent differences in crop weights according to time of day were not found.

Seasonal trends for crop weights for both years were similar. In all groups of bees the lowest weights occurred

during June. Crop weights in nectar foragers corresponded to the daily net colony gain. The amount of food retained by hive bees increased in July and remained at a high level for the remainder of the season. The honey stomach weights of foragers leaving remained at the same level throughout the season.

Seasonal trends in sugar concentration of the crop contents varied with location from which the bees were collected. In nectar foragers the sugar concentration reached its highest level during the nectar flow, and decreased when the flow ceased; in pollen foragers and foragers leaving their colonies there was a slight decrease in concentration over the season, and in workers collected on open brood and on open honey the sugar concentration increased in July and remained at a high level for the remainder of the season.

Pollen load weights did not show any seasonal effect, nor were definite seasonal trends observed in pollen concentration of the crop contents. In general, the pollen concentration was highest in the spring but tended to fluctuate at lower levels for the remainder of the season. As in crop weights and sugar concentration of crop contents, there appeared to be a definite relationship between pollen concentration of the crop contents and the location in which workers were collected.

The effect of various factors on the rate at which

pollen is filtered out of suspension in the crop contents by the proventriculus of worker honey bees was investigated. The following factors were found to significantly affect the rate of filtration: the length of time a pollen suspension is retained in the crop, environmental temperature, and very high sugar concentration.

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CHAPTER I

INTRODUCTION

An abundant supply of both food (pollen and nectar or honey) and water throughout the brood rearing season is a prime requisite for the normal development of a productive honey bee colony. Although adult bees are able to live on a pure carbohydrate diet, pollen is required for the development of the hypopharyngeal glands, fat bodies, and other internal organs, as well as for the elaboration of royal jelly and of brood food. Water is required both for the dilution of honey, as well as the regulation of brood nest temperature.

The present study was designed to determine possible relationships between various environmental factors operating both within the colony and externally to it, and the quantity and quality of food retained by individual honey bees at various locations within the honey bee society. An understanding of some of these relationships will enable beekeepers to manage their colonies more effectively, thereby increasing their value, both for honey production and for pollination.

The balance between food supply and colony development is particularly sensitive when colonies are small. Each spring, in Canada and in the northern United States, approximately 500,000 two-pound packages of bees, each containing between 7,000 to 9,000 workers and a queen, are

CHAPTER II

METHODS AND MATERIALS

The investigations were done during the summers of 1969 and 1970, on the experimental field plots of the Department of Plant Science, and in the Department of Entomology, University of Manitoba. The same general method was followed in both years; differences between years consisted primarily in the number of times honey bee samples were collected throughout the season, the dates of sampling, and the number of samples taken on each sampling date.

Hiving, Hiving Dates, Strain, and Location of Yards

On 20 April, 1969, and again on 14 April in 1970, 8 commercial two pound packages of a yellow strain of bees were hived into brood chambers containing similar quantities of pollen and honey. Starline hybrid queens obtained from commercial queen breeders in the Southern United States were used to replace the queens in all colonies. These were used in order to obtain relatively homogeneous populations and in order to reduce inter-colony differences with regard to colony growth and bee behaviour.

The colonies were placed, in two equal groups (A and B) into locations approximately $\frac{1}{2}$ mile apart. The four colonies of Group A, from which all honey bee samples were taken, were placed on beam scales, facing South, and at

least twenty five feet apart, in order to reduce inter-colony drifting to a minimum. Weight changes were recorded daily, starting on 15 May in 1969, and on 8 June, 1970, respectively.

The B group of colonies was used to obtain supplementary information on daily pollen and nectar income. The group consisted of one colony on a scale, two colonies on OAC pollen traps (See below), and one colony held in reserve. Several reserve Starline queens were maintained in small reserve colonies called "nuclei".

The pollen trap colonies were provided with upper entrances, which were closed on alternate days in rotation so that while pollen was trapped from one colony, the other was free to forage for its own needs. The total amount of pollen collected each day, as well as the average pollen load weight, were recorded. Average pollen load weights of the trapped pollen were obtained by counting the number of pollen loads in a five gram sample of the pollen collected. Pollen trapping was initiated on 1 June, 1969, and on 22 June, 1970. In addition to the data on nectar flows, pollen income, and honey plant blooming periods, a record of daily temperatures extremes was obtained from the official Department of Transport records maintained at the Winnipeg International Airport in both years. A comparison between the Department of Transport temperature records and those

obtained at the Department of Plant Science Field Plots in 1969 show no significant differences. Daily cloud cover and wind conditions were also recorded.

Management of all colonies was carried out as for honey production. Second brood chambers and honey supers were added as required; the queens had free access to all hivebodies throughout the season.

Supplementary spring feeding was required only in 1969. At that time, 50% sugar syrup and pollen supplement consisting of trapped pollen, soybean flour, and sugar, in the ratio of 1:3:2 (Farrar, 1968) were given as required.

In the Spring of 1969 all colonies received two applications of medicated syrup containing fumagillin (for the control of nosema disease) and tetracycline to control a light infection of European Foulbrood. No medication was given in 1970, as no disease was observed.

In order to control swarming, increased ventilation was provided by offsetting supers, the brood chambers of all colonies making preparations to swarm were reversed and queen cells were cut (Cale, 1963; Farrar, 1968). These measures were not completely successful: in 1969 the scale colony of the B group swarmed, requiring the removal of the scale to the reserve colony (A-2) of the group.

In 1970, colony A-2 swarmed with a virgin queen reared under the emergency impulse, following the loss of

the original queen during hive manipulations. This colony was left to recover on its own and periodic collections of adult bees, as well as adult and brood estimations, were continued. Statistical analyses show that the data obtained from this colony do not differ significantly from data obtained from the other colonies. The results obtained from colony A-2 were therefore included in the total averages.

Queen Losses and Replacement

In 1969, three of the four experimental colonies retained their original queens throughout the season. The queen of the fourth colony, (A-2) became drone laying about three weeks after her introduction to the colony, and was replaced with another normal laying Starline Hybrid queen. In 1970, five queens were lost throughout the season. Except in the case of colony A-2, each queenless colony was requeened as follows: All queen cells were removed, and a laying Starline queen, together with her brood and all bees, were placed into the centre of the third story of the colony, using very little smoke. All of the queens introduced in this manner were accepted and continued to lay with very little interruption.

The reasons for the high rate of queen loss in 1970 are not clear. It seemed that in 1970 the bees reacted more excitedly to handling of the combs and hivebodies than they had in 1969; this may have been partly responsible for these

queen losses. However, Nelson (1971) also reported unusually high queen losses for a bee yard situated about five miles from the present location. This suggests that environmental factors operating over a wide area may also have had an effect.

Brood Measurements

Brood measurements, adult population estimations, and sampling, were carried out on a twelve day (±1 day) cycle, starting on 26 May in 1969, and on 1 June in 1970, respectively. A twelve day interval between readings was chosen to allow all sealed brood measured on one reading date to emerge before the next, thus avoiding a double count of sealed brood areas. Both brood measurements and adult estimations were carried out on the day following the collection of bee samples in order to avoid biasing the data due to disturbance of the colony.

In 1969 the brood was measured by tracing outlines of the areas of comb covered by each stage (eggs, larvae, and pupae) onto sheets of plastic. The total areas of brood present were obtained by superimposing a square inch grid over the plastic sheets. This method was discarded in 1970 as being too cumbersome, and the system devised by Smirl (1970) was adopted instead. The brood outlines were drawn directly onto sheets of glass ruled in square inches. An assistant then tallied the amount of each stage present, in

the field, and cleaned the glass. The values obtained throughout the season were plotted for each colony. Because drone brood was not present in large quantities, areas containing eggs, larvae, and sealed brood were not counted separately, but were included in 'Total brood' measurements (Figures 18 through 25). The numbers of queen cells present were recorded.

Adult Estimations

Adult estimations were made on the same days on which the brood counts were obtained, usually between 6:30 and 9:30 A.M., i.e. before large numbers of bees flew from their hives. The technique used was one originally developed by Jeffree (1957) and later modified for Langstroth frames by Nelson (1971). It consists of gently removing each frame from the hivebodies without the use of smoke, and estimating the number of bees on it against a chart showing photographs of combs with known numbers of bees (Figure 1A). Two persons cooperated for each estimation. An assistant removed the frames from the hive and held them for the estimator.

Large numbers of bees can be estimated in this manner within a short time and the manipulations, if performed with care, do not disrupt the normal activities of the colony to a significant extent. Similar observations were made by Free and Spencer-Booth(1963). Tests with 15 observers (Nelson,1971)

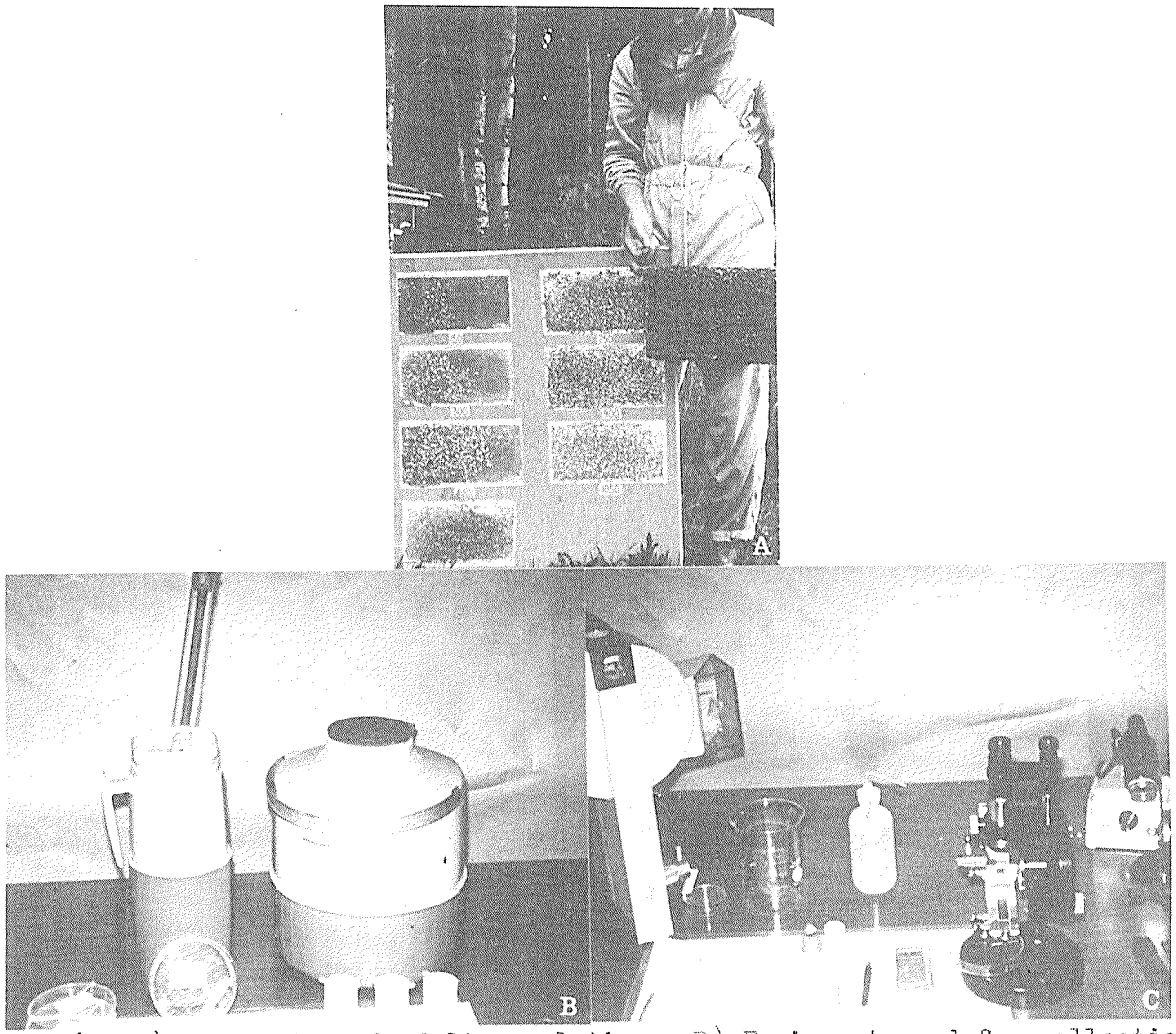

Figure **1** . A) Estimation of adult populations. B) Equipment used for collection of bees. Left to right: Thermos containing alcohol-dry ice mixture into which tube containing bees is immersed, insulated jug for storing vials containing bees while in the field. C) Instruments used in honey stomach analysis. Left to right: torsion balance, hemacytometer, refractometer, microscope.

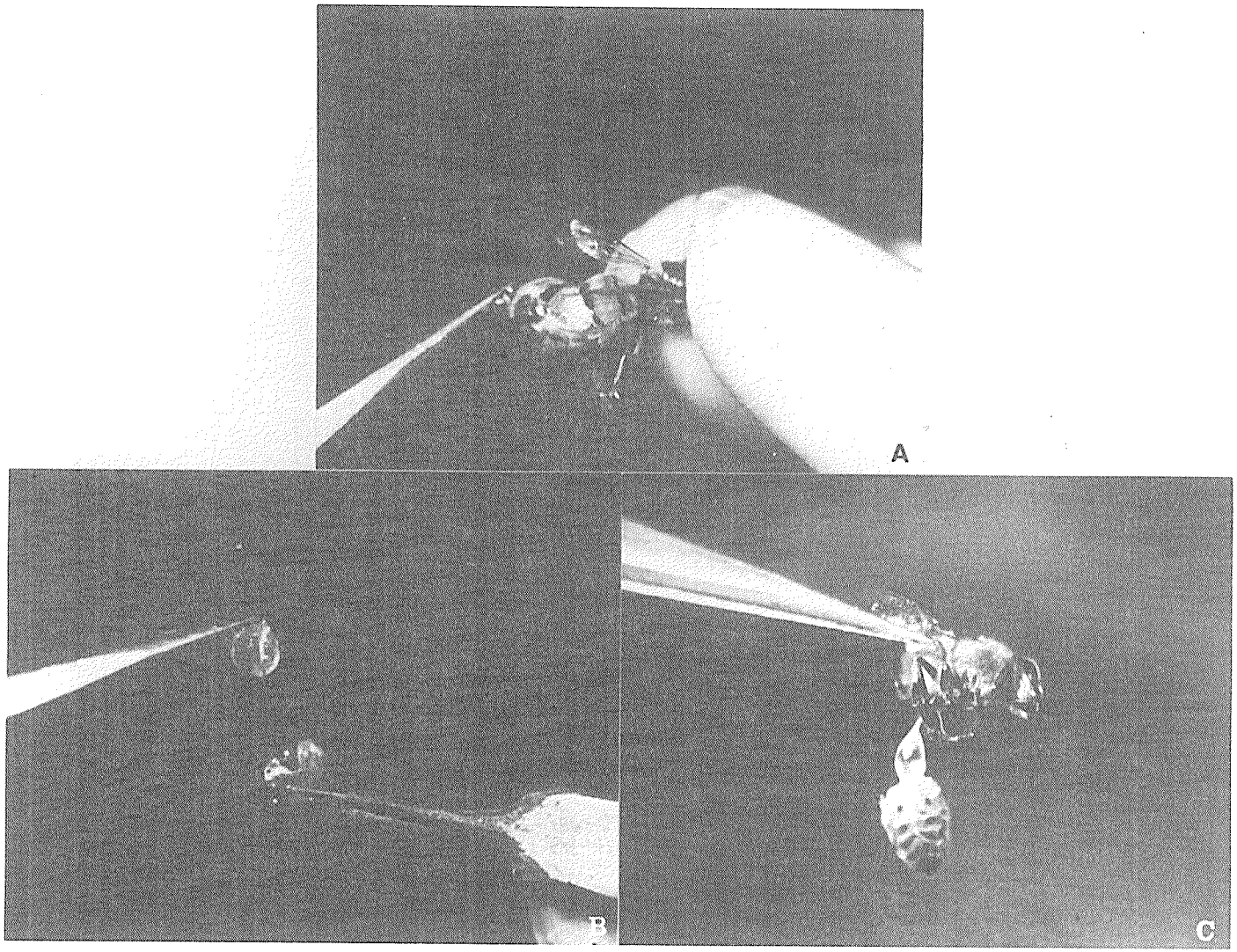

Figure 2 . Dissection of a honey bee worker. A) Honey stomach exposed. B) Honey stomach completely removed from abdomen. C) Honey stomach partly removed from abdomen.

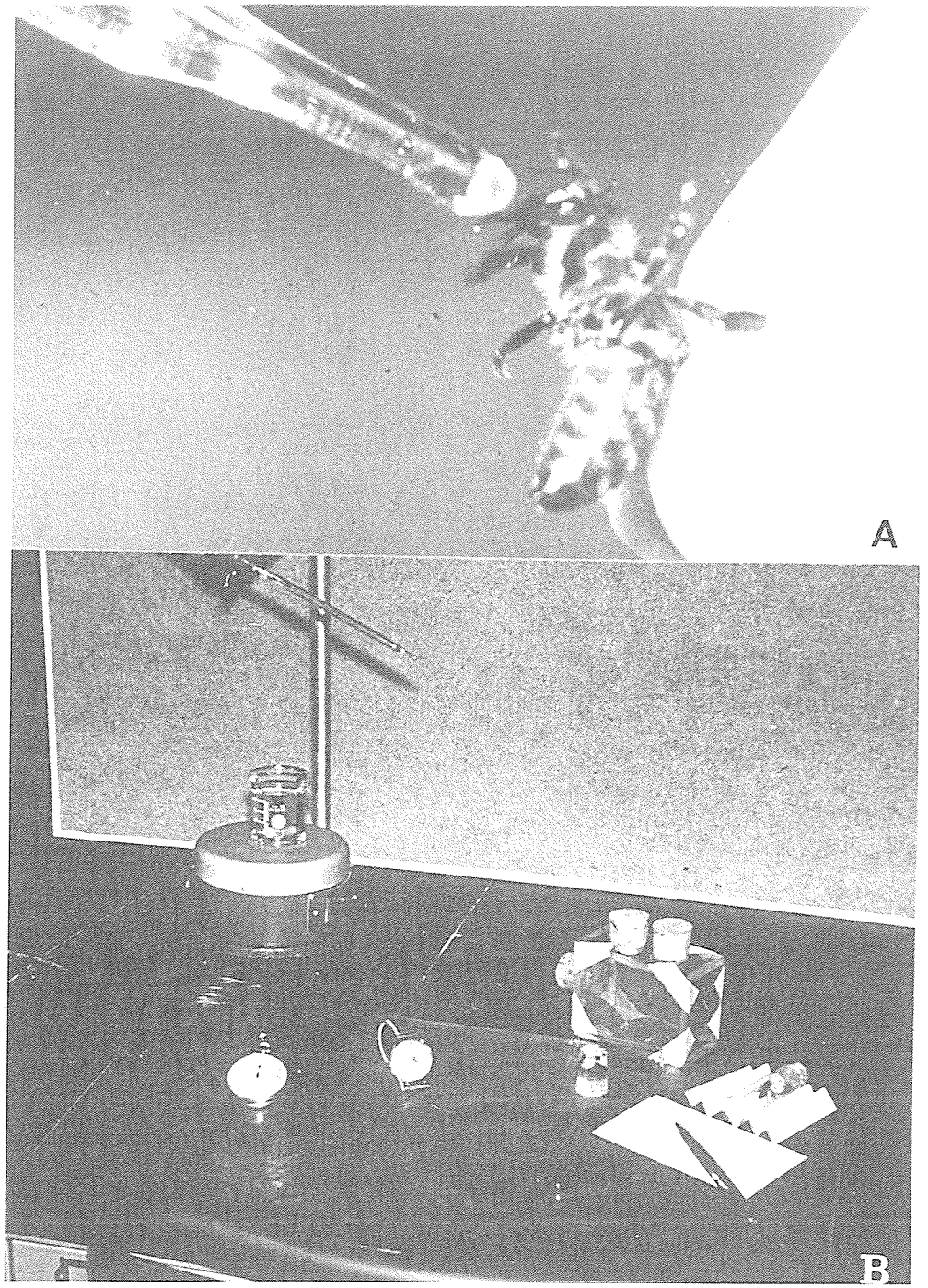

Figure 3 . Equipment used in filtration experiments. A) Feeding worker bee from micropipette. B) Equipment used: Left to right: Pipette (top), pollen suspension on magnetic stirrer, stop watch, cage containing bees, vial for holding bees after feeding.

have shown that the accuracy of estimating populations of entire colonies under normal summer conditions was usually within seven per cent of the actual number of bees present.

Killing Technique

It is essential that bees collected in the field for later analyses of honey stomach contents, be killed as quickly as possible in order to prevent the passage of the liquid or semiliquid material from the honey stomach both backward into the gut or forward through regurgitation. In his attempt to find a practical method of doing so, Feng (1969) experimented with various methods of killing small numbers of bees and included the use of cyanide, carbon dioxide gas, temperatures of -20 to -30 degrees F. (deep-freezer), -60 to -70 degrees F. (dry ice), and -195 degrees F. (liquid nitrogen). Of these, only the dry ice method proved to be of value for field studies. Consequently, this technique was used in the present study.

The bees were killed by placing them into ten-inch test tubes inserted into a mixture of dry ice and ethanol contained in a wide-mouth vaccuum bottle. A lid (plastic Petri dish with holes of the size of the test tubes) held the tubes in place (Figure 1B). When the temperature of the air in the tubes approximated that of the surrounding alcohol-dry ice mixture, individual bees were dropped into the tube where they died within about 20 seconds. Regurgitation did

not occur often enough to significantly bias the data obtained.

Several precautions were necessary. Bees held in the tubes for longer than approximately five minutes usually became so brittle that they fell apart before they could be dissected. Moreover, the honey stomach tissues also became very fragile, greatly increasing the difficulties of removing the honey stomach intact. Similar observations were made by Feng (1969).

In addition, as the number of frozen bees in the tubes increased, the time required for the bees to die also increased, resulting in a greater number of bees regurgitating part of their honey stomach contents. Care was taken, therefore, to empty the tubes frequently.

The bees were emptied into labeled plastic vials and were temporarily stored in picnic jugs containing dry ice (which was also used to recharge the killing jars whenever necessary) until they could be transferred to a deep freezer for storage to be analyzed at a later date. The bees can be kept in this way for several months, with little desiccation or change in the honey stomach tissues (Feng, 1969).

Since a primary objective of the study was to determine possible relationships existing between the environment of individual bees and the amount and quality of food carried by them, the workers were collected on the basis of the

work performed by them at the time of feeding.

While age is another factor which may influence food uptake (Free, 1957, 1967, 1968), it has been shown that worker bees of any age are capable of performing a variety of duties within a brief period of time, even of duties not normally falling within the sphere of work performed at that age (Lindauer, 1952; Sakagami, 1953). It appears that the work performed by a bee, rather than its age, is the dominant factor influencing its food uptake at any given amount; this factor was therefore chosen as the basis on which the bees were categorized.

Sampling

The following categories of bees were chosen for analysis in 1969 and were collected throughout the summer:

	Category	Symbol Used	Year Collected 1969	1970
Hive bees	Workers caught on open honey comb	HO	X	X
	Workers caught on sealed honey comb	HS	X	
	Workers caught on open brood comb	BO	X	X
	Workers caught on sealed brood comb	BS	X	
	Wax producing workers caught on comb foundation	Fo	X*	
Field bees	Nectar foragers entering the hive	FE	X	X
	Pollen foragers entering the hive	PFE	X	X
	Foragers (pollen and nectar gatherers) leaving the hive	FL	X	X
Others	Guard bees	G	X*	
	Fanners	Fa	X*	
	Drones	D	X*	

Table I . Categories of bees collected throughout 1969 and 1970. *Only a few samples were obtained. (See appendix).

As in 1969, the samples were collected throughout the season at approximately twelve day intervals. On several sampling dates in 1969, unfavourable weather inhibited foraging activity to the extent that some of the field bee categories could not be sampled.

The samples of 30 bees each were collected from each of the four colonies between 10:00 and 12:00 A.M., and again from 3:00 to 5:00 P.M. In order to avoid engorgement of honey by the bees, all hive manipulations were carried out without the use of smoke.

At each location, the individual bees selected randomly were picked up with forceps and dropped into the killing jar. Care was taken, when collecting hive bees, to avoid those engorging on honey at the time of sampling. All workers were taken as nearly as possible, from the centre of the comb area (i.e. open honey). It was not possible, however, to ensure that all workers caught on open brood, for example, had actually been engaged in brood-related activities at the time when the colony was being opened. This problem arose especially in the early summer and in the early fall, when the brood areas often were small and intermingled with open cells of honey.

When collecting foragers entering the hive, much time could be saved by blocking the entrance of the colony. The accumulation of both pollen and nectar foragers at the

entrance enabled two persons to work simultaneously without interfering with each other. At the same time the intermingling of aroused guards, foragers leaving the colony, and returning foragers, was avoided. Since the colonies did not remain closed for longer than twenty minutes at one time, problems caused by overheating did not arise.

One of the difficulties encountered in the collection of foragers leaving the hive was that of accurately distinguishing between foragers and guard bees. According to Butler and Free (1952), foraging and guarding of the entrance overlap chronologically in the age sequence of duties performed by worker honey bees and are frequently carried out by an individual on the same day. In this study, it was often observed that field workers, which appeared to be about to leave the hive, reared up suddenly to inspect an incoming worker landing nearby, or made an abrupt about-face to follow a returning forager into the hive. Similarly, workers, apparently on guard duty, sometimes suddenly ran to the edge of the hive entrance and flew away.

The difficulty in distinguishing between the two groups of bees was largely overcome by partially blocking the hive entrance, leaving only an opening large enough to permit the passage of two or three bees at one time. All of the foragers leaving the colony were funnelled through the opening, creating such a flow of bees outward that all

traffic into the colony was stopped effectively for several minutes at a time. Guard bees seemed to avoid the congested area; only occasionally was a worker observed to inspect incoming or outbound bees.

Analyses

On removal from the freezer, the bees were permitted to thaw out completely before dissection was begun. Since tissue breakdown may occur very quickly after defrosting, only as many bees as could be processed within twenty to thirty minutes, were removed from storage at one time.

The abdomen was opened by teasing apart the first and second segments with fine pointed forceps. This operation had to be performed with considerable care, since the relatively tough connective tissue between the honey stomach and the abdominal wall often did not break easily, resulting instead in a rupture of the honey stomach wall and loss of its liquid contents. (Figure 2)

Removal of the honey stomach through the posterior end of the abdomen, as was suggested by Feng (1969), was not attempted, since an accidental break in the midgut or rectum (both of which must be removed first) might have resulted in contamination of the honey stomach with pollen from the gut.

Each honey stomach was weighed to the nearest 0.5 mg. on a torsion balance before being placed into a receiving vial. A small, moistened sponge attached to the lid of

the vial maintained the relative humidity within the vial, and avoided a change in sugar concentration of the honey stomach contents over the time required to dissect the remainder of the sample. In all of these measurements the weight of the empty honey stomach was arbitrarily taken to be one milligram; the values shown in Tables 1 through (Appendix) minus one, represent the mean weights of the honey stomach contents for each sample taken. (Figure 1C)

The honey stomachs were crushed and their contents mixed well. Sugar concentration was determined by use of an Abbê refractometer ("Large Model", produced by Officine Galileo de Milano, Italy). The instrument used is calibrated for per cent of sucrose. However, since the difference between readings obtained for sucrose and for invert sugar is less than two per cent at the same temperature, (Fulmer et al. 1934; Snyder and Hallenburg, 1963), no correction factor was applied.

The concentration of pollen in the honey stomachs were determined by using a Spencer Brightline Double Rule Hemacytometer (improved Neubauer type) at a magnification of 150 diameters. All values are given in terms of pollen grains per mm^3 of liquid.

Single Bee Analyses*

In order to gain more detailed information about the sugar concentration and pollen content of the loads carried

* "Expanded samples" - appendix.

by bees in different locations of the colony, the samples collected on three sampling dates each year were designated for single bee analyses. The sampling dates chosen were such that one collection was taken prior to the honey flow, another fell into the period of the main flow, and the third collection was made after the main flow had ceased. The term nectar flow is defined as a period of nectar availability.

In the analyses of individual bees as in the more general analyses (see page 17), the honey stomachs were individually weighed. Then, fifteen of the thirty honey stomachs per sample were individually measured for sugar concentration and fifteen were inspected for pollen. If any load was large enough, both sugar concentration measurement, and a pollen count were obtained from it. However, in some of the groups collected (e.g. outbound foragers), many bees carried such small loads, that neither the sugar concentration nor the pollen content could be measured. In such samples it was frequently impossible to obtain 15 measurements.

Because many of the honey stomach loads obtained were too small to fill both sides of the hemacytometer and 0.5 mm^3 of liquid was used as the standard quantity in which pollen was counted. The values obtained were multiplied by two, in order to make them equivalent to the values obtained in the general analyses.

Because of the great variation in honey stomach

weights, the mean sugar concentration was determined as follows: The sugar concentration obtained for each honey stomach was multiplied by its corresponding weight. The sum of the products was then divided by the sum of the weights. In making this correction for volume, the weight of the honey stomach was used in the place of volume. The increase in volume of a sugar solution, caused by increasing its concentration, is very small and the difference may be disregarded.

To obtain the pollen load weights, the individual pollen loads were carefully removed from the two corbicula of the pollen foragers with fine-pointed forceps. The loads were weighed to the nearest 0.5 mg. on a torsion balance; the values given in the Appendix Tables represent the weight of pollen (two pollen pellets) carried into the hive by one pollen forager.

CHAPTER III

ENVIRONMENTAL FACTORS, ADULT AND BROOD ESTIMATES

Introduction

Most of the activities occurring within the honey bee colony are in some way related to the gathering, processing and storing of food (Free, 1967; 1968). In the summer, when both pollen and nectar are freely available in the field, much greater quantities than can be immediately utilized by the colony are gathered and stored by its workers. However, when no food is available outside of the colony, the bees, unlike most other insects, are able to remain active, living on food supplies stored in times of plenty.

The food gathering behaviour of the honey bee has been compared to the hoarding instinct of the white rat; in honey bees this instinct has been intensified through breeding (Louveaux, 1959). In both animals the drive to hoard is strongly influenced by the environment; it is dependent on a chronic lack of food, which in the honey bee is out of proportion to the actual requirements of the colony. This hoarding instinct holds for both pollen and for nectar. In the case of nectar, it results in large stores of carbohydrate reserves (honey), while in the case of pollen it results in increased brood rearing and an increase in the

adult population (Louveaux, 1959).

In order to understand more fully the food interrelationships occurring among the members of the honey bee community, it was necessary first to examine a number of the environmental factors influencing not only the individual bee, but also the colony as a whole. The factors investigated more closely include: (a) environmental temperature, (b) the daily amounts of both pollen and nectar brought into the hives, and (c) the amount of brood reared, and the resultant increase in population of each of the experimental colonies. These factors were recorded, and their relationships to each other and to the bees are discussed in this chapter.

The Effect of Temperature on Honey Bee Activity

Environmental temperature influences honey bee activity in several ways. Although individual honey bees are able to raise their body temperature above that of the environment (under some conditions by as much as 20 degrees C., Himmer, 1925; Esch, 1960) through muscular activity, they are able to do so only as long as they carry sufficient carbohydrate stores to meet their metabolic needs (Farrar, 1932). Workers lose the power to fly when their body temperature reaches approximately 50 degrees F., and at about 45 degrees F. they chill and die (Himmer, 1926; Haydak, 1963). The effects of low temperature are avoided by the

colony through the formation of a heat conserving cluster, which forms at a temperature between 65 degrees F. and 57 degrees F. (Wilson and Milum, 1927; Haydak, 1963; Farrar, 1963).

The upper lethal temperature for caged worker bees is between 118 - 122 degrees F. and varies to some extent with relative humidity and access to water (Free and Spencer-Booth, 1962). Although isolated instances of honey bees' continuing to forage at or near these temperatures have been reported (Lensky, 1963), workers generally cease normal activities and remain idle within the hive, or cluster listlessly on the outside when the temperature reaches about 100 degrees F. This, according to Dunham (1931a), is not due to an effort on the part of the bees to control the temperature within the hive, but rather is probably a direct response of the bees to the high temperature.

In a colony which is actively rearing brood, a temperature of 93.5 degrees F. is normally maintained in the brood nest (Dunham, 1931a, 1931b). Although this temperature usually is very constant, a sharp change in external temperature may be followed by a corresponding change in the temperature of the brood nest centre; this change can be as much as 1.5 degrees F. (Dunham, 1931a). In the same series of experiments, Dunham also found that high external temperatures may reduce the rate of oviposition.

The temperature of the outer, marginal area of the brood nest is generally somewhat lower than is that of the center, and is more subject to fluctuations induced by external temperature changes. The temperature in the broodless area of the colony shifts (the extent depending on the strength and condition of the colony) with the rise and fall of the external temperatures (Dunham, 1929). Dunham (1931b) suggests that the much lower temperatures of the area surrounding the brood, together with the constant interchange of worker bees with different body temperatures take heat from the marginal brood area, resulting in the reduced temperature there.

A very high brood nest temperature is counteracted by the bees through the evaporation of water and by increased fanning (Dunham, 1931a). This, in turn leads to an increase in the numbers of bees foraging for water, or nectar of very low concentration (Lindauer, 1955). On the other hand, decreasing temperatures result in the formation of a heat conserving cluster in the brood area, and possibly in increased heat production through muscular activity (Himmer, 1925). Decreased external temperatures, over an extended period of time, may result in the cessation of brood rearing in the marginal brood area, and if continued long enough, in a gradual reduction of the total brood area until brood rearing ceases altogether (Dunham, 1931b).

Environmental temperature also influences honey bee activity indirectly, through its effect on the growth rate of nectar and pollen yielding plants. In general, cool weather retards plant growth and delays flower opening and pollen presentation. Warm weather, on the other hand, stimulates the rate of plant growth and leads to an earlier flower opening and dehiscence of anthers which in turn leads to earlier foraging by the bees. (Synge, 1947; Percival, 1947; Parker, 1926). Percival (1947) observed that on any given day the peak of pollen collection coincided with the peak of flowering in the main crops.

The effect of air temperature on nectar secretion has probably been studied more than any other factor. Nevertheless, the results obtained by various authors conflict probably because of the difficulty encountered in separating the effects produced by temperature alone from those produced by other environmental factors, (Shuel, 1967). Thus, while Beutler (1930) found air temperature to have little influence on nectar secretion by Borago sp. and Asclepias sp., Lovell (1963) and Shuel (1967) found that temperature is an important factor affecting the secretion of nectar in many other plant species. This was also confirmed by Beutler (1953).

Results and Discussion

A comparison of the temperature data for 1969 and 1970 (Figures 4 and 5) shows the following trends: (Table II).

Mean of maximum temperatures	1969	1970
June	65.7°F.	78.0°F.
July	75.5	79.8
August	81.2	79.4
Mean of minimum temperatures		
June	42.7	53.9
July	55.0	57.9
August	57.9	52.5
Overall temperature means		
June	54.2	66.0
July	65.3	68.9
August	69.6	66.0

Table II. Comparison of mean temperatures, by month, for 1969 and 1970.

Table IIshows that both June and July, 1970, had higher mean temperatures (both minimum and maximum temperatures) than did the corresponding months in 1969. The greatest temperature difference occurred between June, 1969

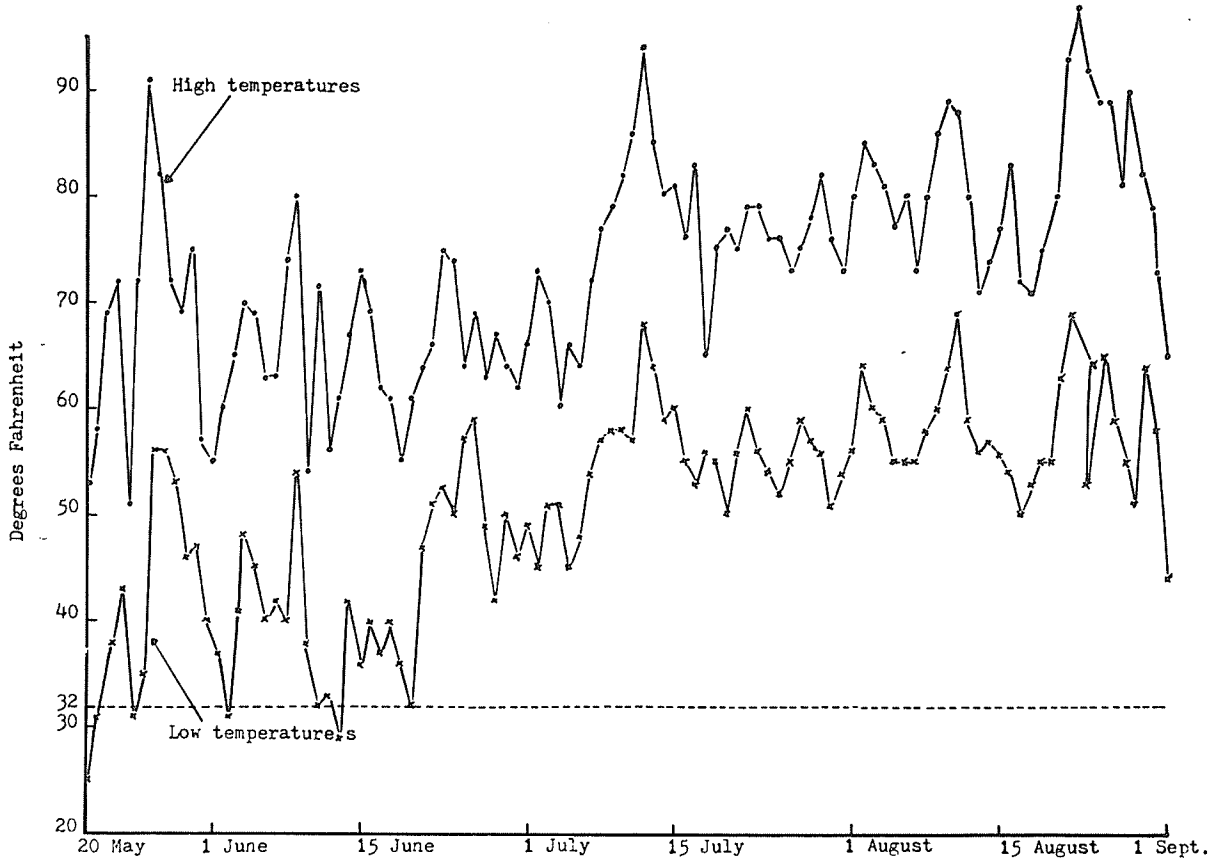

Figure 4. Daily temperatures, 1969. (Recorded by Department of Transport, Winnipeg International Airport.)

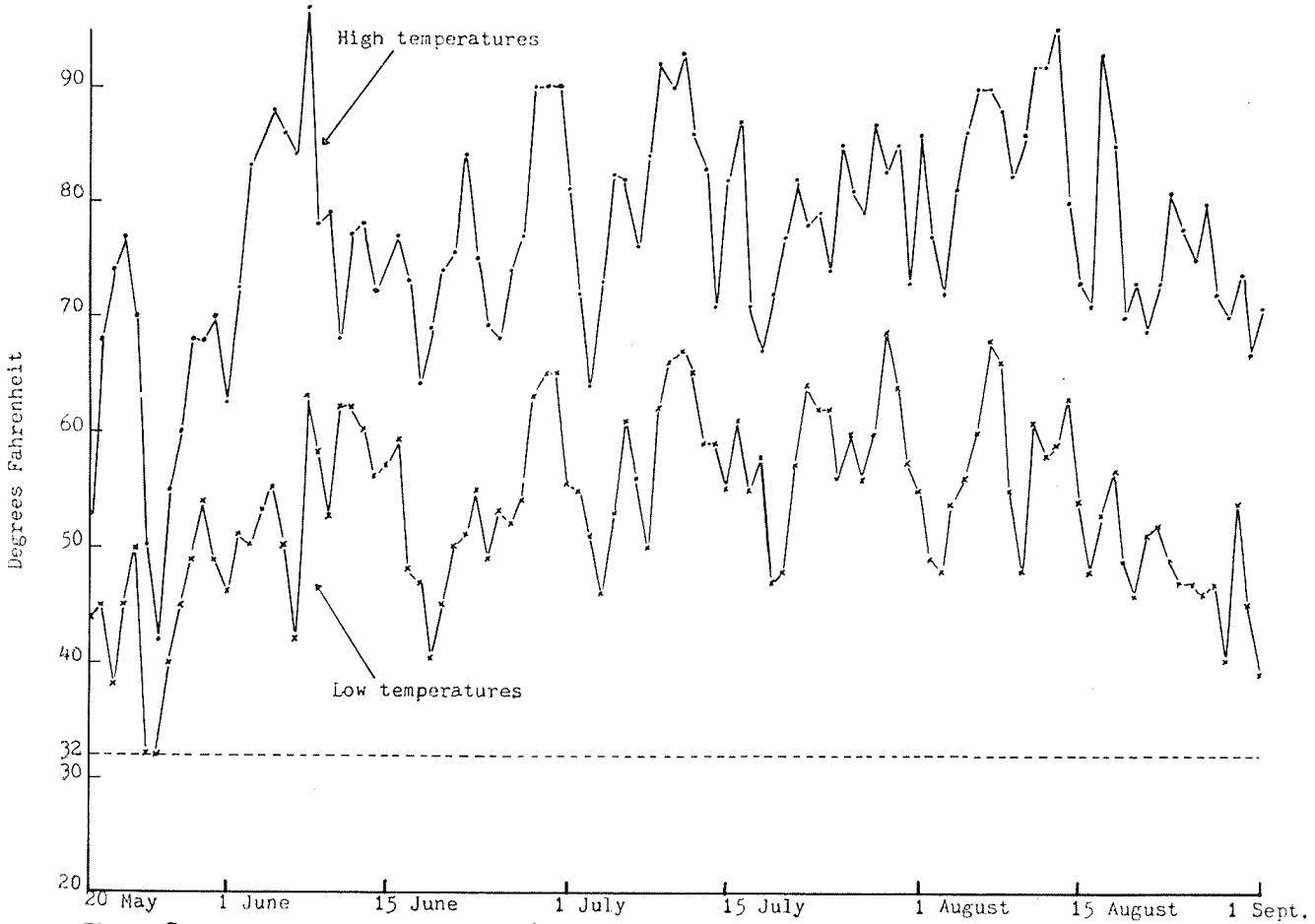

Figure 5 . Daily temperatures, 1970. (Recorded by Department of Transport, Winnipeg International Airport.)

and June, 1970, with June, 1970 showing a mean maximum temperature of 78 degrees F. The reverse situation held true for August, ie. August of 1969 was warmer than was August in 1970.

Temperatures close to the lethal high temperature of honey bees did not occur during either 1969 or 1970. Except during May, and in 1969, the early part of June, flight - limiting temperatures occurred only at night or very early in the morning. It was noted, however, that occasionally on cool mornings a southerly breeze tended to retard development of full flight activity from the A-colonies while hardly influencing the B-colonies which were protected by trees from the south side of the apiary. Similarly, the A-colonies, which were protected from the north by trees, tended to fly somewhat earlier in the day when the breeze came from the north.

Nectar and Pollen Plants

During the months of June, July and August of both 1969 and 1970, periodic tours were made over the Campus of the University of Manitoba and the surrounding area in order to determine the sources of pollen and nectar available to the bees. Some of the more important plant species, together with their approximate flowering dates, are shown in Figures 6 and 7. The difference in the number of plant species listed for both years is due to the lack of information on

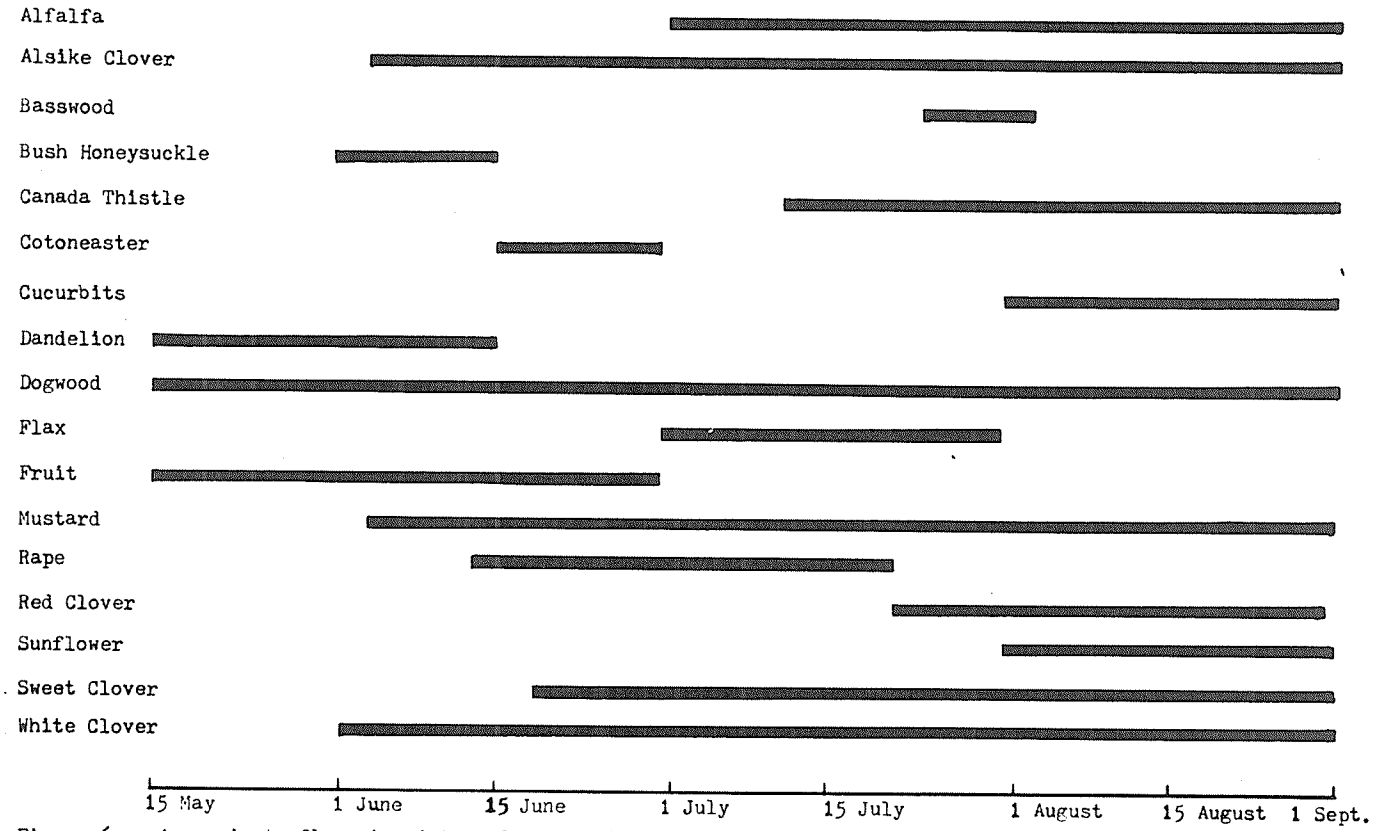

Figure 6. Approximate flowering dates of some major sources of nectar and pollen. University of Manitoba, 1969.

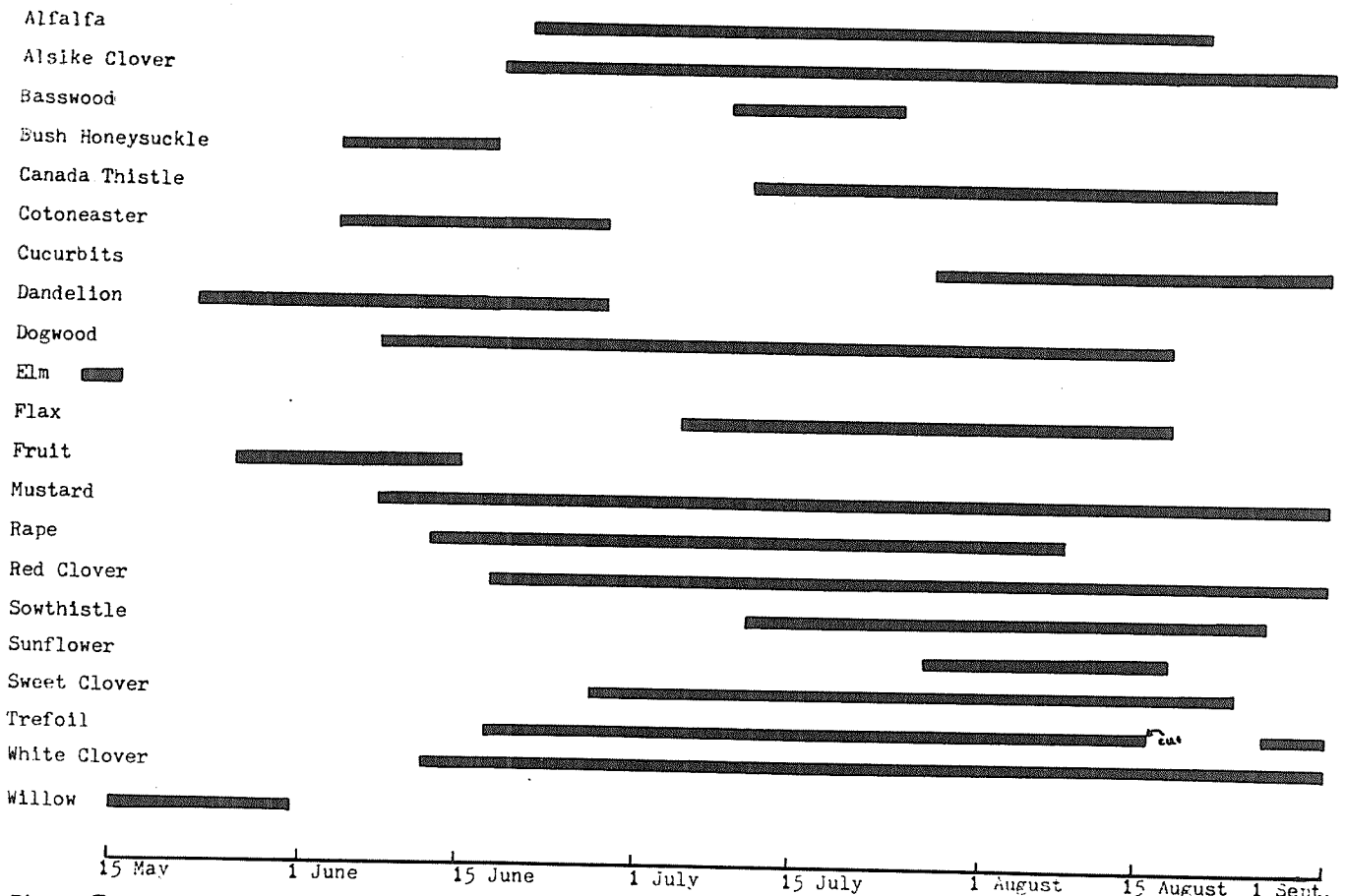

Figure 7. Approximate flowering dates of some major sources of nectar and pollen. University of Manitoba, 1970.

flowering dates in 1969, rather than to the absence of some of the species. Detailed records on bee visitation and the type of forage obtained (i.e. pollen, nectar, or both) were not kept. However, a brief discussion of some of the observations made, may be in order. More detailed information on the relative merits of Manitoba honey and pollen plants may be obtained from Mitchener (1948) and Pellett (1947).

While most of the plant species listed were observed to be actively worked by bees at some time during their period of bloom, considerable differences in apparent attractiveness among those blooming at any given time could be observed. This may have been due either to competition from other species i.e. greater attractiveness to bees because of higher sugar concentration or greater nectar flow, or more attractive pollen (Ribbands, 1949; Free, 1963), or it may have been the result of previous fixation on the part of the bees to another crop (Ribbands 1949; Ribbands 1953). In addition, not all of the plant species were equally attractive over the whole of their flowering period.

Thus, dogwood (Cornus sp.), widely planted on the Campus as an ornamental shrub, and which also occurs wild in waste areas along the banks of the Red River, was heavily utilized as a source of pollen for the first two or three weeks of its flowering period, but was largely ignored by the bees thereafter. During this time, many bees actively

"scrabbled" for pollen (Free and Spencer-Booth, 1964), but only an occasional bee was observed to be probing the florets for nectar. Cornus species are reported by Pellett (1957) to be of minor importance as a source of nectar.

Three other early sources of both pollen and nectar are dandelion (Taraxacum officinale), elm (Ulmus americana), and willow (Salix sp.) in decreasing order of importance (Mitchener, 1948). Dandelion was visited by bees for both pollen and nectar; it is reported to be one of the most important plants to the beekeeper, particularly since it blooms at a time of rapid population build-up in honey bee colonies Mitchener, 1948; Pellett, 1957). Both willow and elm, although reported to be good sources of pollen and nectar, did not appear to attract many foraging honey bees.

Fruit bloom, a good source of both pollen and nectar, consisted of a variety of species, including apple (Malus sp.), plum and several wild species of cherry (Prunus sp.), hawthorn (Crataegus sp.), raspberry (Rubus sp.), gooseberries (Ribes sp.), currants (Ribes sp.) and strawberry (Fragaria sp.). In 1970 the period of fruit bloom was considerably reduced, when compared to 1969. This was probably due to the cool, wet spring of 1970, which retarded plant growth and flower development, and which was followed by a period of considerably higher temperatures in June, resulting in an intensification of flowering and a subsequent

shortening of the flowering period.

Honeysuckle (Lonicera sp.), Cotoneaster, and Caragana (not listed) each were intensively worked by bees for brief periods of time. Caragana yielded both pollen and nectar, Cotoneaster yielded nectar only and the honeysuckle yielded nectar; whether pollen was also collected from it, is not known. All three species were reported to be of value to beekeepers, especially in the Winnipeg, Manitoba area by Pellett (1947), though Mitchener (1948) considered both Caragana and honeysuckle to be of minor importance as honey plants; he made no mention of Cotoneaster.

Mustard (Brassica sp.) started to bloom during the first week of June in both years, and continued throughout the season. Whether one or several species were involved, is not known. It appeared to be a source of both pollen and nectar, particularly during the first half of the season.

With the exception of red clover (Trifolium pratense), the leguminous forage crops are the principal sources of surplus honey in Central Manitoba (Mitchener, 1948). These include white sweet clover (Melilotus alba), yellow sweet clover (M. officinalis), white Dutch clover (Trifolium repens), alsike clover (T. hybridum), and alfalfa (Medicago sativa). All are sources of both nectar and pollen. In addition, small experimental plots of sainfoin (Onobrychis sativa) attracted bees readily. Birdsfoot trefoil (Lotus corniculatus)

appeared to be somewhat less attractive. Although large numbers of bumble bees could usually be found on red clover, this legume was unable to compete with other plants for honey bee visits.

Both rape (Brassica napus) and flax (Linum sp.) were grown by the Department of Plant Science in experimental field plots. Differences in the flowering periods of both crops over the two years are due to the number of varieties used and to differences in planting dates. Rape was a very attractive source of both pollen and nectar, and volunteer plants continued to furnish some nectar and pollen well into September of 1969. However, flax was worked only lightly; nectar and some pollen were gathered. In working on flax blossoms, foragers frequently tried to obtain nectar from the stem end of the flower, by inserting the tongue between the petals and sepals.

Very little honey bee activity was observed on basswood (Tilia americana) in either year. According to Pellett (1947), nectar flows from this species are very irregular. Sow thistle (Sonchus sp.) was regarded by Mitchener (1948) as a good source of nectar. Although this species was common in both 1969 and in 1970, few bees were observed to visit it.

Although sunflowers (Helianthus annuus) are reported to be a very good source of pollen as well as nectar (Pellett, 1947; Bitkolov, 1961; Free, 1964), only a few foragers worked

on sunflowers in 1969 and 1970. Of these, most collected pollen; whether nectar was obtained as well, was not observed. Cucurbits, on the other hand, were highly attractive to bees. The cucurbits grown included several species of melons, pumpkins and cucumbers. Particularly the large flowers of pumpkin (Cucurbita pepo) were highly attractive; often as many as 4-6 bees crowded into one blossom. Both pollen and nectar were obtained.

Rhubarb (Rheum sp.) proved to be very attractive as a source of pollen. Whether nectar was obtained from it as well, is not known.

Of the various plant species listed, dogwood was probably the most important single source of pollen only, while the dandelions were the most important early source of both pollen and nectar. The main nectar flow came primarily from the clover, including the sweet clovers, alfalfa, white clover, and some alsike.

Pollen Collection

In the previous section it was shown that there were no great differences in the sources of nectar and pollen available to the bees over the two years of the experiment. In order to determine whether, as was reported by Louveaux (1959), there existed a seasonal trend in the amount of pollen collected in a given location, from year to year, OAC pollen traps (described by Smith, 1963) were placed

under two colonies. The daily amounts of pollen obtained throughout both seasons are shown in Figures 8 and 9. Although it appears that the greatest daily returns were obtained in the beginning of the season in both 1969 and 1970, and that relatively greater amounts of pollen were collected daily in August 1969 than were collected during the same period in 1970, no seasonal trends could be established, because of the large fluctuations in the daily amounts of pollen obtained. Similarly, seasonal trends are not apparent in the mean weights of single pollen loads in the daily collections (Figures 10 and 11). This suggests that the weight of single pollen loads is independent of the plant species from which they are collected.

The collection of pollen by honey bees is subject to a variety of influences, some of which are environmental, and others inherent in the bees themselves. Thus, the amount of pollen gathered by a colony was found to be roughly proportional to the amount of its brood (Todd and Bishop, 1940; Hirschfelder, 1951; Lavie and Fresnaye, 1963; Free, 1967a, 1967b), under some conditions eggs and larvae stimulated pollen foraging to a greater extent than did sealed brood (Free, 1967b). Similarly, the absence of the queen resulted in a reduction in pollen foraging, before there was a reduction in the amount of brood present (Free, 1967a). Although strong colonies tend to collect and to store more

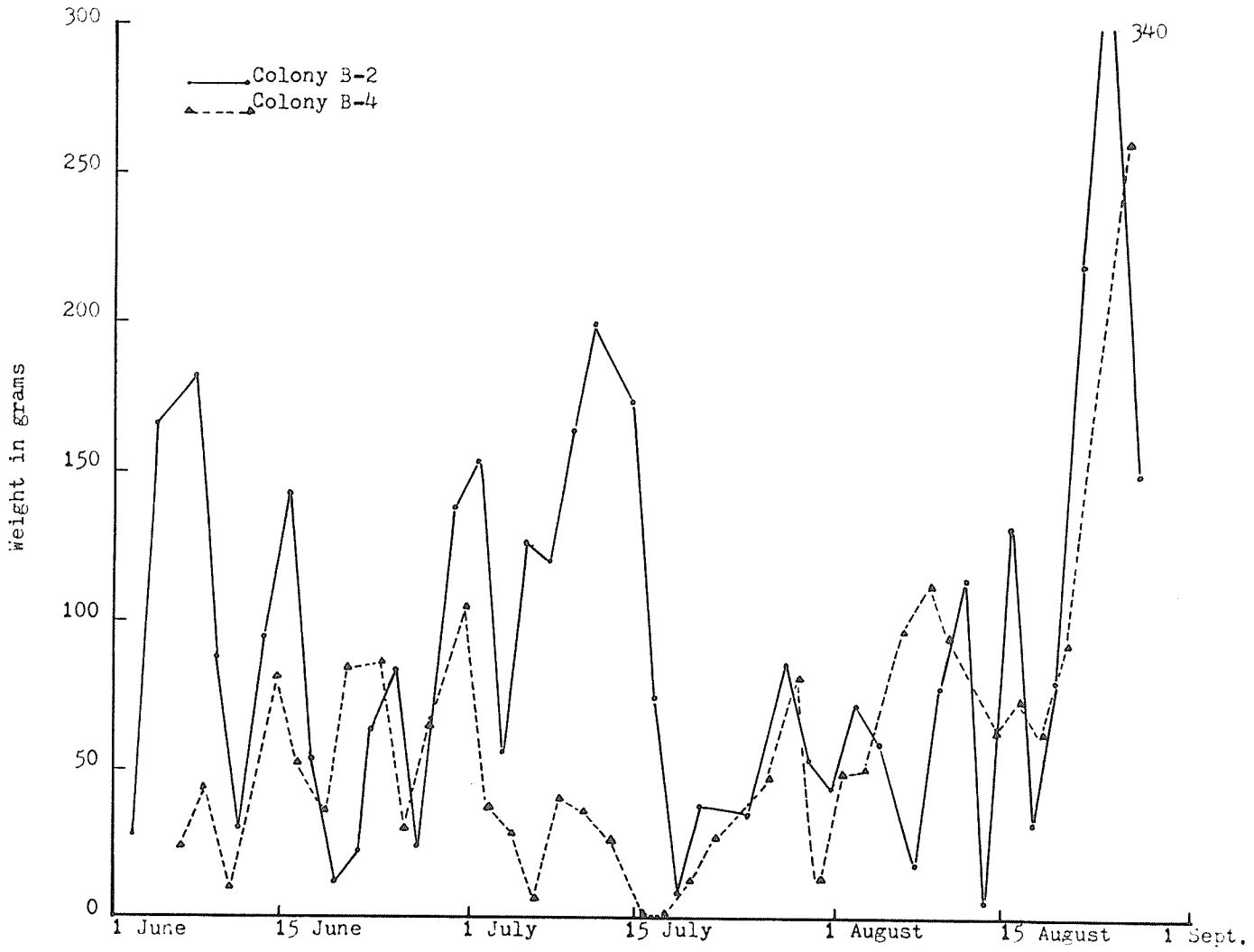

Figure 8 . Daily pollen trap returns. (1969).

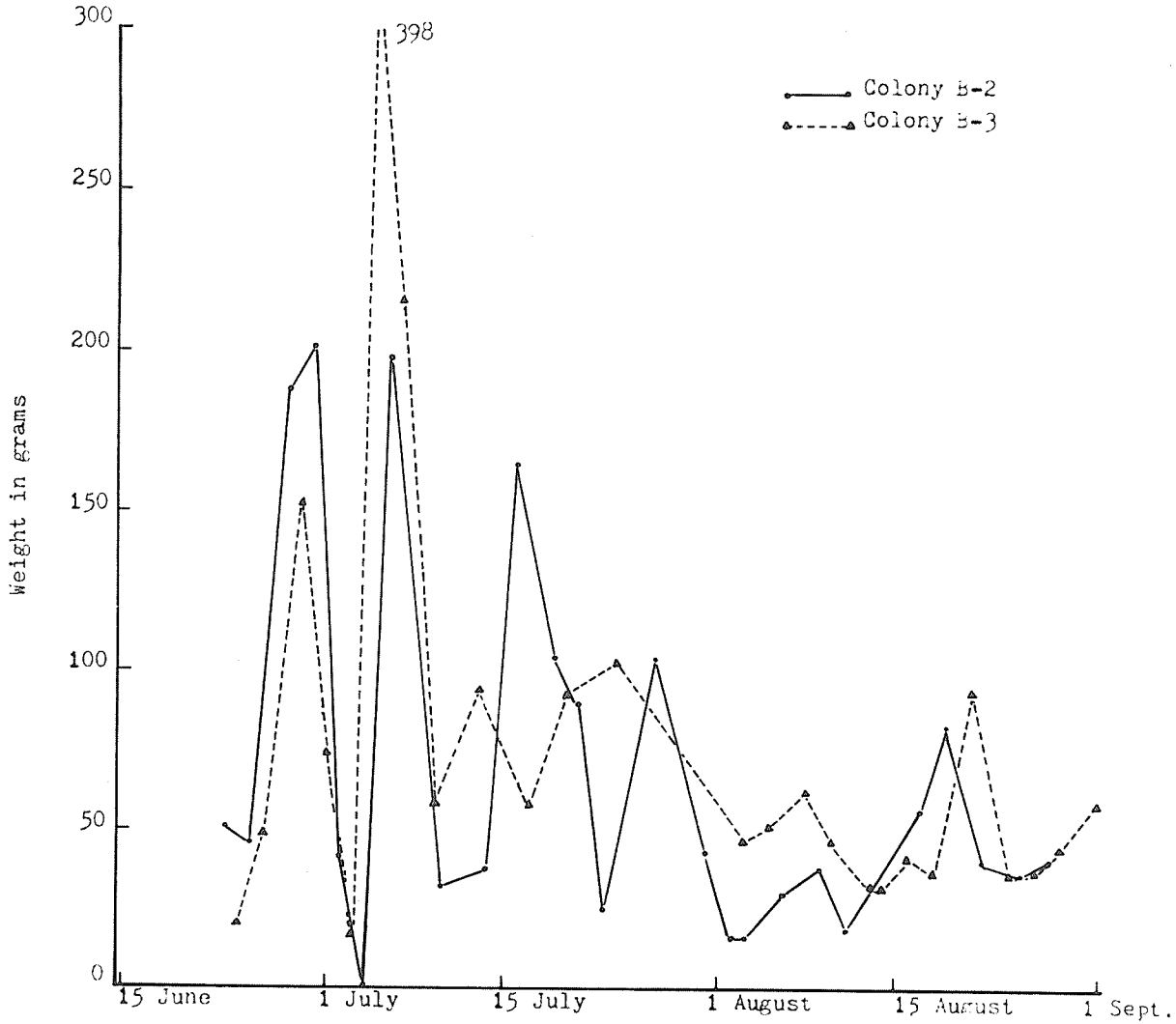

Figure 9. Daily pollen trap returns. (1970).

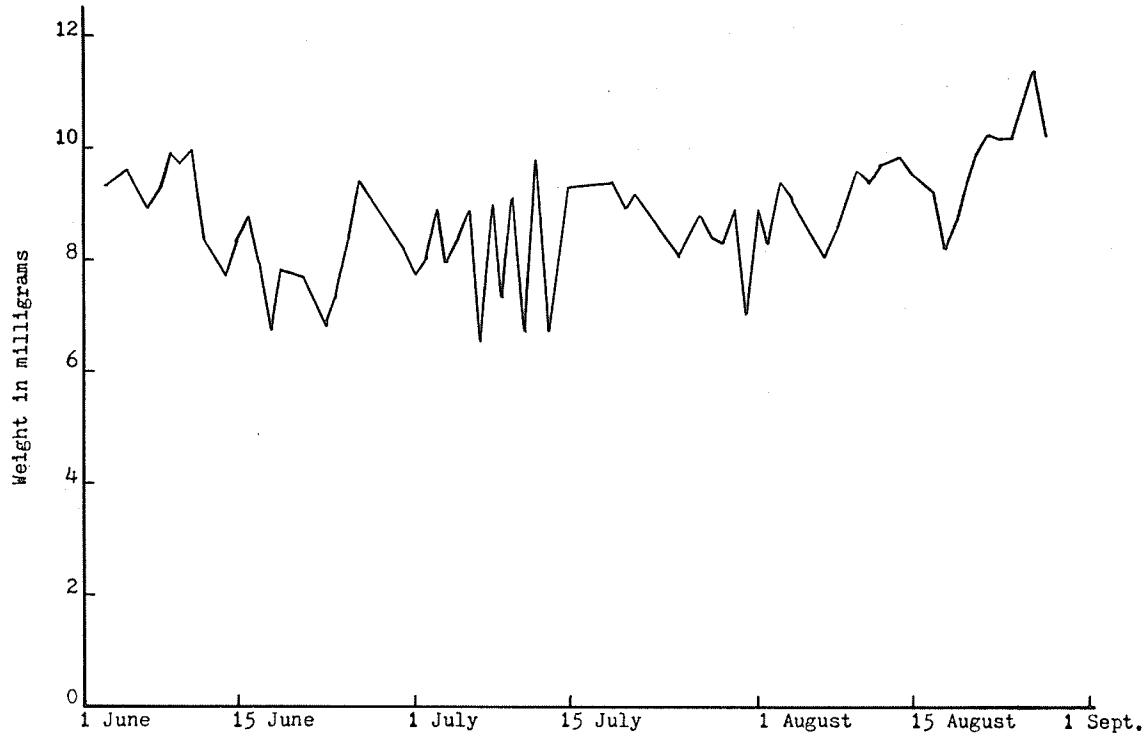

Figure 10 . Weights of individual loads collected in pollen traps throughout the season. (1969).

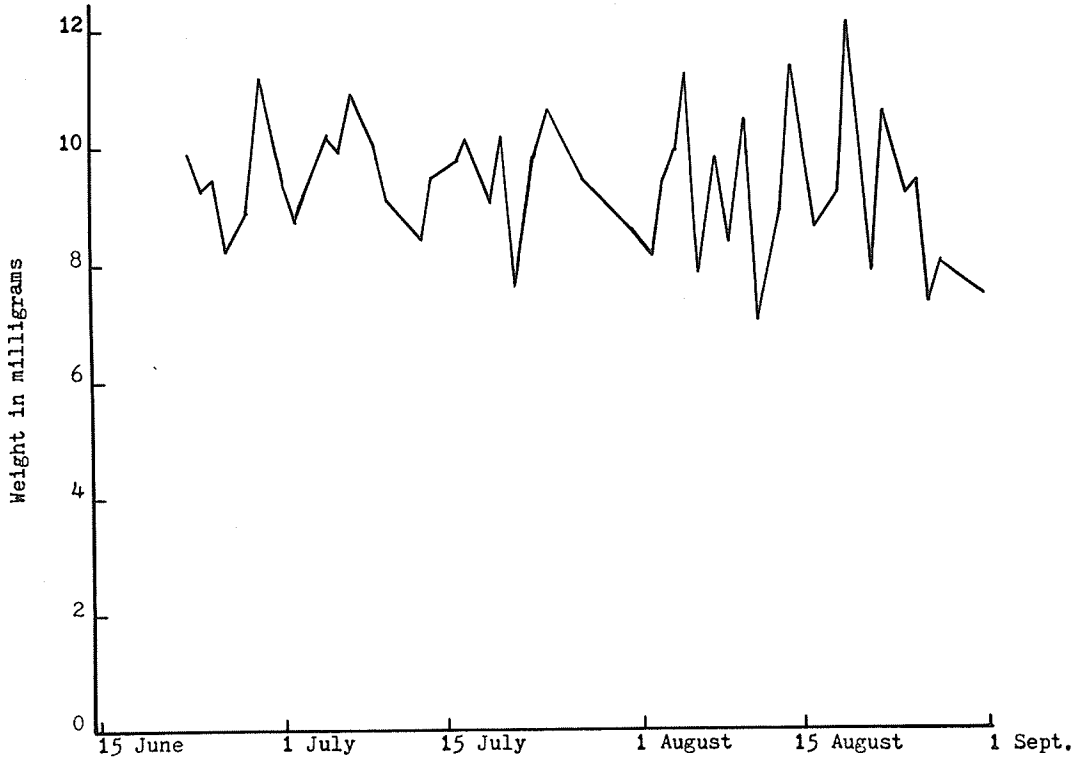

Figure 11 . Weights of individual loads collected in pollen traps throughout the season. (1970).

pollen than weaker ones (Todd and Bishop, 1940; Jeffree and Allen, 1957), they become "discouraged" more easily under marginal foraging conditions, and send out fewer pollen foragers in relation to their population (Free and Preece, 1969). Queenless colonies, although gathering less pollen tend to accumulate more pollen in the combs, because less is used (Jeffree and Allen, 1957).

The genetic background of a colony influences the collection of pollen by its foragers both quantitatively and qualitatively. Some colonies gather and store pollen in far greater quantities than they require (Louveaux, 1959). It has also been found that different races store different relative amounts of pollen throughout the season; this appears to be related to the time of maximum brood in the colony, but is also dependent on genetic makeup. Thus, races which develop early in the season, tend to gather pollen more extensively than they do later in the season (Louveaux, 1959). Strains have been developed through breeding, which show a marked preference for the pollen of alfalfa (Mackensen and Nye, 1969; Cale, 1970; Nye, 1970).

Although many plant species are utilized as pollen sources, most of the pollen collected by bees is derived from a relatively few major crops available at any given time (eg. Percival, 1947; Synge, 1947; Jaxtheimer, 1949; Louveaux, 1959; Louveaux and Albisetti, 1963), and peaks in

pollen collection usually occur during the peaks in the blooming periods of the major species (Percival, 1947). Nevertheless, colonies differ from each other in the percentage of each species collected, and to some degree in the plant species utilized (Jaxtheimer, 1949; Maurizio, 1949; Hirschfelder, 1951; Free, 1963). This, according to Louveaux (1959) is due, in part to the genetically determined preference of the bees for pollen of certain plant species, but it may be due also to the specific area covered by the bees of a given colony and the plant species available, their flowering times, physiological condition, and attractiveness to the bees. The tendency of colonies to collect both pollen and nectar from a variety of plant species, characteristic to each colony, is responsible for the colony odour by which the members of any colony can distinguish hive mates from intruders from other colonies (Kalmus and Ribbands, 1952).

While more pollen came in during a major nectar flow than at other times, a definite relationship between pollen and nectar foraging could not be established (Hirschfelder, 1951; Louveaux, 1959). Nevertheless, Free and Spencer-Booth (1961) found that the feeding of syrup within the colony resulted in increased pollen collection; presumably returning foragers were able to relieve themselves of their loads only with difficulty, and many of them foraged for pollen instead. Similarly, large quantities of stored pollen in the hive

reduced the collection of additional pollen (Free, 1967b). Unlimited quantities of nectar at very high concentration caused honey bee workers foraging in a ¼ acre cage to switch from pollen to nectar foraging almost exclusively (Soehngen, unpublished).

Weather factors exert a considerable effect on pollen collection. The effect of temperature on pollen presentation and on bee behaviour has been discussed in a previous section. Wind, especially when coupled with high temperatures, often dries out flowers, thus influencing pollen presentation. In addition, a wind strong enough to hinder bee flight (i.e. approximately 15 miles per hour), reduces the collection of pollen by foragers (Todd and Bishop, 1940; Percival, 1947; Lavie and Fresnaye, 1963). A change in light intensity reduces bee flight, especially among foragers working in the open and at a distance from the colony (Percival, 1947); even a very light rain results in a temporary cessation in pollen foraging.

The effect of the trap itself on the collection of pollen has also been investigated. In many cases, pollen foraging is reduced during an initial period of several days, until the bees become accustomed to passing through the screen (Eckert, 1942). Thereafter, pollen collection occurs to a greater extent in the trap colonies than in the controls (Moriya, 1955; Jordan, 1958), presumably as an adaptation

to the reduced amounts of pollen brought into the hive. Free, (1963) however, noted that colonies from which pollen is removed by trapping tend to reduce pollen foraging. It is of interest to note that the trap appears to have little immediate influence on the behaviour of the pollen foragers within the hive. Foragers, whose pollen loads are removed, still go through the usual routine of searching for a suitable cell, then "depositing the pollen" into it (McDonald, 1968).

Pollen traps varying in efficiency between 10.0% to 43.0% have been used by Eckert (1942), Smith (1963), Hirschfelder (1951), Jordan (1958), and others, to determine the amounts of pollen collected by normal colonies during the season and to investigate the factors influencing pollen collection by honey bees. Pollen trap efficiency is influenced by uniformity of the openings in the screen used in its manufacture, differences in the size of the foragers, which may be considerable among different colonies (and even within colonies (Kerr and Hebling, 1964), and by the sizes of the pollen loads (Eckert, 1942). In addition, Jordan (1958) found that reduction of the number of holes in the trap through which the bees could enter, increased crowding of the returning foragers, and thereby increased the efficiency of the trap.

It is apparent, therefore, that each colony-trap

combination determines its own pollen collecting efficiency, which varies with changes both in colony and in foraging conditions. It seems that one determination (as has been used by previous workers) of one colony-trap combination is insufficient as a basis on which to draw accurate conclusions regarding quantitative aspects of pollen foraging. However, a pollen curve, such as the one presented here (Figures 8 and 9) is of value, even without the determination of trapping efficiency, as an estimate of the relative amounts of pollen collected over the whole season, and therefore as a means of determining the capacity of an area to support strong colonies.

Nectar Flow

Graphs were constructed, showing the relative daily net gain or loss in weight of each experimental colony throughout the season (Figures 12 to 17). The weight changes were recorded each morning before large numbers of foragers had left the hives for their first flights of the day, and before significant amounts of water, nectar and pollen had been brought in. The data show the relative amounts of "green" honey (nectar from which the bees have removed much of the water during the night; Park, 1925, 1927, 1933) and pollen that had been brought into each hive during the previous day, less the amount required by the colony for its own maintenance (Ribbands, 1952). Thus, if the foragers of

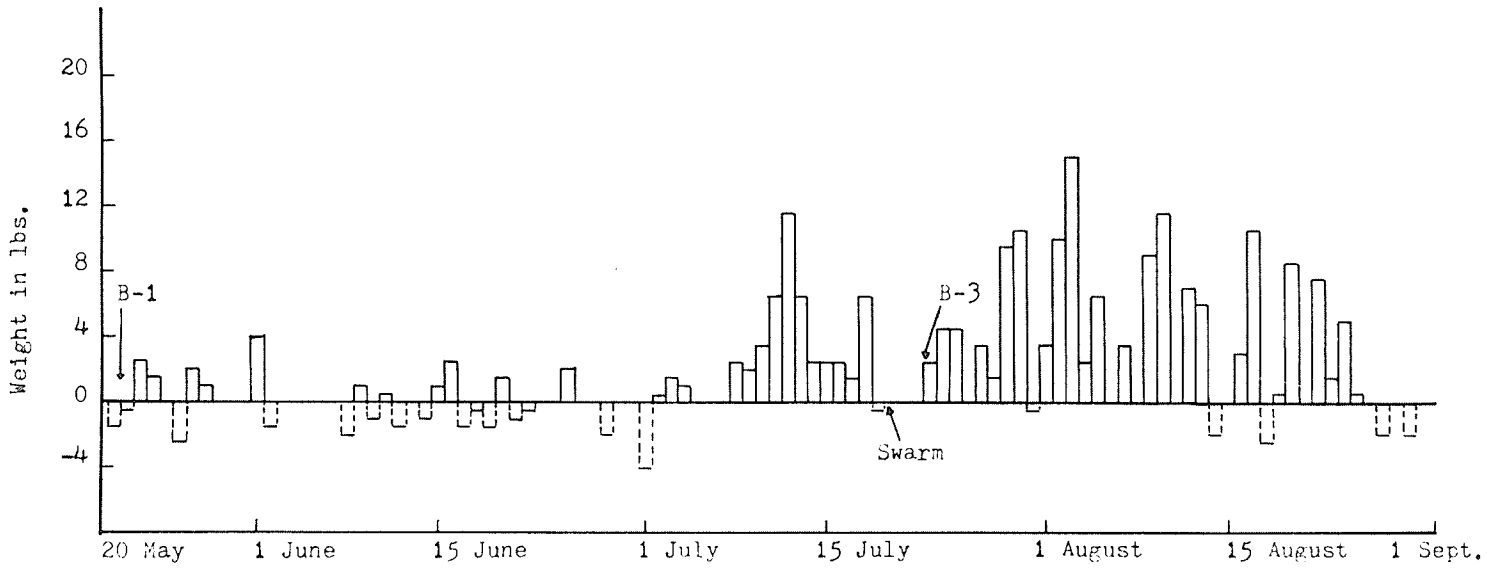

Figure 12 . Daily weight changes. (1969). Colonies B-1 and B-3.

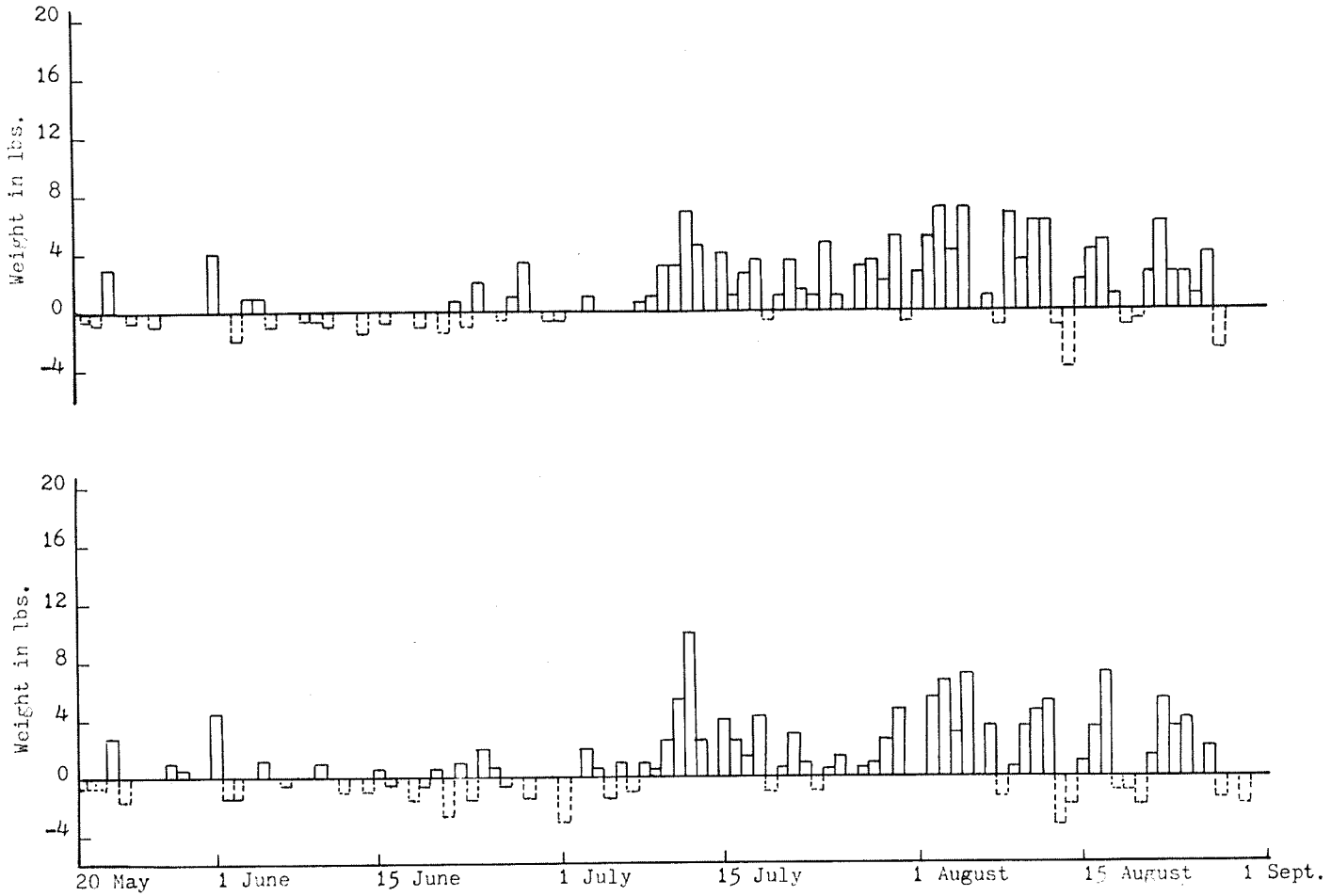

Figure 13 . Daily weight changes. (1969). Colony A-1 (top) and Colony A-2 (bottom).

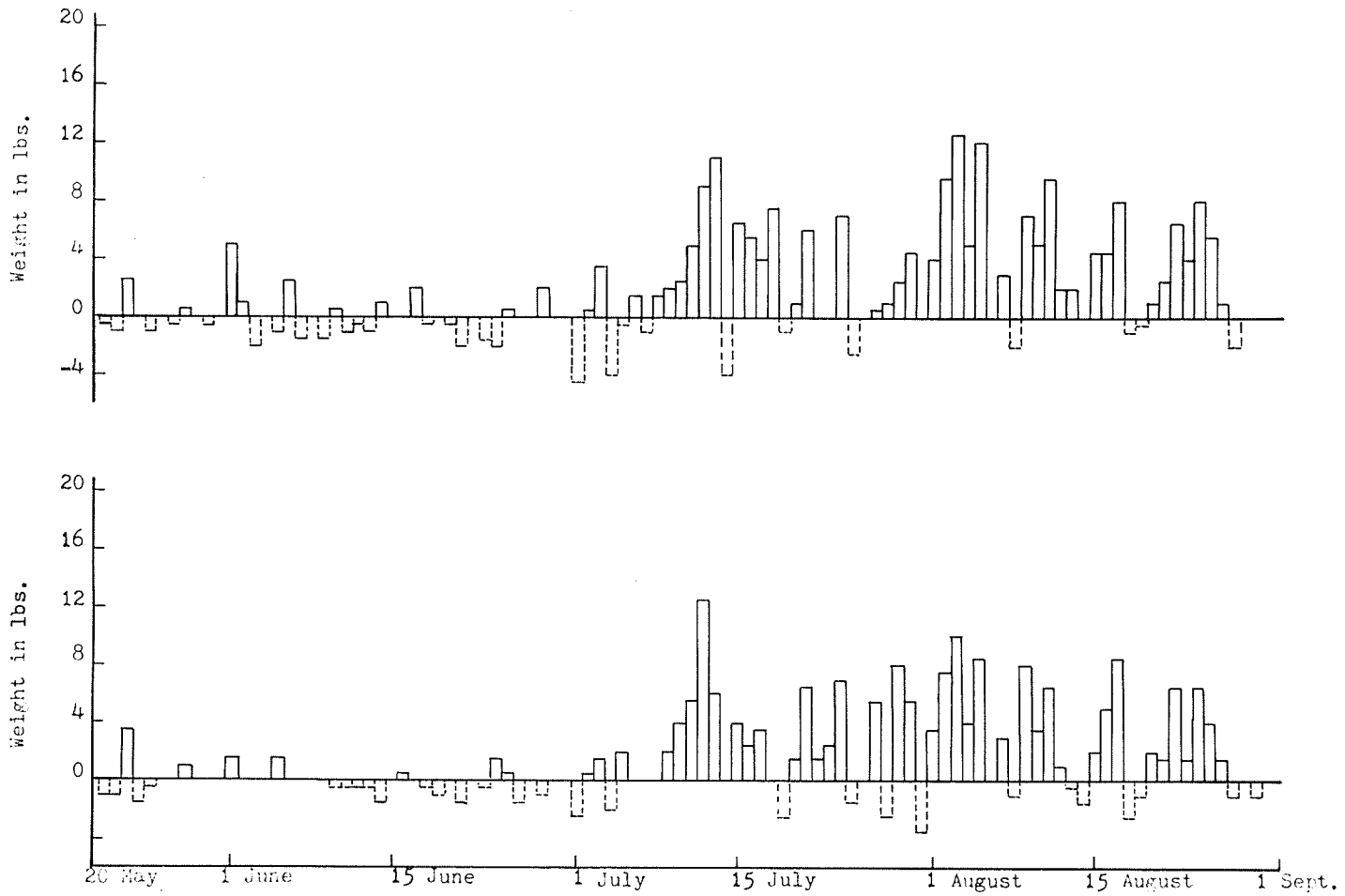

Figure 14 . Daily weight changes. (1969). Colony A-3 (top) and Colony A-4 (bottom).

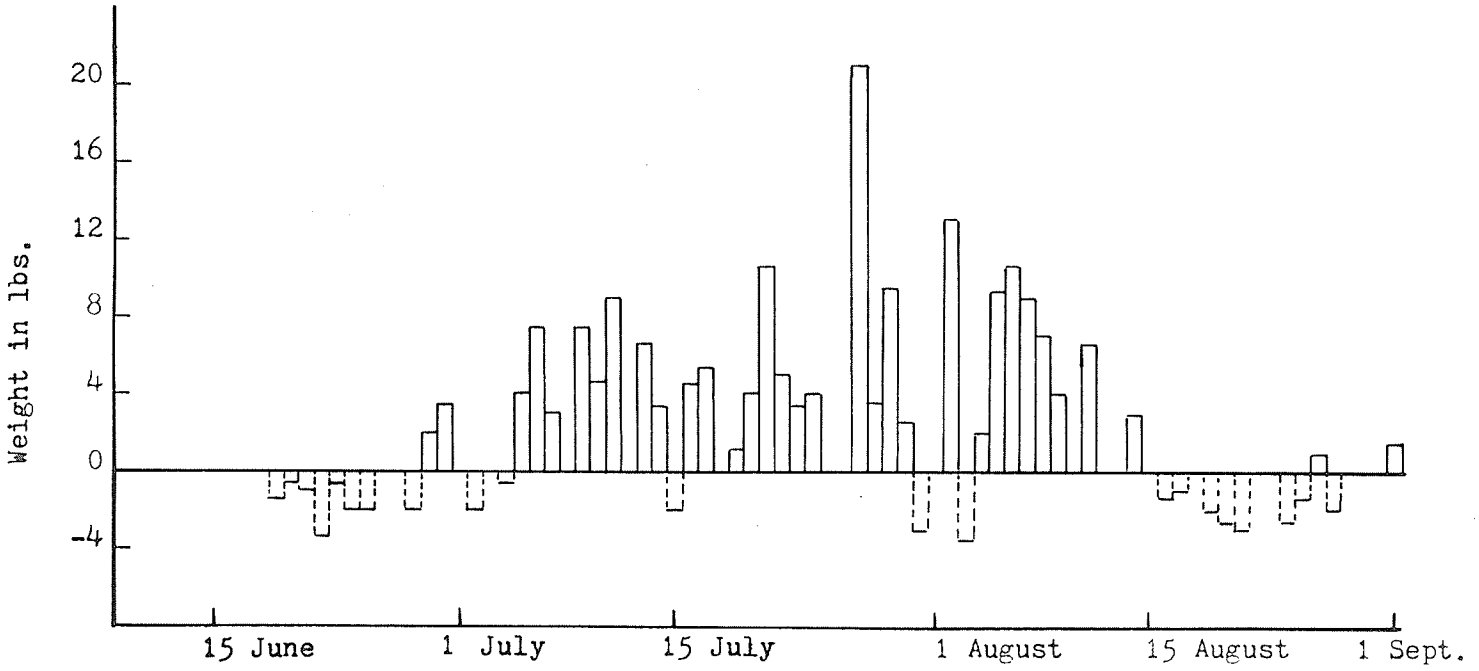

Figure 15 . Daily weight changes. (1970). Colony B-1.

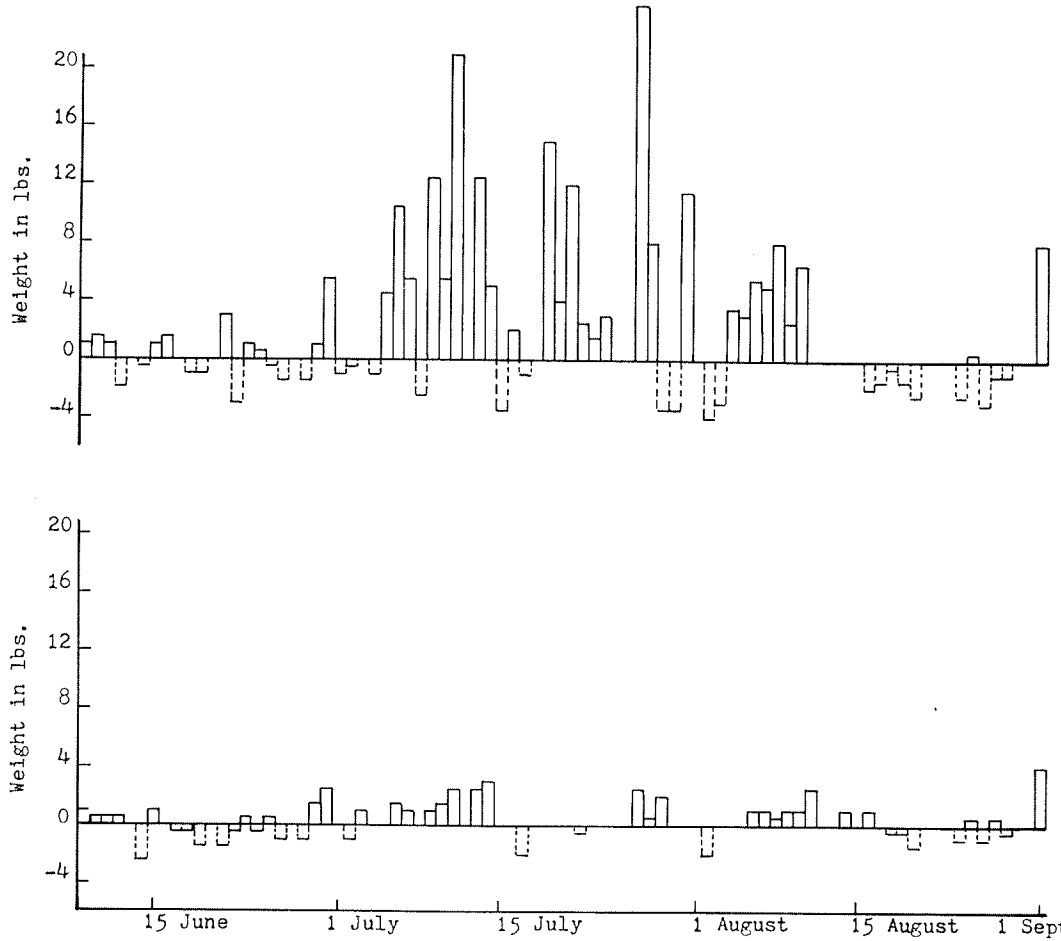

Figure 16 . Daily weight changes. (1970). Colony A-1 (top) and Colony A-2 (bottom).

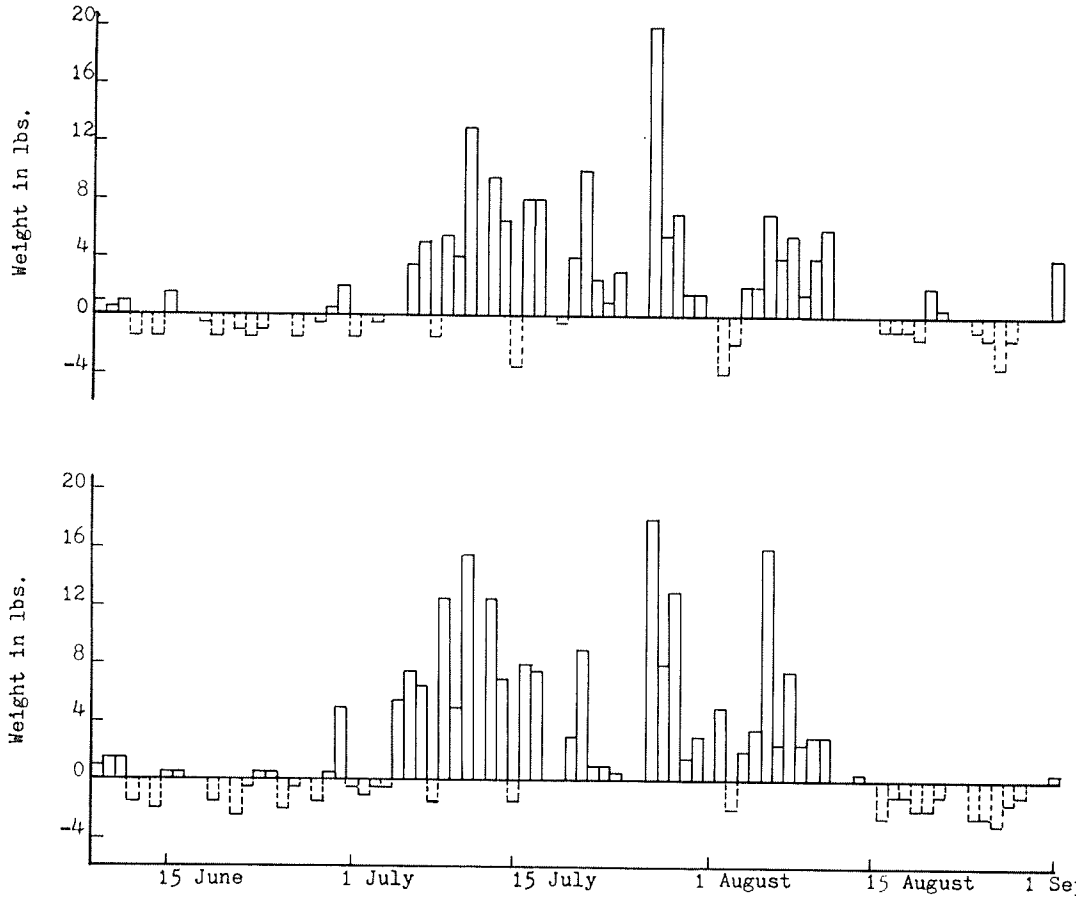

Figure 17 . Daily weight changes. (1970). Colony A-3 (top) and Colony A-4 (bottom).

a colony had brought in three pounds of nectar with a sugar concentration of thirty per cent, and that this had been reduced to one and one-half pounds of green honey by the bees (at a concentration of 60 per cent). If the colony had used, during the same period, one and one-half pounds for its own requirements, the scale would show a net gain of zero pounds for the twenty-four hour period.

Although honey bee colonies may collect an estimated 25-65 pounds of pollen, depending on colony strength and pollen availability, over a season lasting up to five months (Todd and Bishop, 1940; Eckert, 1942; Jordan, 1958; Louveaux, 1959), the average daily amount of pollen brought into the hive is relatively small when compared to the amount of nectar brought into the colony during a flow. Therefore, the weight of pollen collected by the bees will be disregarded in the following discussion.

A comparison of the graphs presented in Figures 12 through 14 and Figures 15 through 17 shows that the honey flows (here defined as the collection of nectar by bees in quantities sufficient to obtain a net gain over a period of at least three consecutive days) in 1969 and in 1970 differed markedly with respect both to intensity and duration. Although in both years the flow began during the first week in July, in 1969 it continued into the fourth week in August, while in 1970 the bees collected very little nectar after 14

August. In both years the flow was within the limits observed by Mitchener (1955).

Although shorter, the 1970 honey flow was of much greater intensity. Maximum daily gains of 24.5 lb., 20 lb., 18 lb., and 21 lb. made by colonies A-1, A-3, A-4 and B-1, respectively, occurred on 26 July. Colony A-2, having swarmed earlier, gained only 2 lb. on that day. In 1969 the maximum gains of some colonies were 7 lb., 10 lb., 13 lb. 13 lb. and 15 lb. and were made on 12 July and on 2 August.

With the exception of colony A-2 in 1970, the experimental colonies used in both years were of nearly equal strength; differences in weather appear to be primarily responsible for the differences in the amount of nectar gathered, both by influencing the amount and quality of the nectar and by their effect on honey bee activity. Although the temperatures in April and May of 1969 appeared to be normal for the time of year, the mean temperatures in June and July were relatively low and were accompanied by frequent rain showers. This probably resulted in a retardation of plant growth and of flowering, and hence reduced the amount of nectar secreted (Beutler, 1953; Lovell, 1963; Shuel, 1967). The increasing temperatures of August, together with the rains received during the previous months, undoubtedly stimulated the plants to continue growing and

flowering and resulted in an extension of the honey flow until the onset of cooler temperatures at the end of August.

In 1970, the months of April and May were cool. They were followed, however, by relatively high temperatures in June and July, through mid-August, when the temperatures began to moderate and the honey flow deteriorated. This confirmed the observations made by Moffett and Parker (1953), and by Demianowicz (1962), who found that a cool May and June was almost always associated with a good honey flow year. They further reported that the maximum daily temperatures most favourable for nectar secretion were 90 to 94 degrees F. in June and July, when sweet clover was the major crop, and 85 - 89 degrees F. in August, when alfalfa was the main source of nectar. Like Mitchener (19??), they found warm days and cool nights to be favourable for nectar secretion.

Although rain during the night often stimulates the secretion of nectar on the following day, a shower during the day, especially if associated with a sudden drop in temperature, often brings a honey flow to an abrupt halt (Lovell, 1963). Rain has been known to wash nectar out of flowers, especially if they are of the "open" type (Lovell, 1963), and the high relative humidity often associated with thunder showers may dilute the nectar (Beutler, 1953; Ribbands, 1953), possibly rendering it less attractive to

foraging honey bees.

Unless the crop is highly attractive to bees, rain will inhibit foraging (Ribbands, 1952) as does low light intensity (Nelson and Jay, 1967; Kefuss and Nye, 1970). During unsettled weather, or when the crop becomes less attractive, foraging honey bees tend to remain close to their hives, leaving many areas of their overall range untapped (Ribbands, 1952; Lee, 1965). When working under poor foraging conditions workers, returning from the fields, tend to remain longer in the hive between trips than they would under favourable conditions, thereby cutting down on the number of trips made per day and the total amount of nectar collected (Park, 1926; 1927; Núñez, 1966). In addition, marginal foraging conditions reduce the numbers of nectar and pollen gathers leaving their colonies for the fields (Taranov, 1961; 1964; Free and Preece, 1969).

Thus, during a cool, wet summer, such as occurred during 1969, a variety of factors may combine to reduce the amount of nectar collected by honey bee colonies. It has been reported, however, that after a wet season in which the nectar-producing plants are especially well developed, a good honey yield may occur in the following year (Jorgensen and Markham, 1946). The results obtained during the summers of 1969 and 1970 seem to confirm this view.

Population Studies

Throughout both years the growth and development of each of the four experimental colonies was monitored in order to gain an insight into the seasonal development of honey bee colonies in Manitoba, and to try to relate the data obtained from the studies of honey stomach contents to the current developmental status of each colony. To this end, each of the three brood stages (i.e. eggs, larvae and pupae) was measured (in square inches of comb surface) and the adult population of each colony was estimated, approximately every twelve days. (Figures 18 through 27). The following brief discussion will cover some of the seasonal trends evident from the graphs and will outline a number of factors influencing brood production by honey bees and, where possible, will relate them to the data obtained. It should be pointed out, however, that the first brood readings and population estimates were obtained approximately one and one-half months after the packages had been hived, and that the seasonal brood curves obtained from them will not show the very steep initial increase obtained from colonies that were hived recently. (See Smirl, 1969).

A comparison of the total brood curves obtained for all colonies shows an initial steep ascent, which either rises to a peak directly, or levels off before rising to a peak; this occurred in June in all colonies but one (A-4/69).

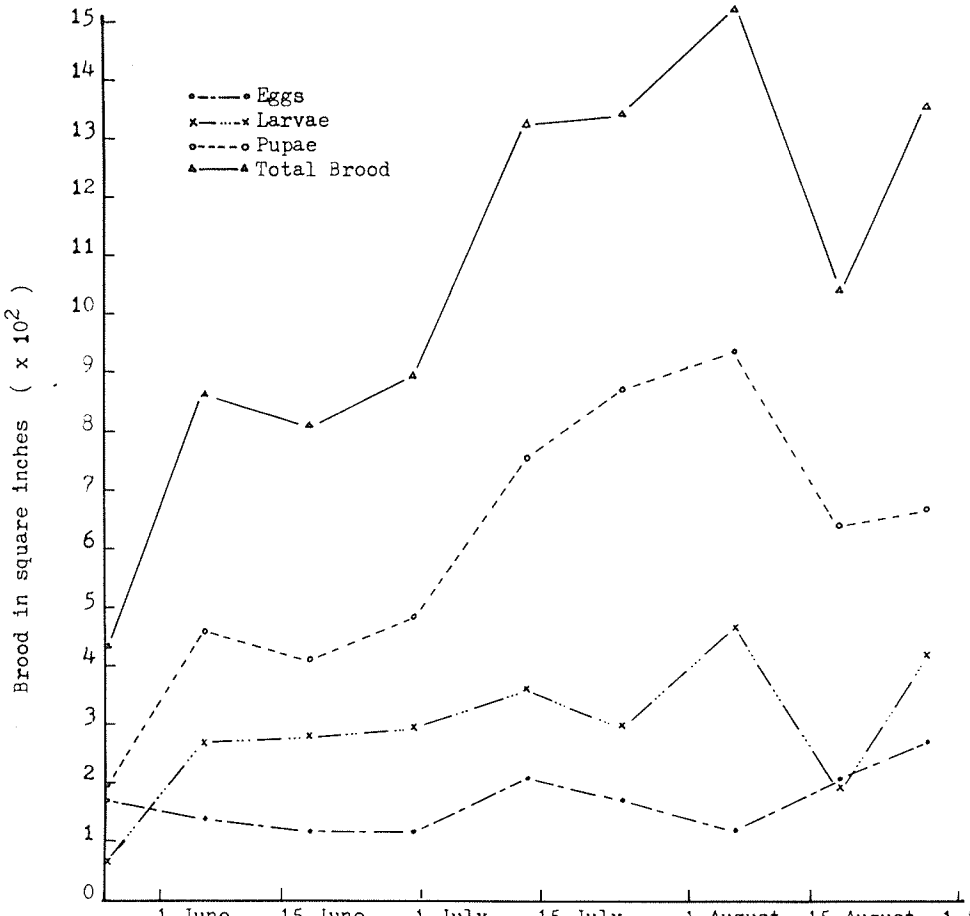

Figure 18 . Honey bee brood: Eggs, Larvae, Pupae, Total Brood. Colony A-1. (1969).

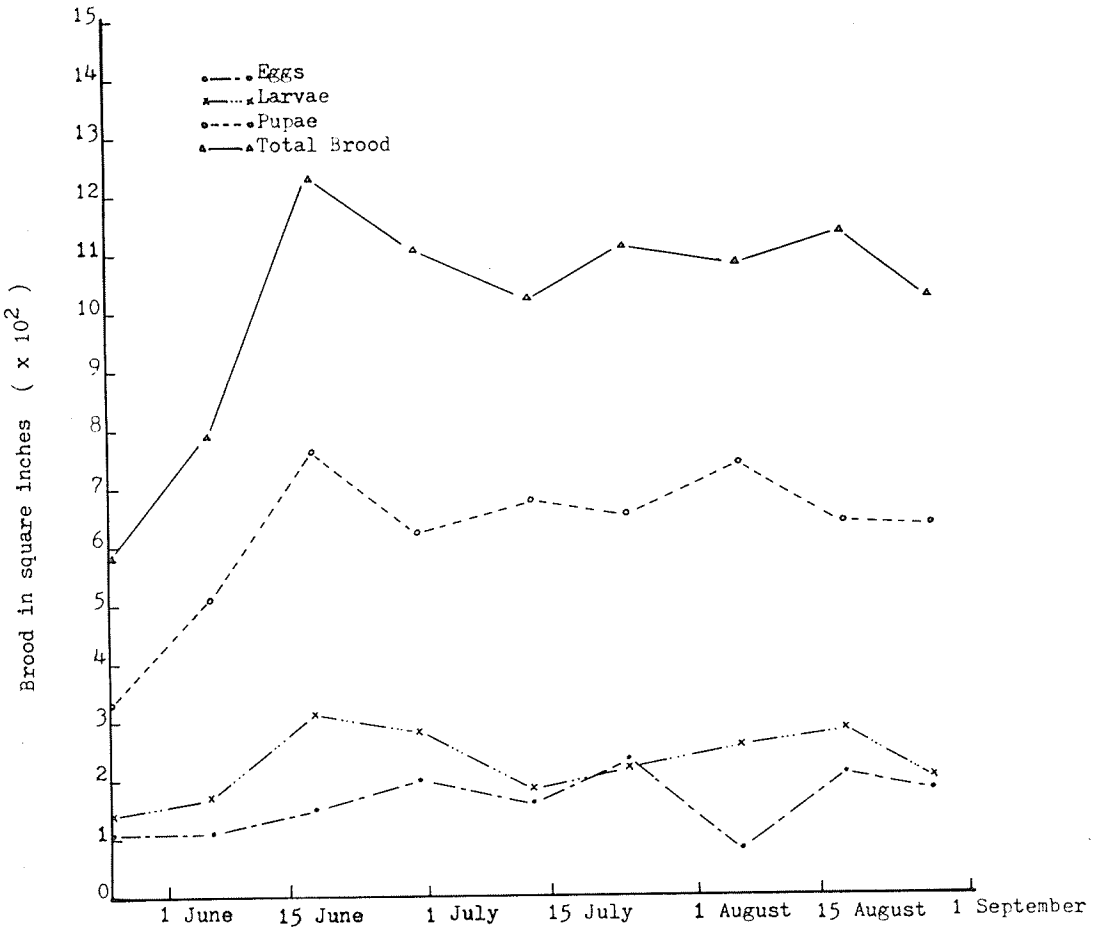

Figure 19 . Honey bee brood: Eggs, Larvae, Pupae, Total Brood. Colony A-2. (1969)

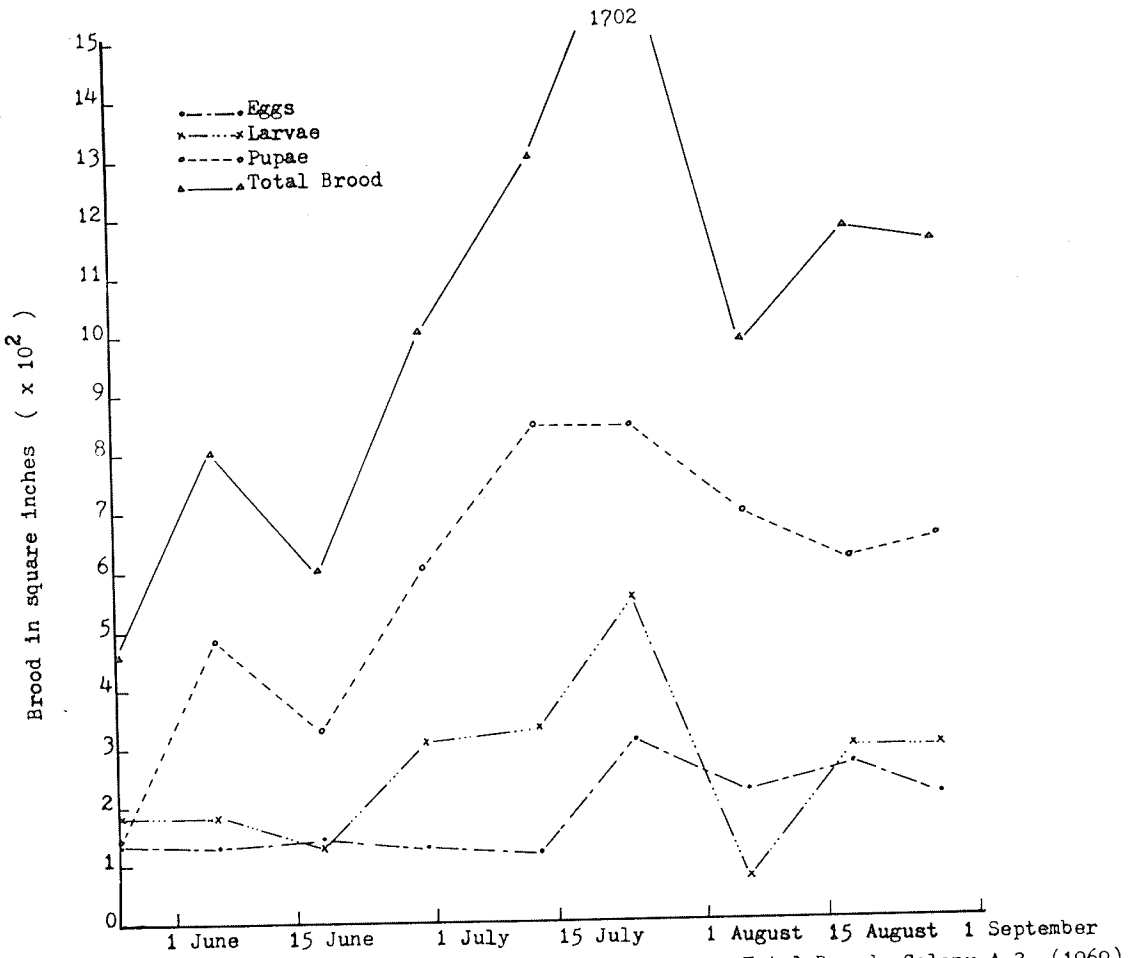

Figure 20 . Honey bee brood. Eggs, Larvae, Pupae, Total Brood. Colony A-3. (1969).

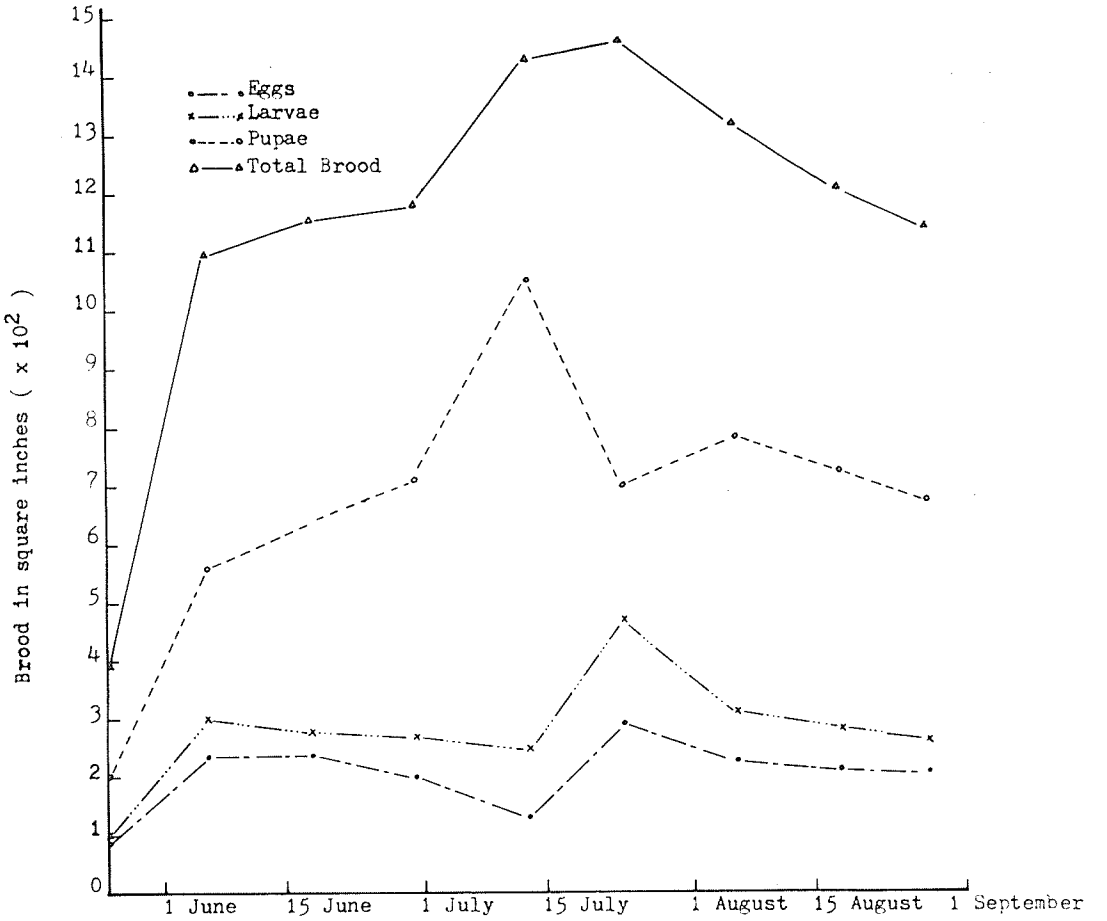

Figure 21. Honey bee brood: Eggs, Larvae, Pupae, Total Brood. Colony A-4. (1969).

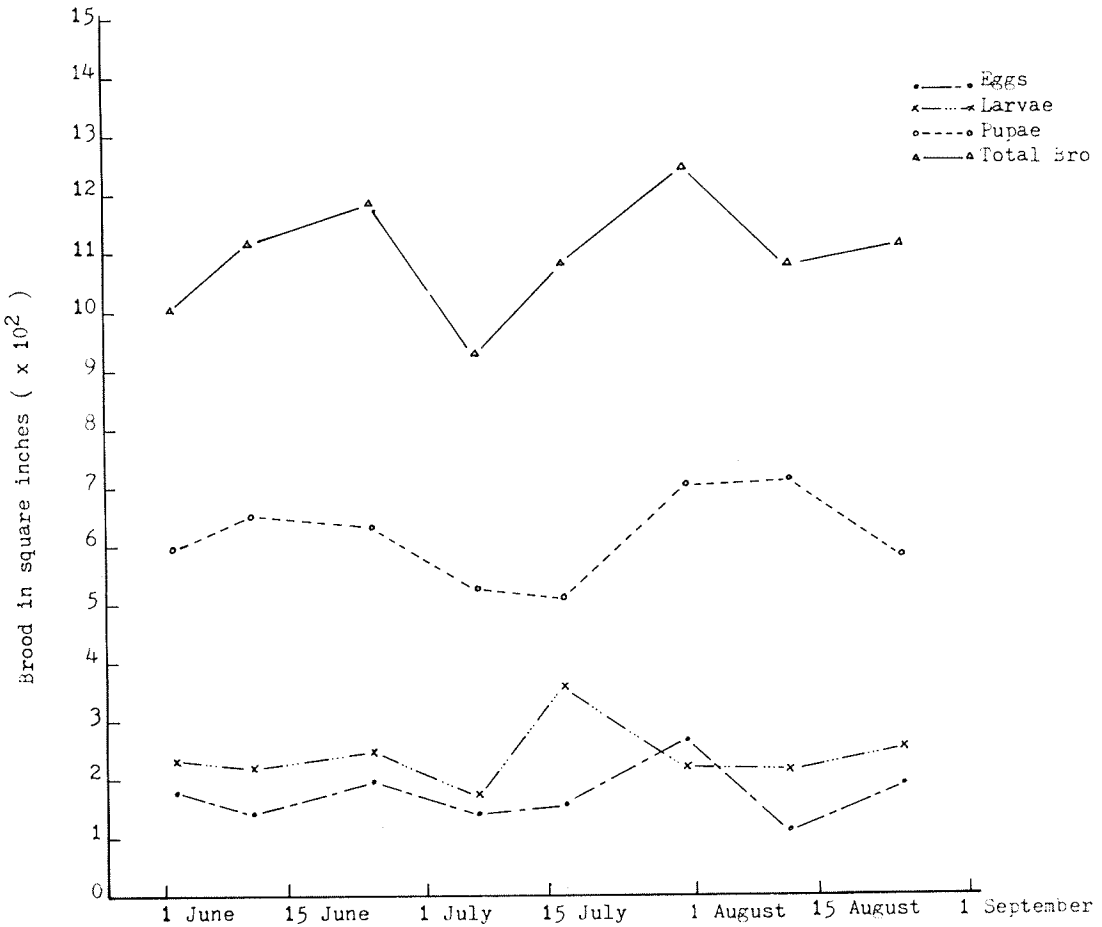

Figure 22. Honey bee brood: Eggs, Larvae, Pupae, Total Brood. Colony A-1. (1970).

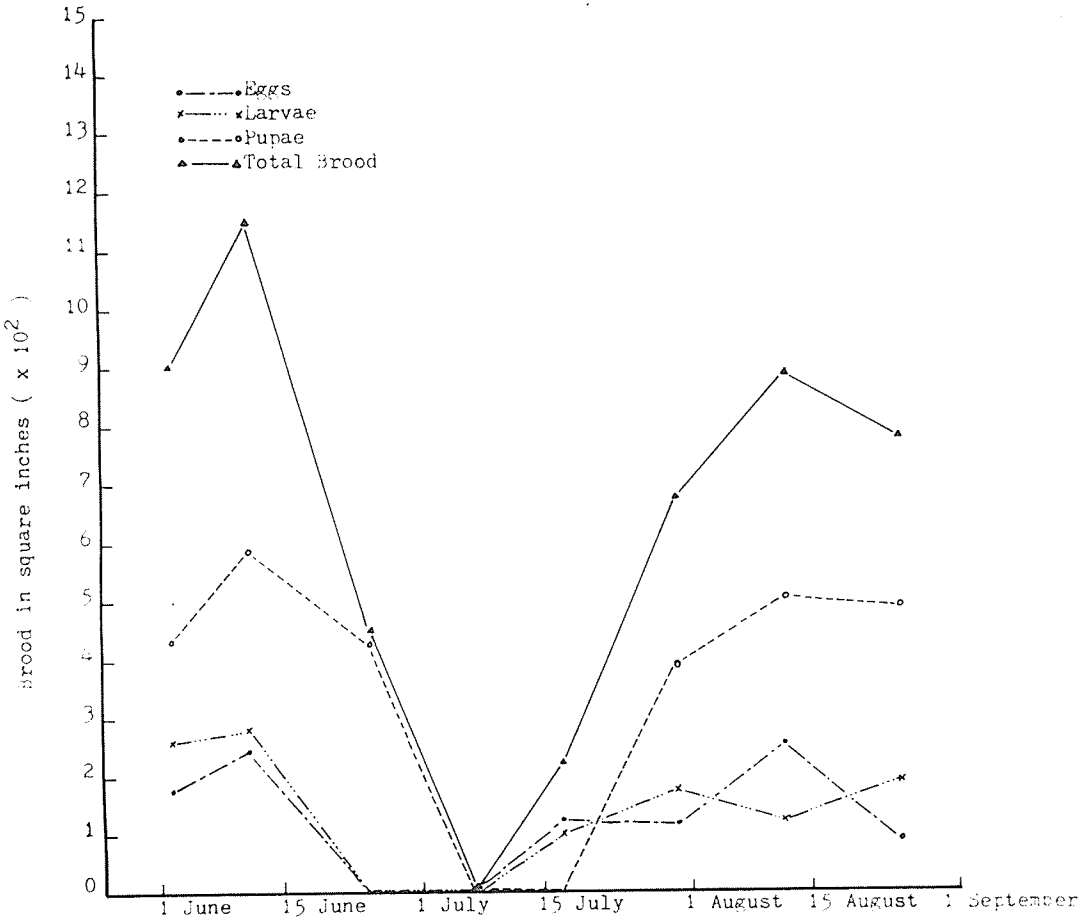

Figure 23. Honey bee brood: Eggs, Larvae, Pupae, Total Brood. Colony A-2. (1970).

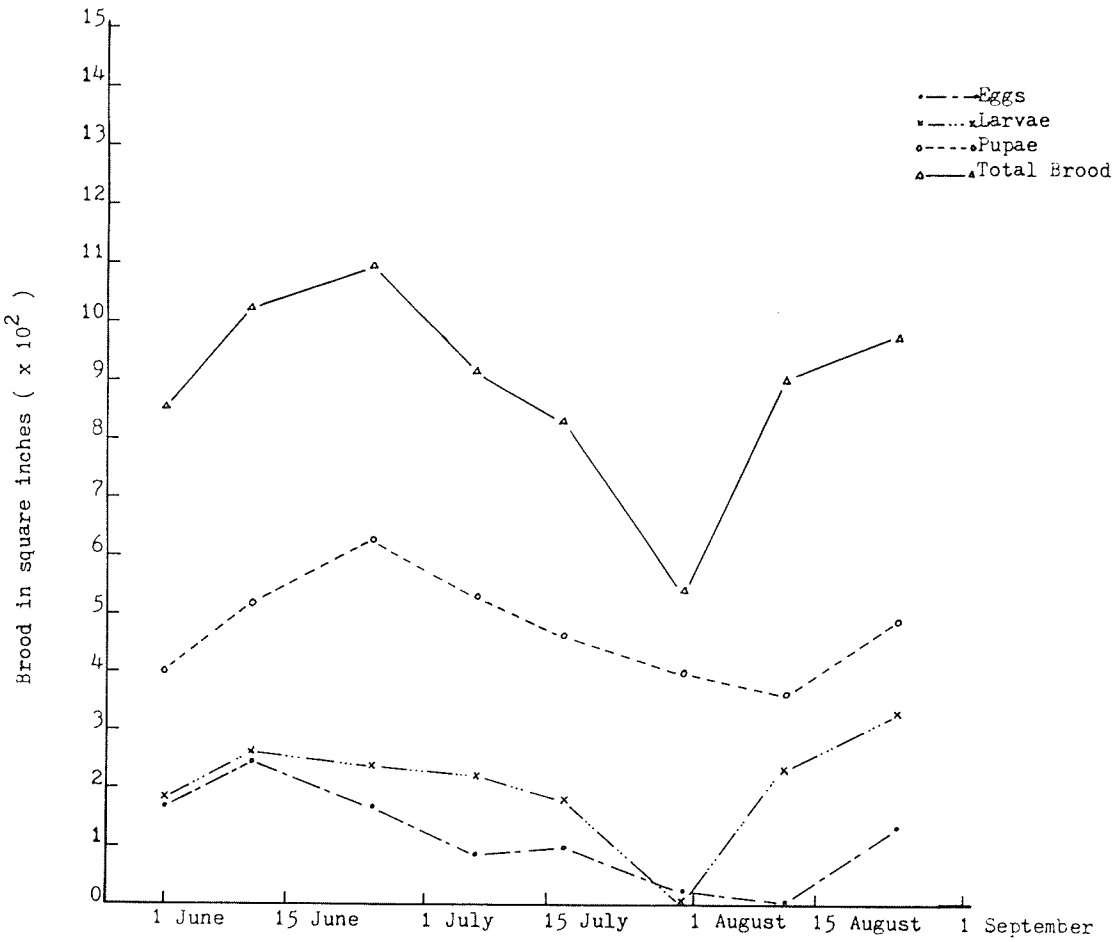

Figure 24. Honey bee brood: Eggs, Larvae, Pupae, Total Brood. Colony A-3. (1970).

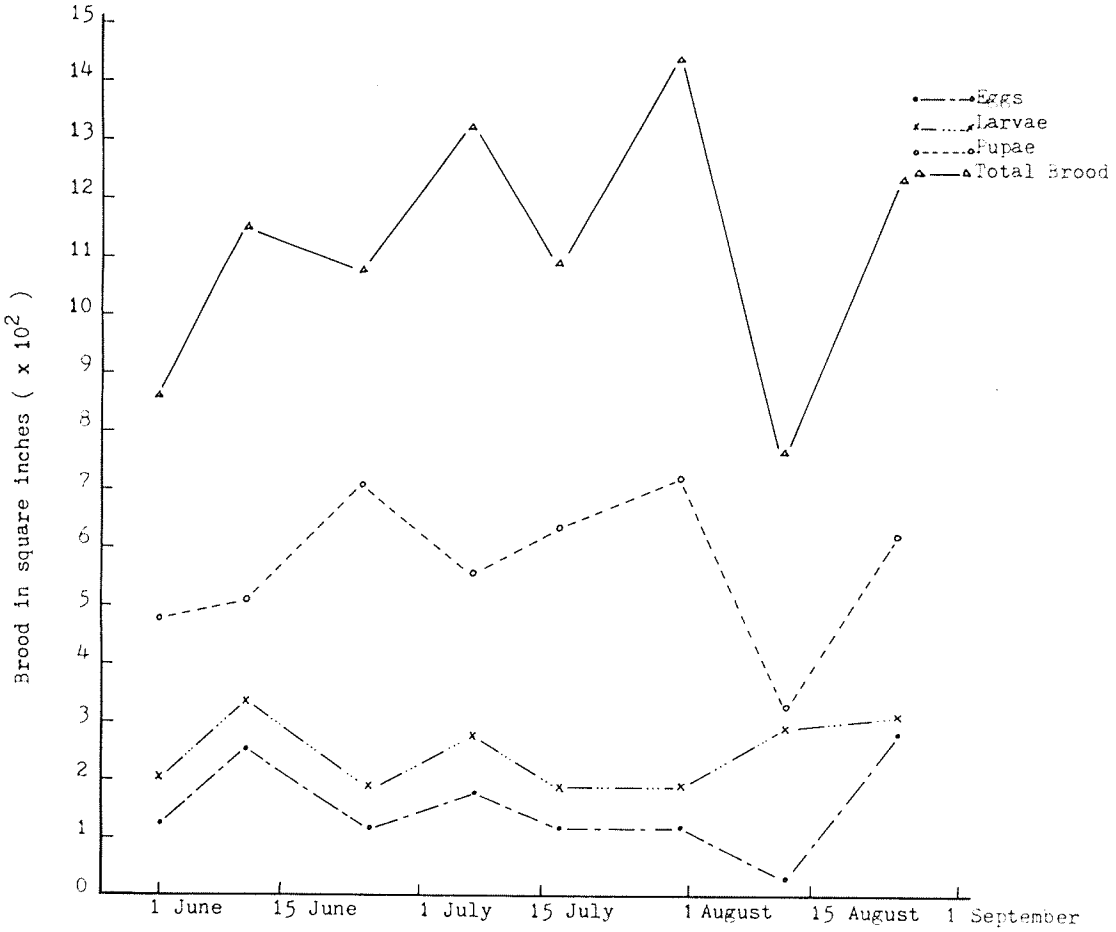

Figure 25. Honey bee brood: Eggs, Larvae, Pupae, Total Brood. Colony A-4. (1970).

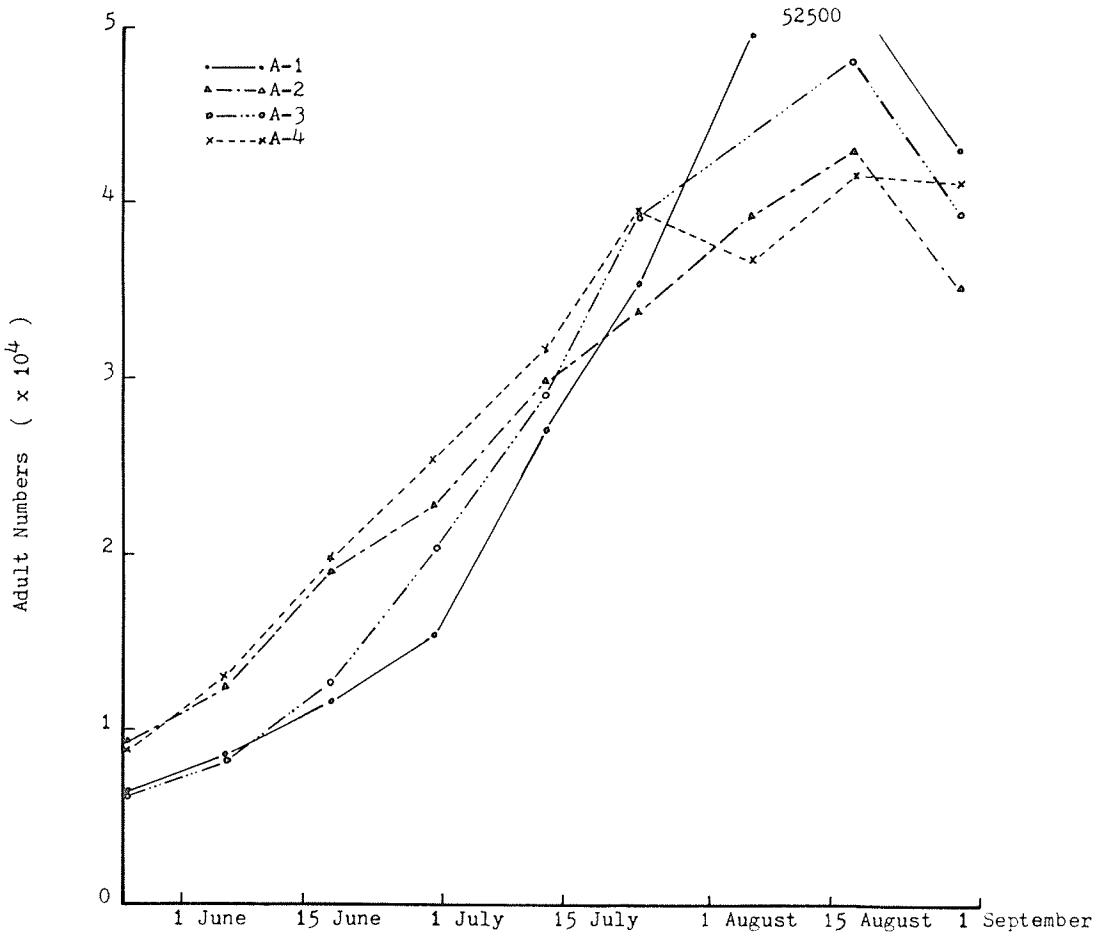

Figure **26**. Adult populations of honey bees: Colonies A-1 through A-4. (1969).

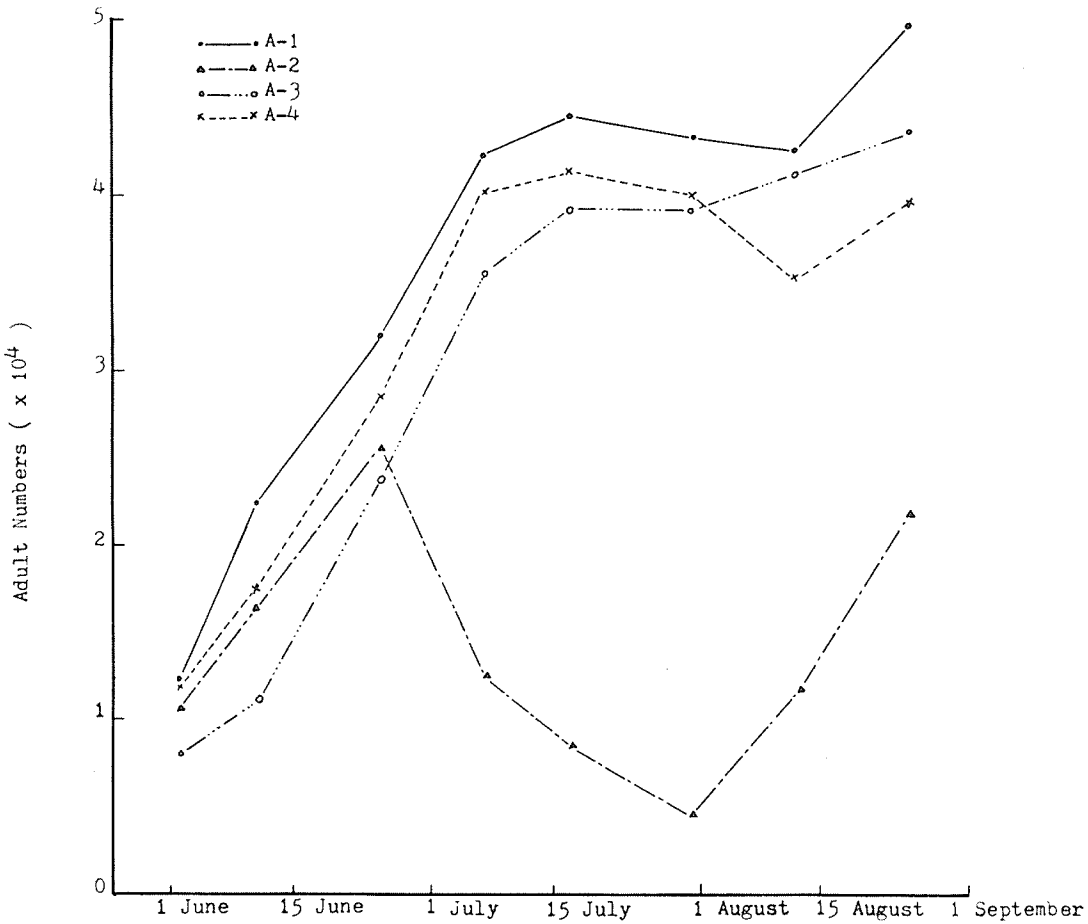

Figure 27. Adult populations of honey bees: Colonies A-1 through A-4. (1970).

The initial peak is followed by a decline, which, in turn, is followed either by one major peak or several of varying magnitude for the remainder of the season. In three out of the four colonies in 1969, the major peak of the season (indicating the greatest amount of total brood) falls either within the last week of July or within the first week of August. The fourth colony (A-2/69) maintained a relatively steady level of brood, slightly below the initial peak, but with only minor fluctuations.

In two out of the four colonies in 1970 the major peak likewise occurred in the last week of July. However, in A-2, which had swarmed on 4 July, and which was left to rear its own queen, all brood had emerged by 7 July, and the young queen had not yet begun to lay and in A-3 the queen was superseded during the last week in July. (An indication of the impending supersedure was given by the steadily declining oviposition rate. Figure 24). The virgin queen was replaced with another laying hybrid queen, two frames of brood (and accompanying nurse bees) resulting in an upswing in the total brood curve.

Thus, the following pattern emerges: an initial steep increase in total brood is followed by a peak in June - in seven out of eight colonies in both years. The major peak of the season occurred in the third week of July or the first week of August in three of the 1969 colonies and in

two of the 1970 colonies. Although the last brood measurements of the season were carried out on the 29 August in 1969, and on the 25 August in 1970, frequent inspections during the autumn of 1969 revealed that brood rearing declined steadily during September and had ceased entirely by the second week of October. Similar observations were made by Jeffree (1959).

A comparison of the individual brood curves obtained in both years further shows that the amount of sealed brood present in the colonies was considerably higher in 1969 than in 1970. Although one of the two "normal" colonies in 1970 showed a somewhat reduced oviposition rate in comparison to that of the 1969 colonies, this would not account for the trend which also occurred in the colony not showing queen problems. Neither brood diseases nor a shortage of pollen (or pollen supplement) were factors in either year. Similar observations were made by Nelson (1970) in an apiary 5 miles from the present site, and in which different strains of bees were used, suggesting that some factor, inherent in the season, and operating over a wide area, may have been responsible for the differences observed.

The adult populations for 1969 show the pattern of increase, as described by Nolan (1932) and Farrar (1968). The initial steep increase continued with only small fluctuations to mid-August, when peak populations between 42,000

and 52,000 bees were reached. A decline followed in all colonies, until 29 August, when the brood readings and adult estimates were discontinued.

In 1970 the initial period of rapid population build up continued in three of the four colonies through June until the first week in July, when the rate of increase began to level off. An initial peak between 39,000 and 44,500 adult bees in mid-July was followed by a slight decrease in colony growth, and by a further increase until the 25 August, when brood measurements and adult estimations were discontinued.

The fourth colony (A-2) (Figure 23) was found to be queenless on 25 June. At that time more than thirty queen cells had been constructed, and it was assumed that the queen had been lost during the last brood reading. In order to determine what changes might occur in the honey stomach contents of the bees as a result of the imbalance in colony population, the queen cells were left intact and the collection of bees from the various locations within the colony was continued as had been planned, with the exception that categories not represented at the time, such as BO (after all brood had been sealed) were omitted. Instead of mating and beginning to oviposit, the virgin queen left with a swarm on 4th July. The swarm was not recovered. By 31 July, when the colony had reached its lowest population (4,600 bees,

covering approximately three frames) young bees were starting to emerge and the population of colony A-2 again increased.

Many factors, operating both within and outside of a honey bee colony influence its development throughout the season, and determine its rate of growth, as well as the ultimate numerical size it may attain. Each of these has a multiple effect, that is, while it may influence the colony directly, it also modifies the effects produced by other factors. As a consequence of these interrelationships, it is frequently difficult to evaluate the direct relationship between a given factor and the colony. In the following discussion the effects of some of the factors known to influence the development of a colony and its activities will be reviewed, and possible applications to the present problem will be discussed.

Although the potential egg laying ability of the queen ultimately determines the numerical size which a colony may attain (Jebsen, 1957; Nolan, 1925; Moeller, 1961; Farrar, 1968), the number of bees present in the colony determines the actual amount of brood which that colony can support (Merrill, 1925; Nolan, 1925; Allen and Jeffree, 1956; Farrar, 1968). Farrar (1968) stated that the average daily rate of egg laying increases with a rise in population up to 40,000 bees. Merrill, (1924b; 1925) found that the

relative number of emerging adults depends not on the numbers of eggs laid, but on the conditions existing within the colony. He observed that during periods of inclement weather, when the bees were confined to the hive, the amount of open brood increased, but that when the weather improved, many of the foragers deserted the brood, and the relative amount of brood reared by the colony remained more or less constant. Merrill (1925) further found that the ratio between the numbers of eggs laid and the numbers of adults reared from them varied from colony to colony, but remained relatively constant for any given colony. This he termed its "brood rearing power".

In general, the ratio between sealed brood and colony population decreases ten to fourteen per cent for each increase of 10,000 bees (Farrar, 1968), so that while a large colony still rears a larger total amount of brood than a much smaller colony, relatively fewer of its bees are engaged in brood rearing, and a higher proportion of its workers is available for field duty (Moeller, 1961). Free and Racey, (1968) suggested that the decreasing proportion of bees participating in the rearing of brood in growing colonies, may be due to a decreasing amount of pheromone received by each worker.

This tendency was observed when the brood and adult population curves of the experimental colonies were compared.

Here, as the amount of sealed brood and the numbers of adult bees increased the amount of open brood increased initially and then levelled off.

The amount of comb space available to the queen may limit oviposition (Farrar, 1937)[1]. Nolan (1925) observed that the use of brood combs for the storage of nectar resulted in a limitation of comb space available for brood rearing, and Farrar (1927), observed a tendency for smaller packages to place nectar into and around the brood nest, thus restricting egg laying by the queen. Similarly, I have frequently observed that the storage of pollen in cells vacated by emerging bees, results in a lack of empty cells for oviposition. Simpson (1969) found that in a cool climate, such as that of Great Britain, a "mature" honey bee colony requires three ten-frame Langstroth hive bodies in order to contain all of its bees, and concluded that confinement of the queen to one hive body did not constitute a restriction in brood area available to her. He stated, however, that during a nectar flow, or in warm climates, more space would be required. Nolan (1925), however, concluded that less brood would be reared if the queen were confined to a single hive body rather than to two hive bodies.

The age of a queen may influence the amount of brood reared by her colony. Results obtained by Nolan (1925)

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[1] Farrar, C.L. 1937. The influence of colony populations on honey production. J. agric. Res. 54:945-954.

suggest that one year old queens, as a rule, are more prolific than are two year old queens. Merrill (1924d) found that old queens ceased egg laying earlier in the fall than did young queens, and that colonies headed by old queens frequently reduced brood rearing during a flow, while colonies with young queens did not.

Pollen is utilized by honey bees in various ways. Young bees feed heavily on pollen, especially during the first two weeks of adult life. (Hagedorn and Moeller, 1967; Maurizio, 1959; Haydak, 1970). This results in the development of the hypopharyngeal glands, fat bodies, wax glands and other organs, and lengthens the life of the individual bee (Maurizio, 1959; 1961; Standifer, 1967). That pollen is essential for brood rearing, has been demonstrated by Haydak (1935), who found that colonies maintained on a pure carbohydrate diet were unable to rear brood for longer than two weeks. Bees reared during that time were found to be low in protein, particularly in the abdomen, when compared to bees of the same age, that had been reared normally.

A similar dependence of brood rearing on the availability of pollen has been found by other workers (Nolan, 1925; Parker, 1926; Spencer-Booth, 1960). A direct relationship exists between the amount of stored pollen and the amount of brood reared (Farrar, 1934; Allen and Jeffree, 1956). The amount of brood reared during the spring and

summer is directly related to the amount of pollen collected by the colony (Todd and Bishop, 1941). The reverse relationship also holds: the greater the amount of brood present in a colony, the more pollen is collected by its foragers (Louveaux, 1959; Spencer-Booth, 1960; Free, 1967a). Not all pollens are of equal nutritive value to honey bees (Louveaux, 1959; Spencer-Booth, 1960; Standifer, 1967), and a diet consisting of pollen from only a few plant species may give rise to nutritional deficiencies which could lower the resistance of brood and make them susceptible to certain brood diseases (Louveaux and Albisetti, 1963). A lack of natural pollen can be circumvented by the beekeeper through the feeding of other types of proteins, such as soybean flour, dried skim milk or dried yeast (Haydak, 1958; Spencer-Booth, 1960; Farrar, 1968), either as part of a pollen substitute or as a supplement to which pollen trapped during the previous season is added.

Brood rearing is also influenced by the amount of carbohydrate food available to the colony (Nolan, 1925; Farrar, 1927; 1968; Free, 1967; 1968). Merrill (1924a, 1924b, 1924c) found that colonies with low stores of honey supported much less brood than did colonies with an abundance of honey. He observed that the latter can maintain brood rearing even during short periods of inclement weather, while colonies with insufficient stores reduce the amount

of brood reared. In the present experiment this became evident during the early spring of 1969, when one of the experimental colonies supported much less brood than did the other three, despite the presence of several combs of sealed honey along the outside walls. It was also noted that no honey was stored in the cells directly above the brood. When sugar syrup was given, the amount of brood reared by the colony increased.

In experiments done by Free and Spencer-Booth (1961) the feeding of sugar syrup resulted in an increase in brood rearing when natural pollen was available; no such effects were noted in the absence of pollen. Similarly, Farrar, (1936) found that colony populations, during the spring flow, increased approximately in proportion to the pollen reserves. However, Todd and Bishop (1941) pointed out that nectar flows are not always related to pollen income, and that nectar flows from orange are associated with a decrease in amount of pollen collected, and a reduction in brood rearing.

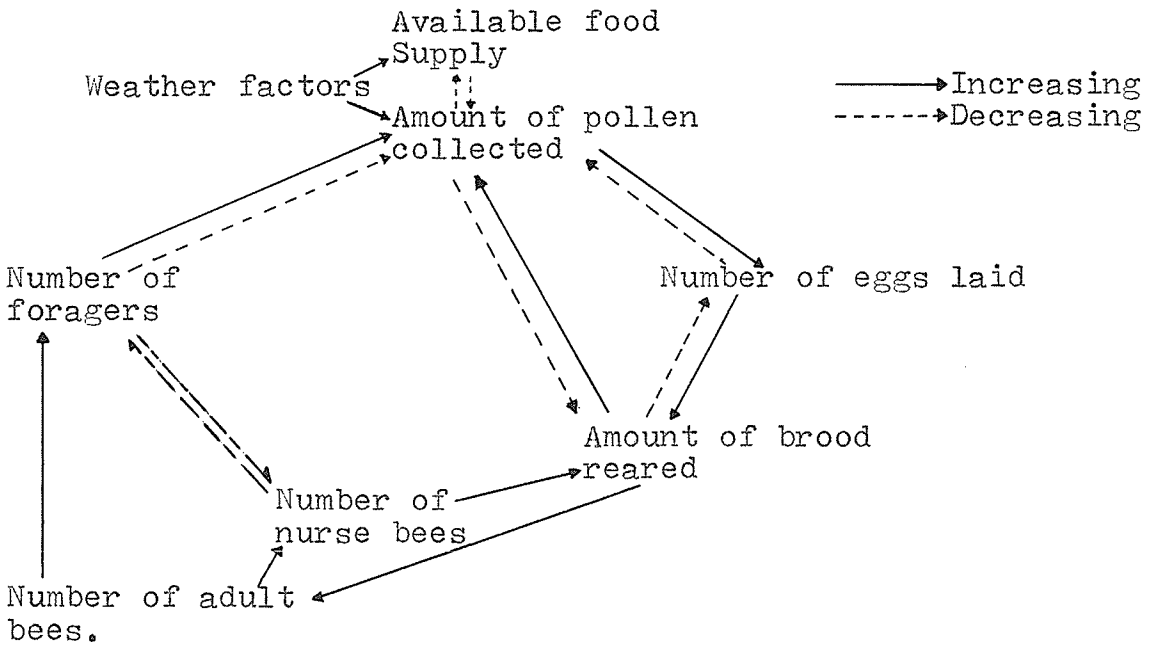
The net influence of temperature on brood rearing is not clear. According to Merrill (1924d) brood rearing, in the spring, is initiated by a brief period of temperatures high enough to permit a general flight, followed by a sharp temperature decrease. The reformation of the cluster is thought to result in a temperature higher than would have

occurred, had the bees not flown, and this in turn stimulates the rearing of brood. In general, during cool weather a colony of bees remains more or less tightly clustered (Wilson and Milum, 1927), and only a little brood is reared. Decreased temperatures occurring after brood rearing had been started resulted in a reduction in the amount of brood reared (Nolan, 1925; Pankiw, 1968). With the approach of warmer weather, the cluster expands, resulting in an expansion of the brood nest and an increase in the amount of brood reared. Warm weather also stimulates plant growth, and the increase in both pollen and nectar brought into the hive stimulates brood rearing, as well (Todd and Bishop, 1941; Free, 1967a). However, Farrar (1927) stated that as a result of the increased forage available in the field at a time when the colony is still small, the desertion of brood by foraging bees may curtail the amount of brood reared by the colony. Similar observations were made by Merrill (1925). The role of environmental temperature in the regulation of the amount of pollen and nectar brought into the colony, and thereby its influence on brood rearing, has been discussed. A direct influence of summer temperatures on brood rearing has not been observed, however (Ribbands, 1953).

The effect of day length on brood rearing has been studied by several authors. Pankiw (1968) using package colonies, was unable to determine any effect of the length

of day on the amount of brood reared. Only those colonies which had been maintained in complete darkness, showed a significant reduction in the amount of brood reared. However, Cherednikov (1968), found the reduction in brood rearing in the autumn to be a reaction of the worker bees to the decrease in day length. Kefus (1967), working with observation hives in controlled environment rooms, found that decreasing day length resulted in a decrease in the amount of brood reared, and that an increase in the length of the day resulted in an expansion of the brood nest.

The relationships existing between the environmental temperature, supply of pollen and nectar, the amount of brood present in a colony, and its population can probably best be expressed in the form of a flow chart adapted from Free (1967):



It is evident from this flow chart that one of the primary factors influencing the activities of honey bees within the colony is the availability of both pollen and nectar, which in turn is influenced by the prevailing environmental temperature. In general a change in one of the factors listed in the chart, will produce a change in one or more of the others. Thus, an increase in the amount of nectar and the amount of pollen collected, will result in a greater number of eggs laid, which may lead to an increase in the amount of brood reared and a corresponding growth of the colony population. However, more brood requires more nurse bees, which possibly reduces the number of younger foragers avilable for field work and the potential amounts of pollen and nectar that may be gathered. This may limit brood rearing. Similarly, the collection of large quantities of pollen and nectar within a short time, may lead to a shortage of comb space and a reduction in brood rearing. Thus, the various factors operating within the honey bee colony are so interrelated, that a change in any one sector of the colony will ultimately influence all parts of it.

CHAPTER IV

ANALYSES OF HONEY STOMACH CONTENTS

Introduction and Review of Literature

One of the most interesting, and at the same time, one of the most important phenomena occurring in the honey bee colony, is that of mutual food exchange or "interfeeding" among its bees. The constant exchange of food by all members of the colony serves both to supply the carbohydrate needs of each bee, thereby maintaining a relatively high level of nutrition within all sections of the community (Ribbands, 1953) and to inform all bees of the needs of the colony at the moment, concerning the resources available in the field (Lindauer, 1955; Free, 1967; 1970). In addition, mandibular gland secretions produced by the queen are passed among the workers with the food, informing them not only of the presence and physiological status of the queen, but also regulating the rearing of young queens and inhibiting ovarian development within the worker bees (Butler, 1954; 1956; Pain, 1961). The development of an odour common to all workers of a colony, by which hive mates can be distinguished from strangers, is a further result of the constant food exchange between the bees of a colony. It is thought that the colony odour consists of volatile waste products derived from the catabolism of the food circulating within the hive,

and that, since the composition of food stores varies with each colony, the odour produced by each is also different (Kalmus and Ribbands, 1952). Experiments done by Ribbands (1953) confirmed that the food of the colony is the source of colony odour.

Although the rapid distribution of both liquid food and water among large numbers of workers in honey bee colonies has been observed by various researchers (Park, 1923; 1925; Lindauer, 1952; 1955; Nixon and Ribbands, 1952; Kiechle, 1961) and the influence of isolated factors, such as age, on food exchange has been investigated by Pershad (1966), Lensky (1961, 1964), and Istomina - Tsvetkova (1953), only Free (1956; 1957) has done a detailed analysis of the various factors influencing the transfer of food from one bee to another. In general, there is a tendency for food to pass from older to younger bees. Nevertheless, there is considerable food passage in the reverse direction, and among the members of any given age group (Free, 1957). The tendency of food passing from older to younger workers roughly parallels a similar trend existing in the division of labour among honey bee workers, as was described by Rösch (1925), Lindauer (1952), and Free (1967). The foragers, which comprise the oldest group of workers in the colony, deliver their loads of nectar to the younger hive bees, who process and store it. The nurse bees, which constitute the

youngest group of workers, receive the nectar needed for brood rearing from them. While drones are frequently fed by the workers, they have never been observed to reciprocate (Mindt, 1962; Free, 1967). Queens, likewise, are normally fed by the workers; there is evidence, however, that under some conditions a queen may feed workers (Mindt, 1962).

It has been suggested that continuous food exchange, among the workers of a colony, quickly results in a homogenization in the concentration of food carried by most of its workers. Exceptions occur only in those workers which are active in limited areas of the hive, where temporary deviations from the "normal" situation exist, i.e. overheating in a part of the brood area (Kiechle, 1961). According to Kiechle, it is in this way that foragers are informed of the concentration of food required, even before leaving the hive on their first flights of the day. Lindauer (1955) investigated the honey stomach contents of foragers leaving their hives and of hive bees taken from the top bars (i.e. from the feeder hole built into some German bee hives), and found considerable differences in sugar concentration among individual workers of each group, which he presumed to be due to the duties performed by each bee prior to its capture. However, the mean concentrations of the honey stomach contents were found to be very similar in both groups; Lindauer therefore concluded that foragers choose the forage collected

in the field at least in part on the basis of the concentration of the food received in the hive.

In general, the sugar concentration of honey stomach contents appears to be closely related to the duties performed by the bee at any given time. Thus, Park (1932) found that the sugar concentration in the honey stomach of a foraging bee approximates that of the nectar in the flowers on which she has been working. Water foragers and 'reservoir bees' (Park, 1923) tend to have honey stomach contents of very low sugar concentration, while hive bees processing nectar may contain sugar solutions varying in concentration between that of incoming nectar and nearly ripened honey (Park, 1925; 1927; 1928). In addition to pollen and honey, considerable quantities of water are required for brood rearing (Lindauer, 1955; Haydak, 1970). It seems reasonable to assume that the honey stomach contents of nurse bees are relatively high in water content and relatively low in sugar concentration. It may be concluded therefore, that the sugar concentration of worker bee honey stomach contents may vary considerably, subject to a variety of factors, including the duties performed by the individual bees, the amount of brood in the colony and the availability of food and water in the field. Although a few studies have been done on honey stomach sugar concentration, data on the sugar concentration in the honey stomachs of bees taken from

various locations within the same hive and at the same time, are not available.

A detailed study of the amount of food carried by honey bee workers performing a variety of tasks in the same hive at the same time has only been done by Feng (1969), Department of Entomology, University of Manitoba. He concluded:

> "Regardless of time of day or season the gradation of honey stomach weights can be expressed generally as follows: honey comb> brood comb> nectar gatherers > pollen gatherers > leaving hive. Bees on open cells had heavier honey stomachs than those on sealed ones and bees returning to the hive (pollen and nectar gatherers) had heavier honey stomachs than those leaving it. The heaviest loads of nectar and pollen were collected at 1700-1800 and 1300-1400 hours respectively. The honey stomach weight patterns of both nectar and pollen gatherers followed closely the honey flows. The honey stomach weights of bees on honey and brood combs varied considerably throughout the day but they had patterns similar to each other throughout the season with two peaks occurring, one in July and one in August.
>
> It is concluded that the weight of honey stomachs of bees is affected by the time of day and season when they are foraging, as well as by their location in the hive at these times."

The effect of environmental factors on honey stomach weight has also been investigated. As in most biological reactions, no one factor appears to govern the amount of syrup or nectar carried by individual bees. Rather, a bee reacts to a complex of influences, each of which interacts with the others. Thus, von Frisch (1965) found that under the conditions of his experiment, foraging bees took

greater quantities of concentrated than of dilute sugar solution. Núñez (1966) was able to confirm the results obtained by von Frisch, and found in addition that increasing air temperature (but not syrup temperature) resulted in an increased uptake of sugar syrup. The "quality" of syrup or nectar strongly influenced the amount of syrup taken back to the hive by a forager, in experiments done by Núñez (1966). He found that by increasing either the sugar concentration, the rate of flow or both (i.e. by increasing the "quality" of the syrup) he could induce a forager to take a greater amount of syrup back to the hive. However, Wells and Giacchino (1968) were unable to find any correlation between sugar concentration and the amount of syrup taken. They did find, however, that the size of a bee was positively correlated with the amount of syrup taken; the capacity of the honey stomach appeared to be the determining factor.

The distance between the hive and the feeder also seems to influence the amount of syrup taken. Schuå (1952) observed that at distances greater than approximately 1000 meters, foragers tended to increase the load taken at the feeder. The extra amount was found to correspond to the amount of sugar used on the flight to the feeder. Schuå also reported that changes in the electropotential of the air during unsettled weather appeared to be related to changes in the amount of syrup taken at the feeder.

Both Free (1957) and Feng (1969) found previous experience to be of importance in determining the amount of food retained in the honey stomach. Thus, bees which had been fed constantly retained smaller quantities of sugar solution in their honey stomachs than did bees which had been fed intermittently, or which had been starved for several hours. Bees which had been starved for 24 hours and then offered syrup of different concentrations retained more of the concentrated syrup than of the dilute (Free, 1957). An improvement or deterioration of a natural crop had similar effects. Although bees about to give food generally carried more in their honey stomachs than did bees about to receive food, there was considerable overlap in the relative amounts carried by both groups (Free, 1957); not infrequently the donor retained less food in its honey stomach than did the bee about to be fed.

Most of the work done on the incidence of pollen in the honey stomach contents of worker bees has been confined to studies of the filtering action by the proventriculus and the mechanism of pollen digestion, and on the identification of pollen grains found in honey and nectar, with reference to the identification of the floral sources of honey. For a review of the pertinent literature, see Chapter V.

Although little work has been done to determine the

concentration of pollen in worker honey stomach contents relative to the division of labour among bees, it may be worthwhile to review what is known about some of the factors influencing the amount of pollen found in the honey stomachs of worker bees. It has generally been assumed that pollen is pushed or shaken into the nectar of a flower, as the insect brushes against the anthers in its attempt to reach the nectaries (Maurizio, 1951; Pritsch, 1957; Demianowicz, 1964). The quantity of pollen reaching the nectar in this fashion is further influenced by a number of factors, including flower structure (Free, 1960; 1962), the position of the flower, i.e. whether it is upright or pendant (Maurizio, 1949), manner of reproduction (monoecious or dioecious, Melville, 1945), time of anther dehiscence in relation to first flowering (Synge, 1945), and the amount of pollen produced by the plant species being worked (Maurizio, 1948). A bee actively "scrabbling" for pollen (Free and Spencer-Booth, 1964) would tend to force more pollen into the nectar, particularly in a flower that is upright, than would a bee gathering nectar only. Throughout the time during which a load of nectar is being collected by a forager, pollen is removed from its honey stomach through the action of the proventriculus (Todd and Vansell, 1942). The same activity also occurs within the hive bees who process the nectar before storing it in the combs as honey.

Very young workers and nurse bees engaged in brood rearing activities frequently consume large quantities of pollen (Moeller and Hagedorn, 1967; Haydak, 1970). Although workers of these age groups usually receive food more often than they feed others, the feeding of older bees does occur (Free, 1967). It may therefore be assumed that some pollen is transferred to the older workers also, including those engaged in the processing of nectar. It has been shown that not all pollen grains are removed from the honey stomach before its contents are stored in the comb (e.g. Berner, 1952; Maurizio, 1958; Demianowicz, 1964).

Thus, it seems that there are two sources of pollen: (a) that which has been accidentally pushed into the nectar, before being gathered by bees, and (b) pollen derived from that stored within the colony, and eaten by young bees and nurses. Although the proventriculus is highly efficient in the removal of pollen from the honey stomach, rarely is all pollen removed from the honey stomach contents, and therefore some pollen is almost always transferred to other bees along with the liquid food.

Method

In this study worker bees (and some drones) were collected twice daily from various locations within four honey bee colonies approximately every twelve days throughout the summers of 1969 and 1970. The mean honey stomach weight, the sugar concentration, and the concentration

of pollen of the honey stomach contents were determined for each category of bees collected; the results obtained for each of the five major categories (i.e. those which were collected throughout both seasons) are shown in Figures 28 through 45 . The results obtained for categories of which only a few samples were collected (in 1969), are not presented graphically; however, the mean values obtained for each 30-bee sample, of all categories collected, are given in the Appendix Tables I through XIX . The discussion of the results will be divided into three sections, i.e. (a) honey stomach weights, (b) sugar concentration, and (c) pollen content. These will be followed by a brief summary and conclusion.

Results and Discussion

Honey Stomach Weights

Figures 28 through 33 , and Table III , show the mean honey stomach weights of bees collected in various locations within the four experimental colonies. In the curves each point represents the mean weight obtained from the four sample means (A.M. or P.M.). Using the t-test, intercolony differences were found to be non significant at the 5% level.

Foragers entering hives - Figure 28 shows the honey stomach weights obtained from nectar foragers returning

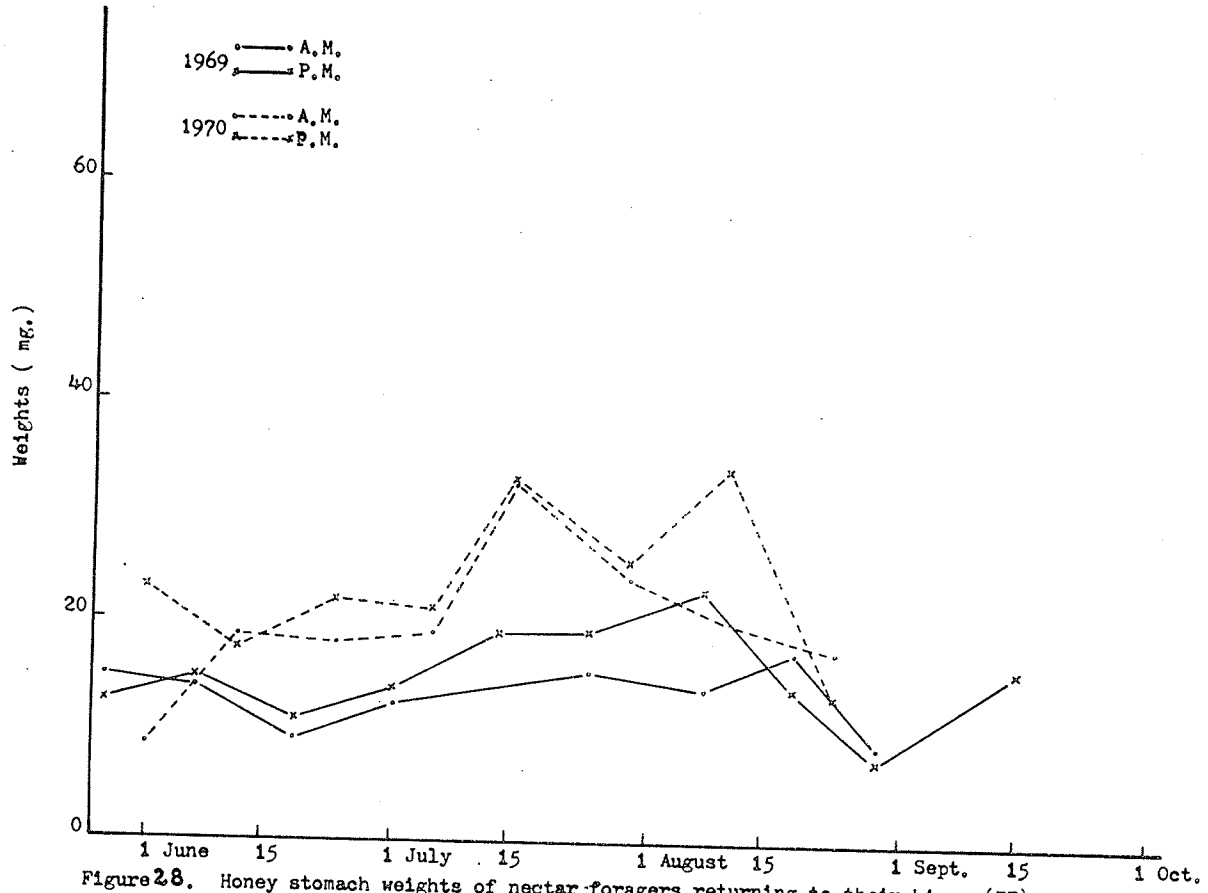


Figure 28. Honey stomach weights of nectar foragers returning to their hives (FE).

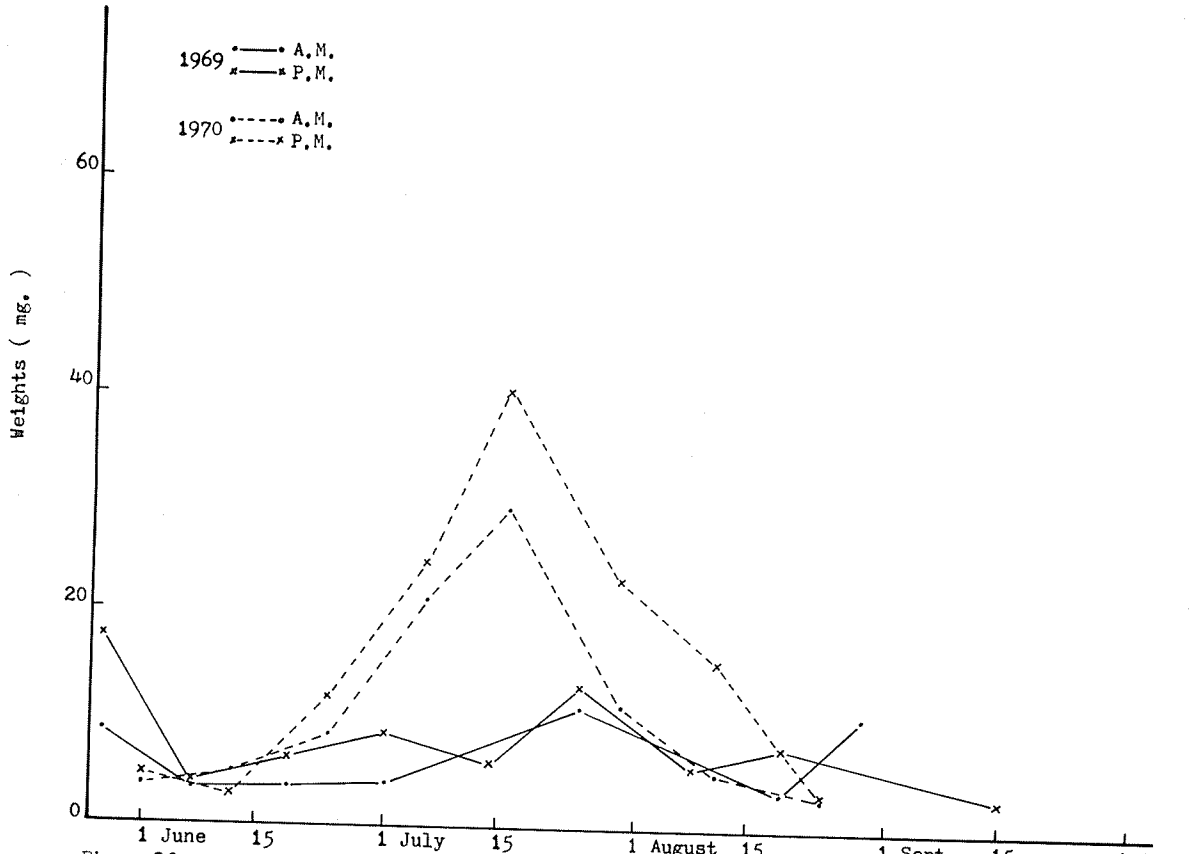


Figure 29. Honey stomach weights of pollen foragers returning to their hives (PFE).

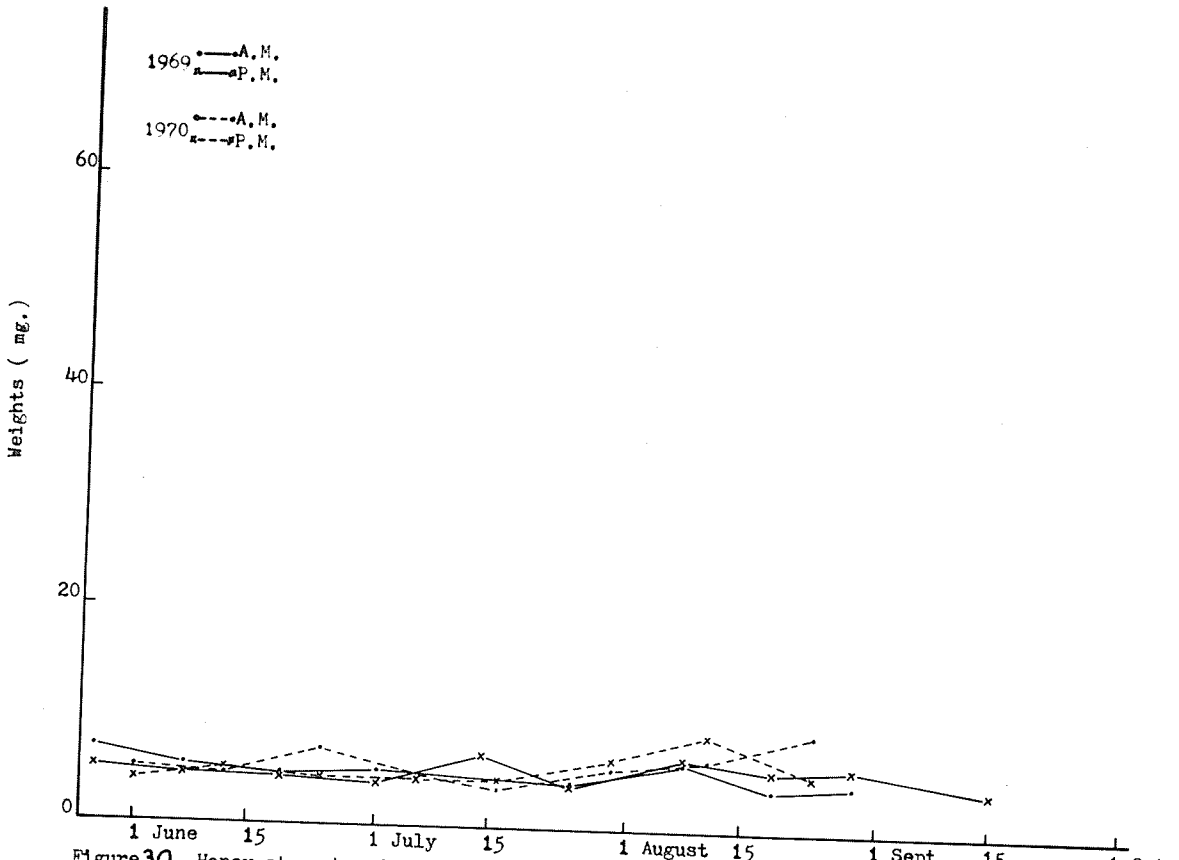


Figure 30. Honey stomach weights of foragers leaving their hives (FL).

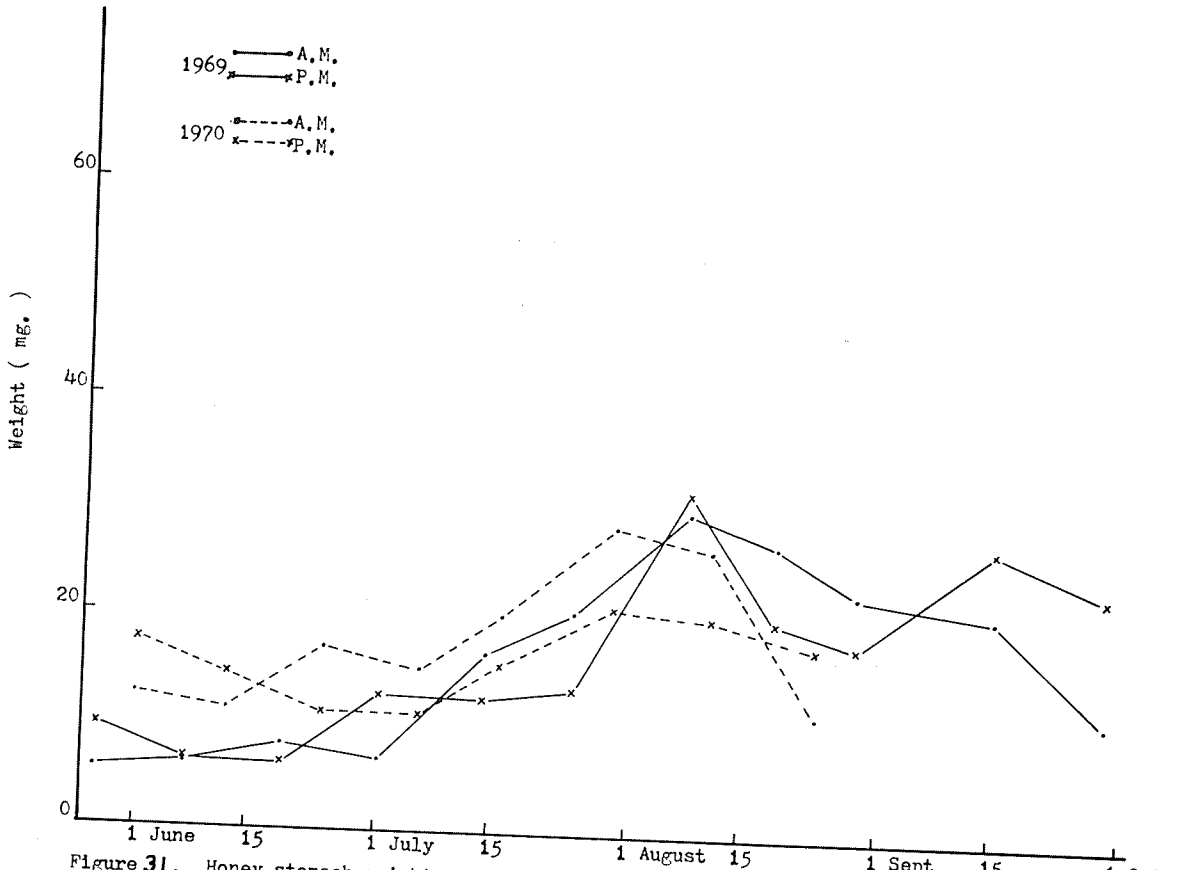


Figure 31. Honey stomach weights of bees caught on open brood (BO).

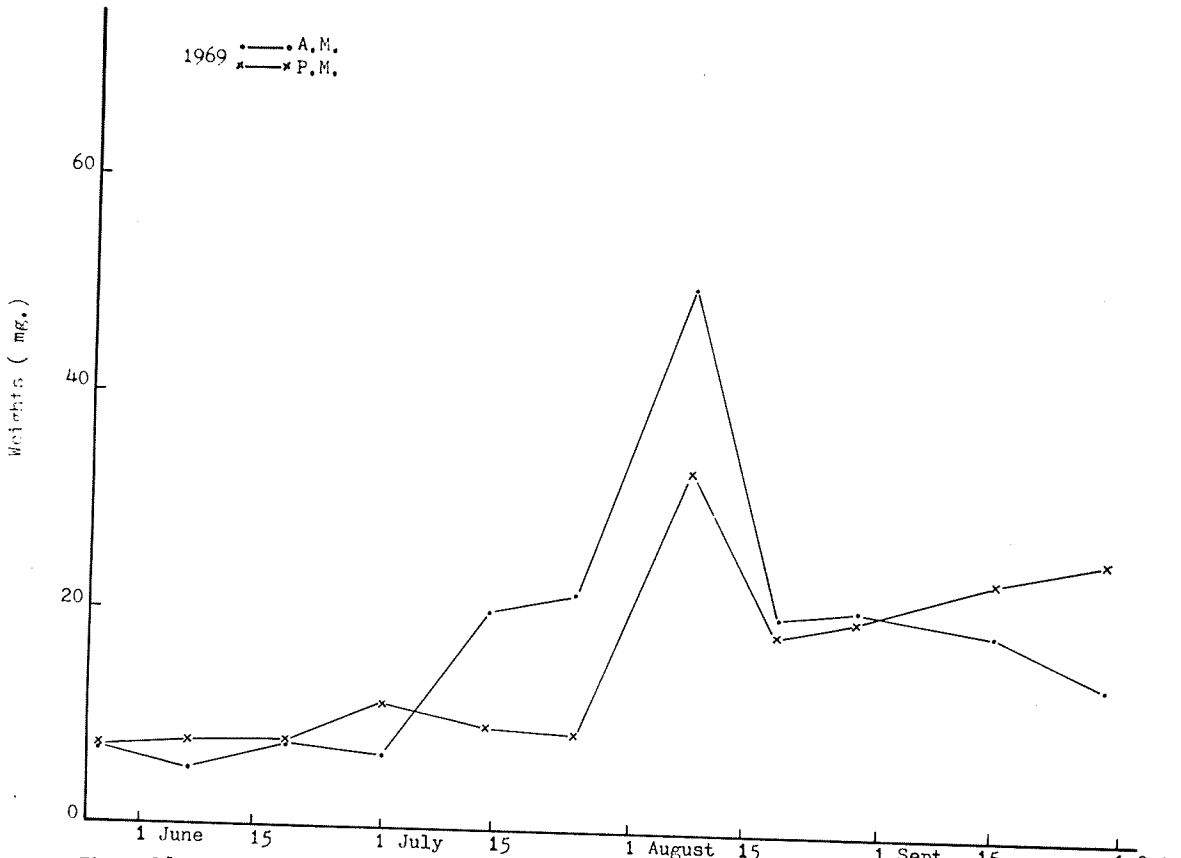


Figure 32. Honey stomach weights of bees caught on sealed brood (BS).

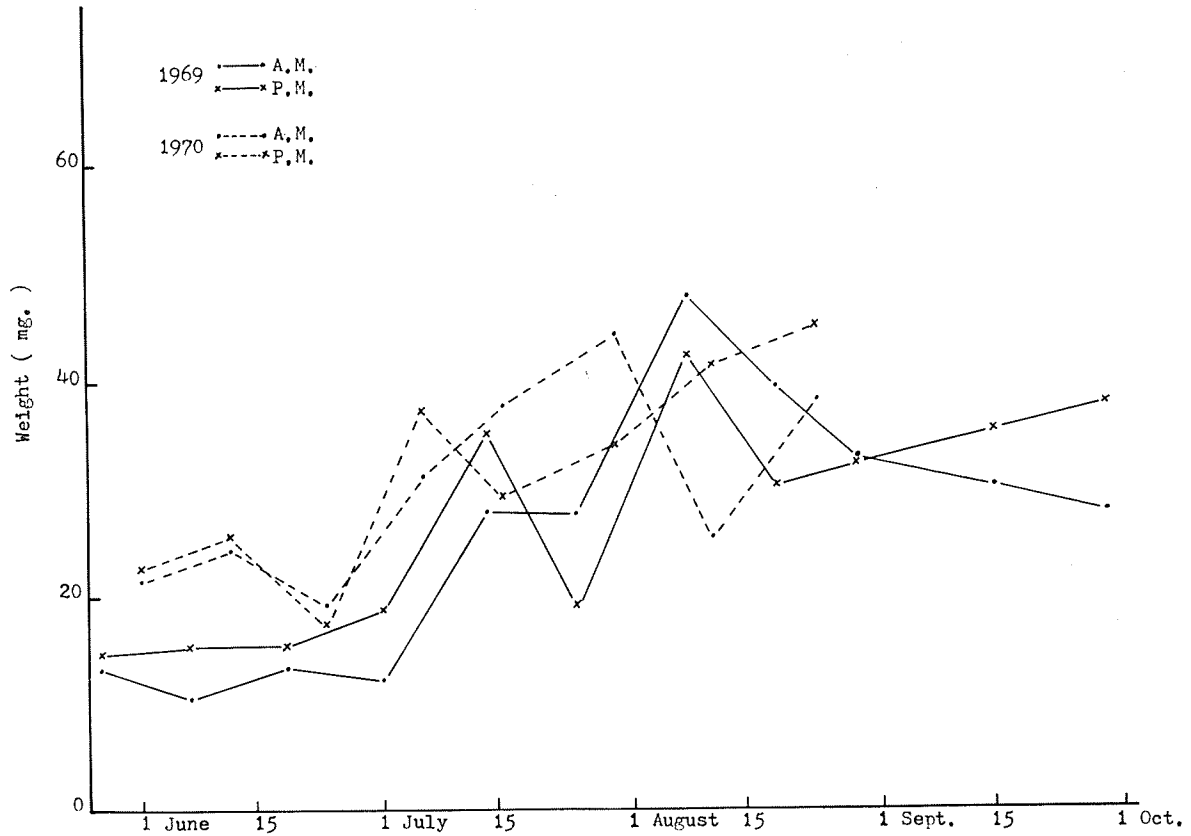


Figure 33. Honey stomach weights of bees caught on open honey (HO).

	FE				PFE				FL				BO				HO			
	1969		1970		1969		1970		1969		1970		1969		1970		1969		1970	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
June vs July	-	+*	+*	+*	-	-	+*	+*	-	-	*+	-	+*	+*	+*	-	+*	+*	+*	+*
June vs August	-	-	-	-	-	-	-	-	-	+*	+*	+*	+*	+*	-	-	+*	+*	+*	+*
July vs August	-	-	-	-	-	-	*+	*+	-	-	*+	+*	-	-	-	-	+*	+*	-	-

Table III a. Statistical comparison of honey stomach weights, by month, within each year. Statistic used: Student's t-test.

Symbols:

1. FE = Foragers caught entering their hives.
2. PFE = Pollen foragers caught entering their hives.
3. FL = Foragers caught leaving their hives.
4. BO = Worker bees caught on open brood.
5. HO = Worker bees caught on open honey.
6. + = Difference is significant at the assigned level of 5%.
7. - = Difference is not significant at the assigned level of 5%.
8. * = Position of asterisk indicates which of the two months compared had higher values.

	FE				PFE				FL				BO				HO			
	1969		1970		1969		1970		1969		1970		1969		1970		1969		1970	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
June	-	-	-	+	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-
July	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
August	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	+

Table III b. Statistical comparison of honey stomach weights, by time of day. Statistic used: Student's t-test. Symbols: As above. + placed according to time of day at which heavier honey stomachs were collected.

For statistical analysis, the values obtained from the 26 May, 1969, collections were combined with those of June, 1969, and values obtained in September with those of August, 1969.

Location	Month	Time	Statistical Significance		
			Weight	CHO	Poll.
HO	June	AM	+*	+*	-
		PM	+*	-	*+
	July	AM	+*	-	-
		PM	+*	-	-
	August	AM	*+	*+	+*
		PM	-	*+	-
BO	June	AM	+*	+*	-
		PM	+*	+*	-
	July	AM	-	-	-
		PM	-	-	-
	August	AM	-	-	+*
		PM	-	*+	-
FE	June	AM	-	*+	-
		PM	+*	-	-
	July	AM	+*	-	-
		PM	+*	-	-
	August	AM	-	-	-
		PM	-	-	-
FL	June	AM	-	-	-
		PM	-	-	-
	July	AM	-	-	-
		PM	-	+*	+*
	August	AM	+	+*	+*
		PM	-	+*	-
PFE	June	AM	-	-	-
		PM	-	-	-
	July	AM	+*	-	-
		PM	+*	+*	-
	August	AM	-	+*	-
		PM	-	+*	-

Table IV . Statistical comparison of honey stomach contents, by month, 1969 versus 1970.

Symbols:
+ Difference is significant at the 5% level.
- Difference is not significant at the 5% level.
* Position denotes the year in which the higher values were obtained (i.e. *+ = 1969, +* = 1970).

to their colonies, throughout both 1969 and 1970. A seasonal trend which is similar for both years is apparent: relatively small loads were brought in during June in both years; there was an increase in the amount of nectar gathered by each bee during the first week of July, i.e. in the beginning of the main nectar flow (also see Feng, 1969). The largest average loads were brought into the hives in mid-July, and again during the second week in August. This was followed by a decrease in the average amount carried by the foragers during the final two weeks in August, when the main nectar flows ceased. The reduction in honey stomach weights measured in bees collected in the morning during the second week in August, 1970, may have been due to decreasing temperatures (also see Feng, 1969). In 1969, an extended autumn period which enabled the bees to forage on sunflowers, cucurbits, mustard and some volunteer rape, probably accounted for the slight increase in the mean honey stomach weights which occurred during the first two weeks in September.

Overall differences between the flows of both years are reflected in the mean honey stomach weights measured during both seasons. As is shown in the graphs, the mean honey stomach weights measured through the 1969 season are lower than those obtained in 1970. For a statistical comparison*

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*In this and the following discussions, only differences in honey stomach weights that were significant at the 5% level are mentioned.

between years, see Table IV.

As can be seen from Table III a, in 1969 the bees collected in the afternoons during July had heavier honey stomachs than did those collected on June afternoons, while in 1970, all collections made in July had significantly higher mean weights than those made in June.

Pollen foragers caught returning to their hives - The mean honey stomach weights of pollen foragers collected in 1969 and 1970 are shown in Figure 29 . Unlike the curves obtained from the mean honey stomach weights of nectar gatherers, which show a similar seasonal trend for both years, no such tendency is apparent here. Thus, in 1969, the highest pollen forager honey stomach weights were obtained in the beginning of the season. Pollen foragers caught during the first week in June carried much less food in their honey stomachs. A gradual increase in the honey stomach weights occurred through June and the first three weeks in July, followed by a decrease, with fluctuations, for the remainder of the season. However, in 1970, the pollen foragers collected during the first two weeks in June carried very little in their honey stomachs on returning to the hive. Through the remainder of June and until mid-July, the amount of nectar carried increased rapidly; in mid-July the mean honey stomach weight of the pollen foragers collected in the afternoon was 40.2 mg., approximately 6 mg. more

than was recorded for nectar gatherers at any time during the 1970 season. The rapid increase was followed by an equally rapid decrease for the remainder of the season.

For a statistical comparison between years, see Table IV. A comparison of the honey stomach weights between months within either year (Table III) shows that in 1970 the honey stomach weights of the pollen foragers were significantly higher in the afternoons of July and August, than in the mornings, and that they were significantly higher in July (both A.M. and P.M.) than in either June or August.

The reasons for the differences in the results obtained in 1969 and 1970 are not known. It is possible that under the marginal foraging conditions frequently encountered in 1969, only those bees foraged for pollen, which actually "specialized" in this task (Ribbands, 1952), but that under the much better foraging conditions of 1970 nectar as well as pollen were gathered by the same bees.

Although the nectar flow did not start until the first week in July (Figures 12 through 17), an increase in honey stomach weights of pollen foragers was already found in the bees collected during the third week of June, 1970. The term "nectar flow" (as defined on page 53 ,) signifies a net increase in colony weight due to nectar gathered by its foragers over a period of several consecutive

days. Although the scale colonies did not show such net gains until approximately two weeks later, sufficient nectar may have been available in the field in late June to account for the increases in honey stomach weight observed.

Foragers caught leaving their hives - As can be seen from Figure 30 , foragers carried very small loads in their honey stomachs when leaving their hives to return to the fields. Although minor fluctuations did exist, the quantities carried were very similar in both years and throughout both seasons. Nevertheless, a statistical analysis shows some significant differences. (Tables IIIa and IIIb). These differences can probably be explained as follows. According to von Frisch (1965) foragers leaving their hives take with them enough food to meet their metabolic needs on the flight to their foraging areas. The amount of food taken is dependent on the energy expenditure; the differences in the amount of food taken may be due either to differences in distance flown, or to some other factor, such as wind resistance, which requires an increase in energy expended.

The small degree of variation in the amount of food taken seems to indicate that throughout both years much the same area was covered by the bees, and that the distances flown between the crops and the hives did not vary by much.

Bees caught on open honey - Although subject to considerable fluctuations, the seasonal trends indicated in the

graphs (Figure 33) follow those of the nectar flows both in 1969 and in 1970. In the two years worker bees collected on open honey carried less food in their honey stomachs in June than at any other time during the season. A sharp increase in mean honey stomach weights was noted during the first week in July; the increase in mean weight became more gradual through the remainder of July and the first week in August, 1969, and was then followed by an overall decrease in mean honey stomach weight. In 1970, however, a slow increase was still apparent at the time of the last collection; it is possible that, had the collection of bees been continued, a decline in the amount of food held in the honey stomachs would have occurred through the month of September in 1970, as well.

Table IV shows the statistical comparison between years. It should be noted that the honey stomach weights of bees caught on open honey were significantly higher in June and July of 1970 than in the corresponding months in 1969. However, in August of 1969 the honey stomach weights were higher in the mornings, than they were in the mornings of August, 1970. A comparison of honey stomach weights of bees collected in the mornings and in the afternoons (Table III b.) shows that a significant difference occurred only in August, 1970; the honey stomachs were heavier in the afternoons.

In 1969, the honey stomachs of bees caught on open honey were heavier in August (A.M. and P.M.) than in July, and heavier in July than in June. However, in 1970, the weights were greater in July than in June, but no significant differences existed between August and July (Table IIIa).

Worker bees caught on open brood - As in bees on open honey, the amount of food carried by nurse bees (i.e. those caught on open brood Figure 31) appears to be related to the amount of nectar brought into the colony by the foragers (Figure 28). An initial period of low average honey stomach weights, which lasted through June of both years, was followed by a gradual increase, through July and the first week in August. For the remainder of the season, the bees tended to retain decreasing amounts of food, which appear to be correlated to the decreasing amounts of nectar available to the foragers. In general, the amount of food retained by the nurse bees at any given time throughout both years was considerably less than that held by workers collected on open honey, on the same date. Similarly, the fluctuations in the mean weight of the honey stomachs obtained from nurses over both seasons were considerably less than were those of honey stomachs obtained from workers found on open honey.

As can be seen from Table IIIa , significant differences between years were only found in June, when the honey

stomachs were heavier in 1970. Table IIIa shows that in 1969 the honey stomachs of nurse bees were significantly heavier in July and August (A.M. and P.M.) than in June, and that in 1970, the nurse bees contained significantly more honey in July (A.M.) than in June (A.M.).

Workers collected on sealed brood - Honey bee workers were collected on sealed brood only during the summer of 1969 (see Chapter III). With the exception of one major peak which falls into the first week of August, the seasonal curves obtained from the mean honey stomach weights of bees caught on sealed brood (Figure 32), closely resemble those obtained from bees collected on open brood (Figure 31). The relationships of the peaks obtained from workers collected on 29 July, 1969, to the remaining data is not clear. These are the highest mean honey stomach weights recorded for any groups of workers during the entire two year study. They do not appear to be linked to any of the environmental factors studied.

In addition to the categories listed above, which were collected throughout the summers of 1969 and 1970, isolated samples of several other groups of bees were collected, as time permitted. With the exception of the drone samples, not enough samples were collected of any one kind to establish seasonal, or even daily trends, or to form any definite conclusions from them. They are presented here in

order to give the reader further insight, however slight, into the food relationships occurring within the honey bee colony.

Drones - Studies on the life and food consumption of drones were done by Free (1957), Levenets (1956a; 1956b), Morse et al (1967), and Mindt (1962). Of these only Free (1957) investigated the amounts of food retained by drones in the honey stomach; his findings showed that the quantity retained depends on the activity of the individual drone at the time. Thus drones about to leave the hive carried a mean amount of 20.0 mg. of honey, drones returning from a flight contained 2.5 mg. on the average, and drones collected within the colony held an average amount of 3.6 mg.

In 1969 the following 30-drone samples were collected from combs: (Appendix tables V, VIII, X, XI).

Month	No. of Samples	Mean Honey Stomach Weight
July	4	4.3 mg.
August	8	4.9
September	16	6.2

Table V . Mean honey stomach weights of drones collected on combs in July, August, and September, 1969.

The overall mean honey stomach weight of 5.5 mg. differed only slightly from the average value obtained by Free for drones occurring within the colony. Differences

in environment, strength of colonies and race of bees used, all may account for the difference found.

The average value of 6.2 mg. of food contained by drones collected in September, at the time when drones were being driven from the colonies by the workers, confirms the observation made by Mindt (1962), that drones are not starved by the workers prior to their removal from the colony.

Other categories of workers - The average honey stomach weights of other categories of workers are recorded in the following table:

Category	Month Collected	Number of Samples	Mean Honey Stomach Weight
Guards	July	8	5.5 mg.
	August	4	1.5
Workers "resting" in hive entrance	July	4	5.0
Wax producing workers caught on foundation	July	8	25.2
Fanners	August	1	1.5
		3	21.7

Table VI. Mean honey stomach weights of "minor" categories of worker bees collected in 1969.

Little or no previous work has been done on the food relationships of any of the groups of bees listed above and

much more research is needed before valid conclusions regarding the interrelationships between these and other groups of bees within the colony can be made. However, a few comments regarding the "work-relationships" of these bees to other groups may be in place.

Guard bees are closely related to foragers in the "age-duty" sequence of honey bees. Although guard duty is normally performed by workers which have more or less terminated their period of hive duties and are about to become foragers (Rösch, 1930; Butler and Free, 1952; Lindauer, 1952; Ribbands, 1953; etc.), I have frequently observed foragers which were about to leave the colony turn suddenly and inspect incoming foragers, instead.* The mean honey stomach weights obtained for guard bees corresponded closely to those obtained for foragers leaving their hives (Figure 30).

The "bees resting" (Table VI) were caught in the entrances of the experimental colonies during a period of low flight activity. Since there was little guard activity at the time, I assume that these bees were foragers which were temporarily out of work.

Most of the workers caught on foundation appeared to be active in the production of wax. Considerable quantities of sugar are required for wax production (Ribbands, 1953;

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*Similarly, Butler and Free (1952) concluded from their experiments that many guard bees were foragers as well, and alternated between these duties.

Grout, 1954) and estimates of the amount of honey used by bees to produce one pound of wax have varied between five and 25 pounds. However, the mean values obtained for wax-producing worker bees are somewhat lower than expected. This may have been due to the conditions of poor honey flow which frequently occurred during the summer of 1969, resulting in sporadic production of wax. Many of the workers collected in this experiment contained little or no honey.

Very little information is available regarding the place of fanning within the age-duty sequence of honey bees. I have frequently observed both nectar and pollen foragers returning from the fields to join the bees fanning in the colony entrance, and assume that most of the fanners were either foragers or of near-foraging-age. The two values listed show the extremes in mean honey stomach weights found in this group of bees.

Sugar Concentration of Honey Stomach Contents

Figures 34 through 39 , and Table VII show the mean sugar concentration of the honey stomach contents obtained from bees collected in various locations within the four experimental colonies. As in the curves showing honey stomach weights, each point represents the mean sugar concentration obtained from the four sample means (A.M. or P.M.); using the student's t-test, intercolony differences were found to be non significant at the assigned level of 5%.

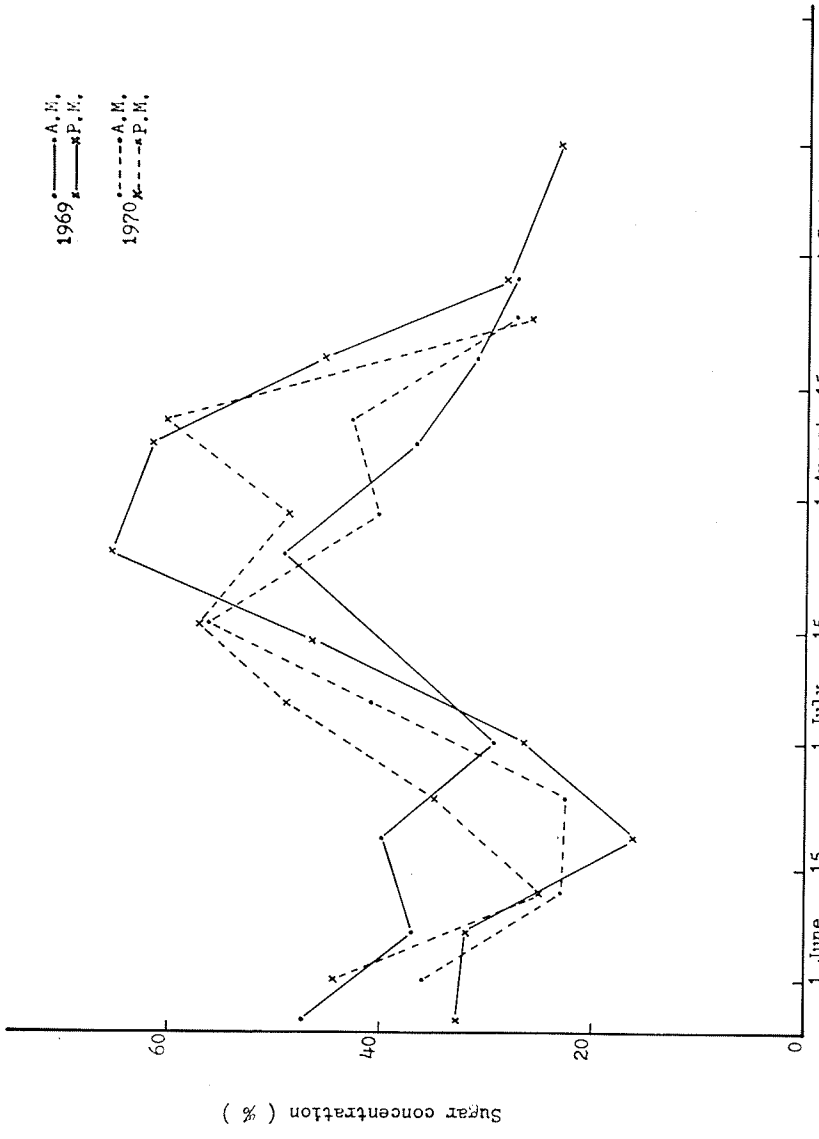

Figure **34.** Sugar concentration of honey stomach contents from nectar foragers returning to their hives (FE).

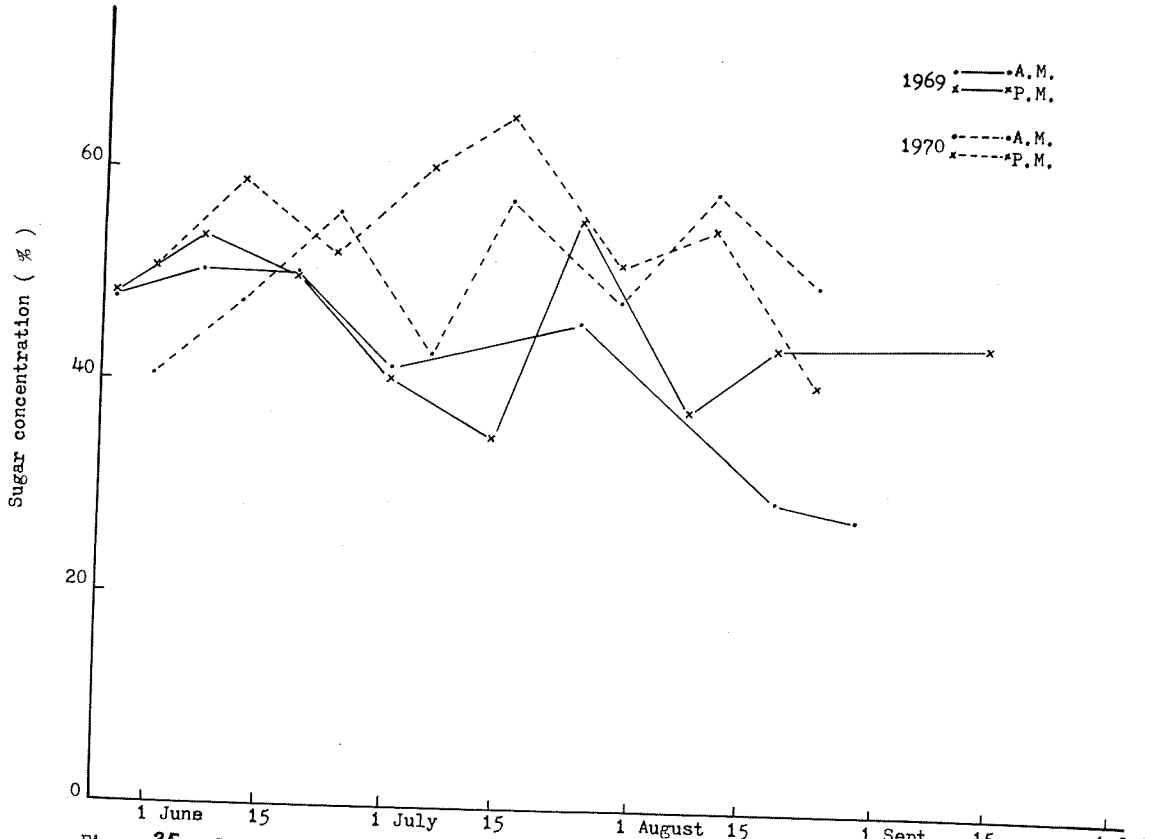

Figure 35. Sugar concentration of honey stomach contents from pollen foragers returning to their hives (PFE).

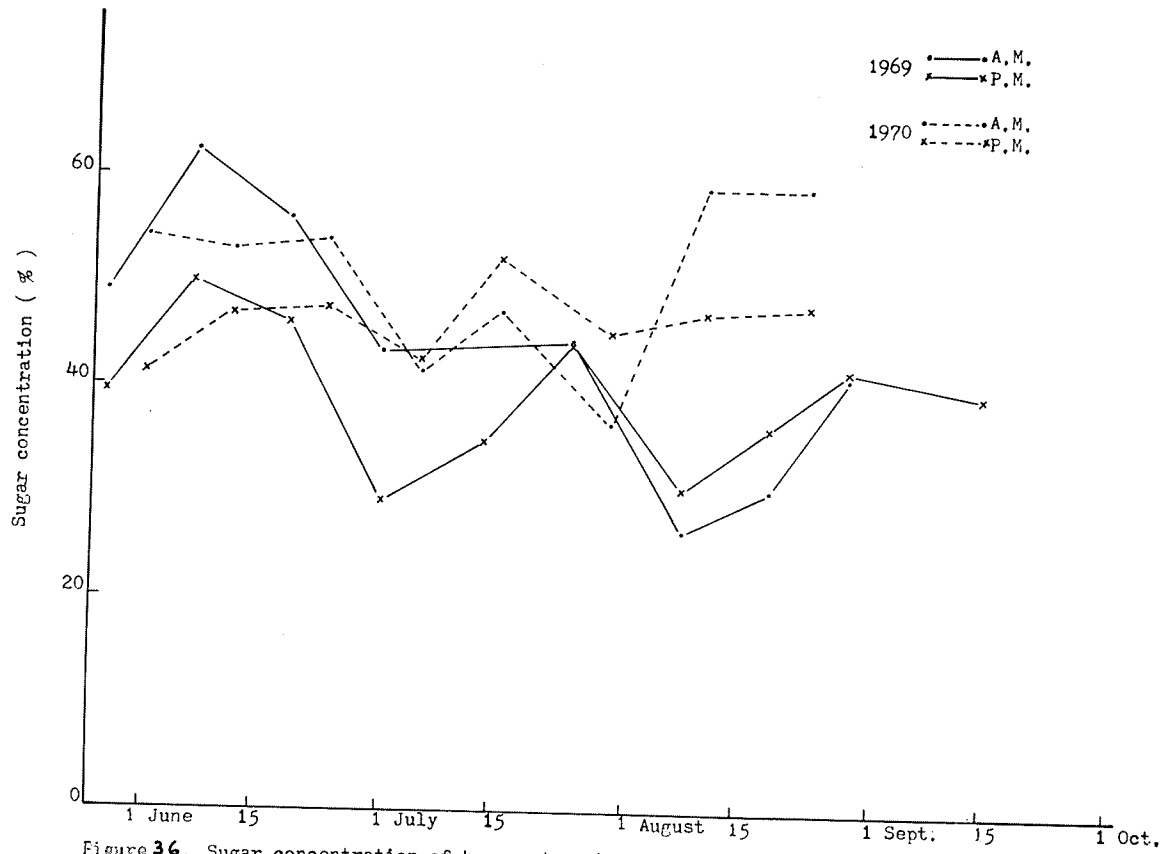

Figure 36. Sugar concentration of honey stomach contents from foragers leaving their hives (FL).

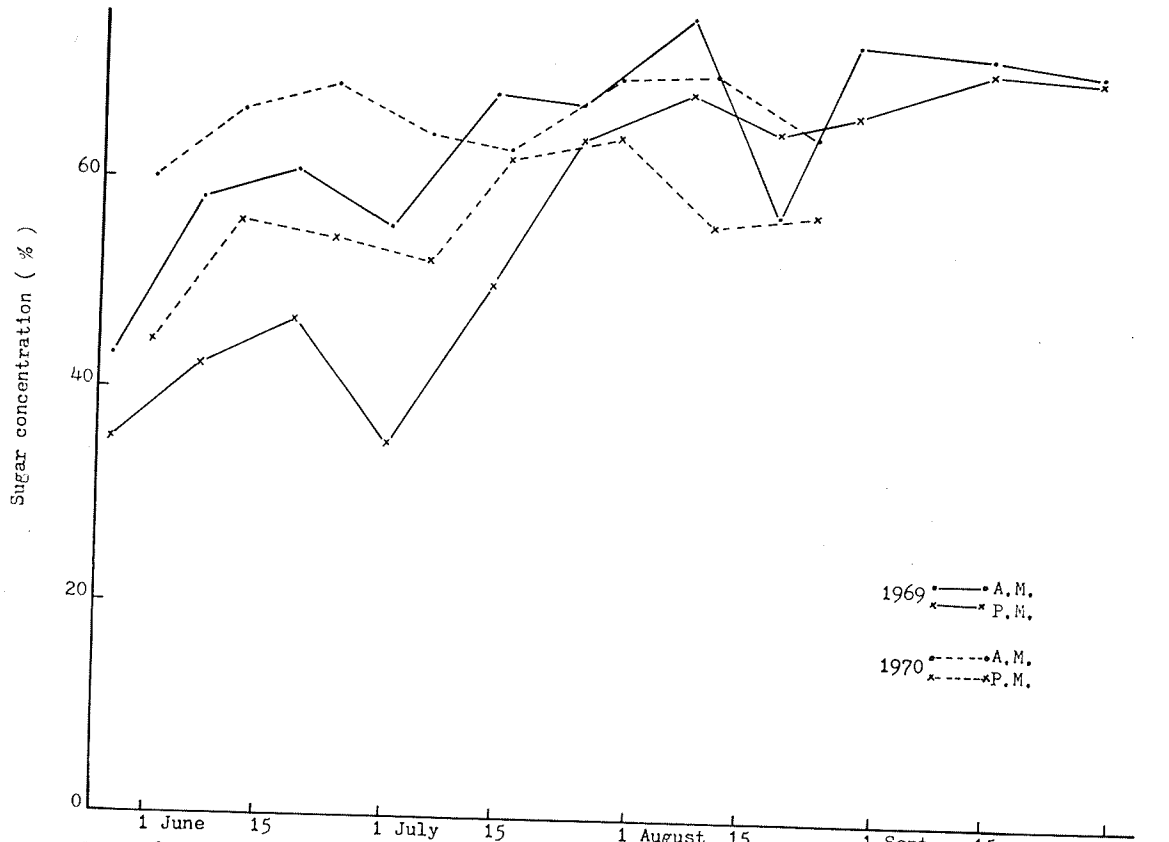

Figure 37. Sugar concentration of honey stomach contents from bees caught on open brood (30).

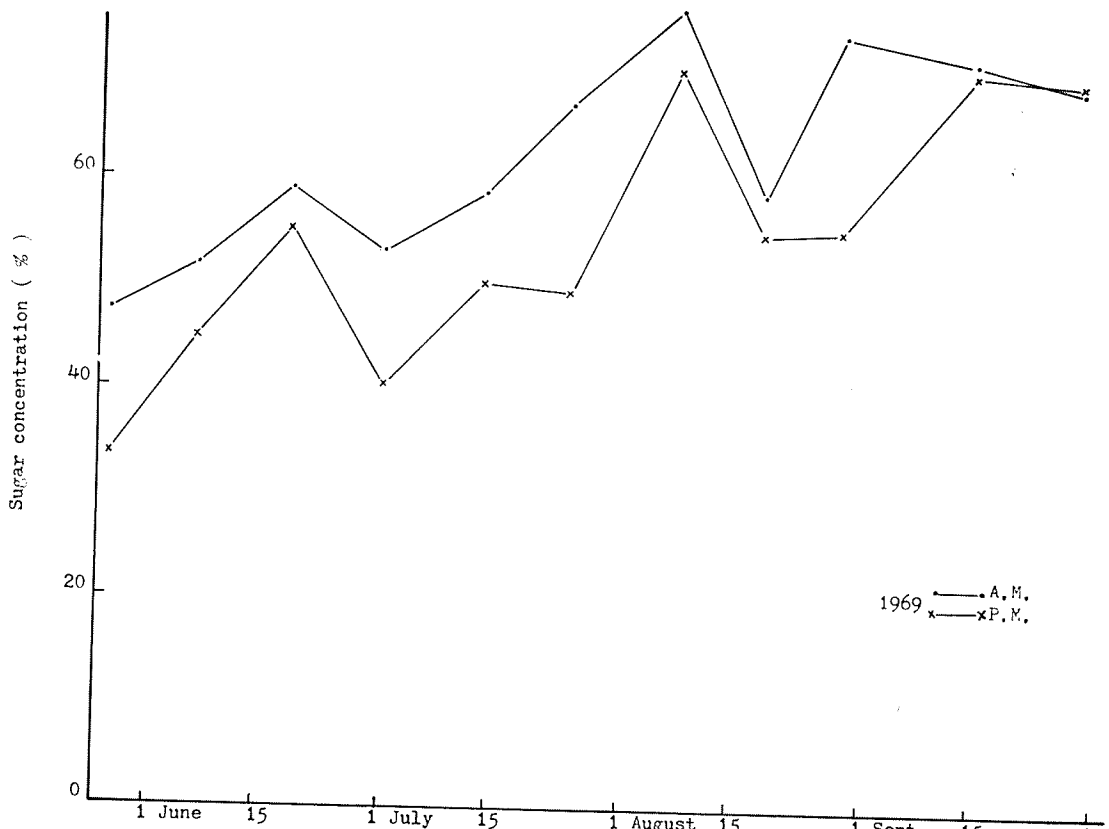

Figure **38**. Sugar concentration of honey stomach contents from bees caught on sealed brood (BS).

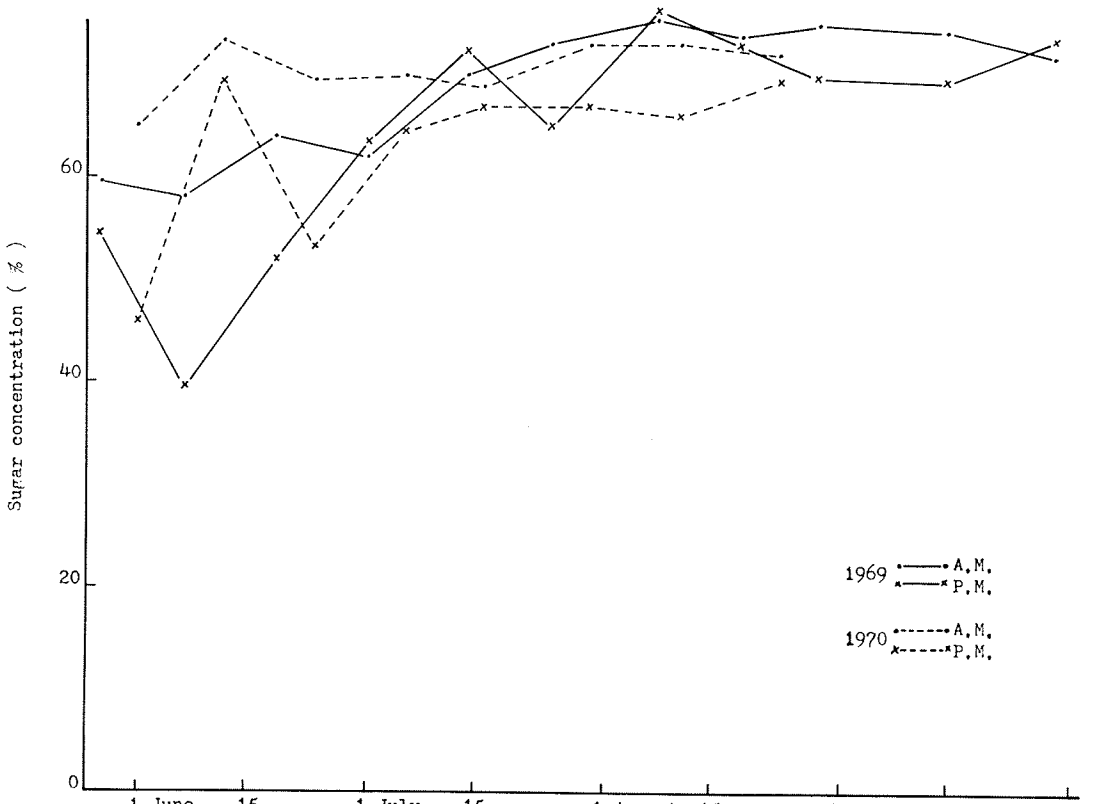

Figure 39. Sugar concentration of honey stomach contents from bees caught on open honey (HO).

	FE				PFE				FL				BO				HO			
	1969		1970		1969		1970		1969		1970		1969		1970		1969		1970	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
June vs July	-	+*	+*	-	-	*+	-	+*	*+	*+	*+	-	+*	-	-	+*	+*	+*	-	+*
June vs August	-	+*	-	-	*+	*+	-	-	*+	*+	-	-	+*	+*	-	-	+*	+*	-	+*
July vs August	-	-	+*	-	*+	-	-	*+	*+	-	+*	-	+*	+*	-	-	+*	+*	+*	-

Table VIIa . Statistical comparison of honey stomach sugar concentration by month, within each year. Statistic used: student's t-test.

Symbols:
1. FE = Foragers caught entering their hives.
2. PFE = Pollen foragers caught entering their hives.
3. FL = Foragers caught leaving their hives.
4. BO = Worker bees caught on open brood.
5. HO = Worker bees caught on open honey.
6. + = Difference is significant at the assigned level of 5%.
7. - = Difference is not significant at the assigned level of 5%.
8. * = Month in which sugar concentration was higher: *+ indicates June or July, +* indicates July or August.

	FE				PFE				FL				BO				HO			
	1969		1970		1969		1970		1969		1970		1969		1970		1969		1970	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
June	+	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
July	-	-	-	+	-	-	-	+	+	-	-	+	+	-	+	-	+	-	+	-
August	-	+	-	-	-	+	-	-	-	-	+	-	-	-	+	-	+	-	+	-

Table VIIb . Statistical comparison of honey sugar concentration by time of day. Statistic used: student's t-test. Symbols: As above. + placed according to time of day at which nectar of higher sugar concentration was collected.

Foragers caught entering their hives - The curves obtained for the mean sugar concentration of the honey stomach contents brought back to the hives by foragers returning from the fields (Figure 34) indicate that a similar trend occurred throughout both seasons. After an initial concentration which varied between 35% and 45% in late May and early June, a concentration decrease occurred in mid-June, which was followed by a gradual increase through the first two weeks of July. In 1969 the highest concentration of nectar was collected by the bees during the third week of July; this was followed by a steady decline in sugar concentration for the remainder of the season. In 1970, however, the period between mid-July to mid-August was characterized by considerable fluctuations in the mean sugar concentration of the food brought in by the foragers; this was followed by a rapid decrease in sugar concentration.

The mean sugar concentration of the honey stomach contents within any given group of worker bees is determined by a balance between the volume and concentration of nectar or honey available to them and the relative quantity of water to which they have access. Water is required particularly by the nurse bees for the elaboration of brood food (Lindauer, 1955; Kiechle, 1961) and on very hot days for the temperature regulation in the brood area (Ribbands, 1953; Kiechle, 1961). The actual amount of water required by a colony of bees

depends on the amount of brood present, and on the temperature conditions occurring within the brood nest (Lindauer, 1955). However, the relative quantities of nectar and water required are highly interdependent; less water is needed by the colony when large quantities of nectar of low sugar concentration are collected in the field.

The effect of weather on the secretion of nectar has already been discussed (Chapter III). Since the weather conditions change from day to day, and even from hour to hour, considerable fluctuations in the amount and concentration of the nectar gathered, and therefore also in the amount of water collected by the foragers at any given time, can be expected. Such fluctuations are apparent in the data presented here.

The conditions indicated by the curves may be explained as follows. The initial high sugar concentration recorded for returning foragers may be due to nectar gathered from the last of the dandelion bloom. Throughout much of June of both years only small quantities of nectar were available to the bees and even these may have been of low quality. This, and the relatively high quantities of water required for brood rearing (see expanded Appendix Tables), resulted in a decrease in the overall sugar concentration of forager honey stomach contents. Toward the beginning of July increasing temperatures resulted in

increase in quantity and quality of nectar secreted by the major honey plants, such as the legumes and rape, and continued until mid-August, when such factors as, aging of the plants, and decreasing temperatures resulted in a deterioration of the nectar flow.

A statistical comparison of the mean sugar concentrations found in nectar foragers entering their colonies in 1969 and in 1970 is presented in Table IV . Comparisons by time of day and by month within each year are given in Tables VIIb and VIIa, respectively. It should be noted that in 1969 sugar concentration was significantly higher in the honey stomach contents of foragers collected in the afternoons of July and August than in those collected in June at the same time; in 1970, however, foragers collected on July mornings carried food of higher concentration than did bees caught at the same time in June. Nectar gatherers collected on August mornings also carried supplies of higher sugar concentration than did those collected on July mornings.

Foragers caught leaving their colonies and pollen foragers caught as they entered their hives - A forager leaving the hive usually takes with her a sufficient quantity of sugar (in the form of dilute honey) to meet her metabolic needs during the flight to her foraging area (von Frisch, 1969; Beutler, 1936). Results obtained by Beutler in her studies on the comparative blood sugar levels of

nectar and pollen gatherers suggest that because of their sustained high level of activity in the field, pollen foragers require greater quantities of sugar than do nectar gatherers for the same amount of time spent in the field. The food reserve is obtained either from other workers in the immediate area, or it may be obtained directly from cells of open honey (Lindauer, 1952). How much nectar is retained from the previous foraging trip is not known, but results obtained by Park (1932) indicate that "carryover" of nectar from previous foraging trips is so low that little influence is exerted on sugar concentration of nectar collected on a subsequent foraging trip.

The relatively high sugar concentration of the honey stomach contents obtained for both groups in the first two weeks of June probably was due to the carbohydrate reserves taken by the foragers on leaving the hives. Since it was difficult to distinguish between pollen foragers and nectar gatherers among bees leaving the hives, no attempts were made to determine differences in amount or sugar concentration in the honey stomach contents of pollen and nectar foragers leaving for the field.

During July of 1970 the pollen foragers collected considerable quantities of nectar. This is indicated by a peak in concentration (Figure 35), which coincides with similar peaks as shown in Figure 34 (nectar foragers) and

in Figure 29 (honey stomach weights of pollen foragers). In 1969, however, the pollen foragers, and the foragers leaving (in both years) appeared to depend primarily on stores obtained in the hive. The reason for the slight decrease in the overall sugar concentration observed in both years, is not known. It is possible that the foragers, unlike the hive bees living in the "controlled environment" of the colony require more water for the regulation of body temperature under field conditions and therefore food of lower concentration is taken at increasingly higher environmental temperatures (Free and Spencer-Booth, 1959).

As can be seen from Figure 34 , the mean sugar concentration of honey stomach contents obtained from foragers leaving their colonies and from pollen foragers returning to them was significantly higher in the bees collected in July (P.M.) and August (A.M. and P.M.) of 1970, than it was in bees collected in 1969 during the corresponding period (Table IV). A statistical comparison by month within each year (Table VIIa) shows that in foragers leaving their hives the sugar concentration was greater during the early part of the 1969 season than it was later in the year, but that in 1970 the differences between months were much less pronounced, with differences only between June and July and July and August being significant. For pollen foragers, significant differences in 1969 existed between June and July, between

June and August (P.M.) and between July and August (A.M.). In 1970, the sugar concentration was significantly higher in the afternoon of July than in either June or August.

Workers caught on open honey - Figure 39 shows the mean sugar concentration of honey stomach contents recorded for worker bees collected on open honey. Here, considerable fluctuations occurred through the month of June in both years; the fluctuations decreased with the advent of the honey flow and continued to a much lesser degree for the remainder of both summers. The overall seasonal trend for both years was one of increasing sugar concentration until approximately mid-July, when it held steady for the remainder of the season.

The trends observed may be explained as follows. As can be seen from the honey flow data presented in Chapter III, very little nectar was brought into the colonies in June. Thus, many of the worker bees collected on open honey probably were engaged in reworking honey stored during the previous season, much of which had crystallized during the winter. Considerable quantities of water are required to reliquefy crystallized honey and the bees collected on open cells of honey probably contained honey in various stages of processing, thus accounting for the differences in mean concentration observed at this time. Because of the relatively great homogeneity observed in the honey stomach

contents of workers collected on open honey during July and part of August, it is apparent that they were engaged in the processing of nectar coming into the colony at this time.

Table IV shows significant differences only between August of 1969 and 1970, and in the morning collections taken in June of both years. Significant differences occurred also between most months of 1969 but only between June and July (P.M.) in 1970. The morning collections contained significantly higher mean sugar concentrations than did the afternoon ones (Tables VIIa and VIIb.).

Workers caught on open brood - The mean sugar concentration of nurse bee honey stomach contents (Figure 37) followed a seasonal trend similar to that observed for the bees collected on open honey (Figure 39). Although there were wide fluctuations in the values recorded throughout both seasons, the general tendency was toward an increase in sugar concentration, as the season progressed.

As was explained (page 82), considerable quantities of water are required by honey bee colonies both for brood rearing and for the control of the brood nest temperature. Hence, bees engaged in duties related to brood rearing are the primary recipients of much of the water brought into the colony (Lindauer, 1955). It is not surprising, therefore, to find considerable variations in sugar concentration in the food retained by workers found on open honey. It should

be noted, however, that probably not all workers caught on open brood were directly engaged in the care and feeding of larvae. According to Lindauer (1952), worker bees spend a considerable amount of time "patrolling" through the hive. These bees, which are not actively engaged in any given task, are receptive to stimuli presented by tasks that need to be performed, i.e. they are "looking for work". Such bees may have come from outside of the brood area, could have been collected as nurse bees, and hence could have influenced the results obtained. Water foragers and perhaps even some nectar foragers could have been collected along with nurse bees, especially on combs close to the entrance, adding to the variation observed.

As can be seen from the graphs, the sugar concentration of the food held by bees on open brood, was usually more concentrated in the mornings than in the afternoons. This difference, which is significant at the 5% level (Table VII b.), was likely due to the evaporation of water from the nurse bees' honey stomach contents at night when no additional water could be brought into the hives (Lindauer, 1955; Kiechle, 1961). By the time bees were again collected in the afternoon, sufficient water had been brought into the colonies by the foragers, to alleviate the lack of water and to reduce the sugar concentration of the honey stomach contents.

Table IV shows that the sugar concentration was significantly higher in June of 1970 than in June, 1969. However, a higher concentration was found in bees collected in the afternoons of July in 1969. A comparison by month within each year (Table VIIa) shows that in 1969 the sugar concentration generally increased as the summer progressed. However, in 1970, only the bees collected on July afternoons contained food of higher concentration than did bees collected in June.

Workers collected on sealed brood - Since areas of sealed brood are frequently found on the same comb and are adjacent to open brood and/or open honey, the workers collected from sealed brood probably included bees from several different categories. Aside from emerging bees (which can easily be differentiated from older workers, but which were not collected), bees with relatively heavy honey stomachs were frequently encountered; it was assumed that these were workers engaged in the processing of nectar (Park, 1925). Also, especially at the margins between open and sealed brood, nurse bees were probably often collected. In addition, some of the bees may have been workers patrolling through the colony, which were caught as they were "resting" on the sealed brood (Lindauer, 1953).

The curves obtained from the mean sugar concentration of bees collected on sealed brood in 1969 (Figure 38) are

very similar to those obtained from bees collected on open brood, and to a lesser degree, to those collected on open honey. The same seasonal trend is apparent; from an initial concentration of around 40%, there was a general increase in sugar concentration with the advance of the season. The fluctuations in these curves are very similar to those in the curves of workers collected on open brood; it is possible that in these collections nurse bees predominated. Here too, the curves indicate a higher sugar concentration in the morning collections than in bees which had been collected in the afternoons.

Drones - During the first few days after emergence, drones are almost exclusively fed by worker bees (Levenets, 1956b; Free, 1957; Mindt, 1962). As they become older, the drones pass through a period of transition in which they come to rely on honey taken from open cells. Although workers of any age may be solicited, most of the workers observed to be feeding drones were between one and two and a half weeks old (Free, 1957).

The honey stomach contents of flying drones, ie. those over eight days of age, were found to be very similar in sugar concentration to that of the honey stored in the combs (Free, 1957; Mindt, 1962). In young drones, however, the honey stomach contents most closely resembled the mixed food offered to the older worker larvae. The honey stomach

contents consisted of several different fluids which frequently contained considerable quantities of pollen (Mindt, 1962), and were thought to be derived from the honey stomach contents of the workers, possibly mixed with glandular secretions. The sugar concentration of this material varied between 12 and 48% (Mindt, 1962).

The sugar concentration in the honey stomach of the drones collected in the present study is shown in the following table:

Month	No. of Samples	Mean Sugar Concentration
July	4	46.2%
August	8	53.1
September	16	66.7

Table VIII. Mean sugar concentration of honey stomach contents in drones collected on combs during July, August, and September, 1969.

Although the number of samples taken is too small to permit the formulation of any firm conclusions, a seasonal trend, similar to that observed in workers on open honey, appears to exist.

The increase in sugar concentration may have been due either to an increase in the concentration of the food circulating among the workers with the advance in season,

or it may have been due to a shift in the mean age and hence a shift in the feeding pattern of the drones collected.

Other categories of bees collected - The sugar concentration obtained from the honey stomach contents of the "minor" categories of bees collected, are shown in the following table:

Category	Month	No. of Samples	Mean Sugar Concentration
Guards	July	8	44.2%
	August	4	23.5
Bees "resting" in entrance	July	4	36.1
Bees collected on foundation	July	8	66.3
Fanners	August	1	24.0
	August	3	65.3

Table IX. Mean sugar concentration of honey stomach contents in the "minor" categories of workers collected in 1969.

Because of the small number of samples involved, no daily or seasonal trends are apparent, and no obvious relationships between the data presented above and those presented in the "major" categories appear to exist. However, it seems that most of the bees working on the "outside" of the colony, i.e. the guards, foragers "resting" in the entrance, and

the one group of fanners, all carry relatively small quantities of food of low sugar concentration. Much more research is needed to clarify the relationships existing between these and the other "work groups" of bees within the colony.

Pollen Concentration in Honey Stomach Contents

Foragers caught entering their colonies - As was indicated in the introduction of this chapter, very little is known about the incidence of pollen in the honey stomach contents of worker bees under normal conditions, with the possible exception of pollen that had been ingested by very young workers, or by those engaged in the rearing of brood. It has generally been assumed that pollen grains in nectar, brought back to the hive by foragers, have been "accidentally" pushed into the nectar by the insect (or by some other factor) and that the pollen has been taken up from the flower along with the nectar by the bee as she gathers her load. Thus, the amount of pollen present in the honey stomach contents of a forager returning to her colony is determined by the relative quantity of pollen initially present in the nectar before it was collected by the bee, less the amount of pollen removed from its honey stomach by the filtering action of the proventriculus.

Figure 40 shows the concentration of pollen (per mm^3 of fluid) in the honey stomach contents obtained from

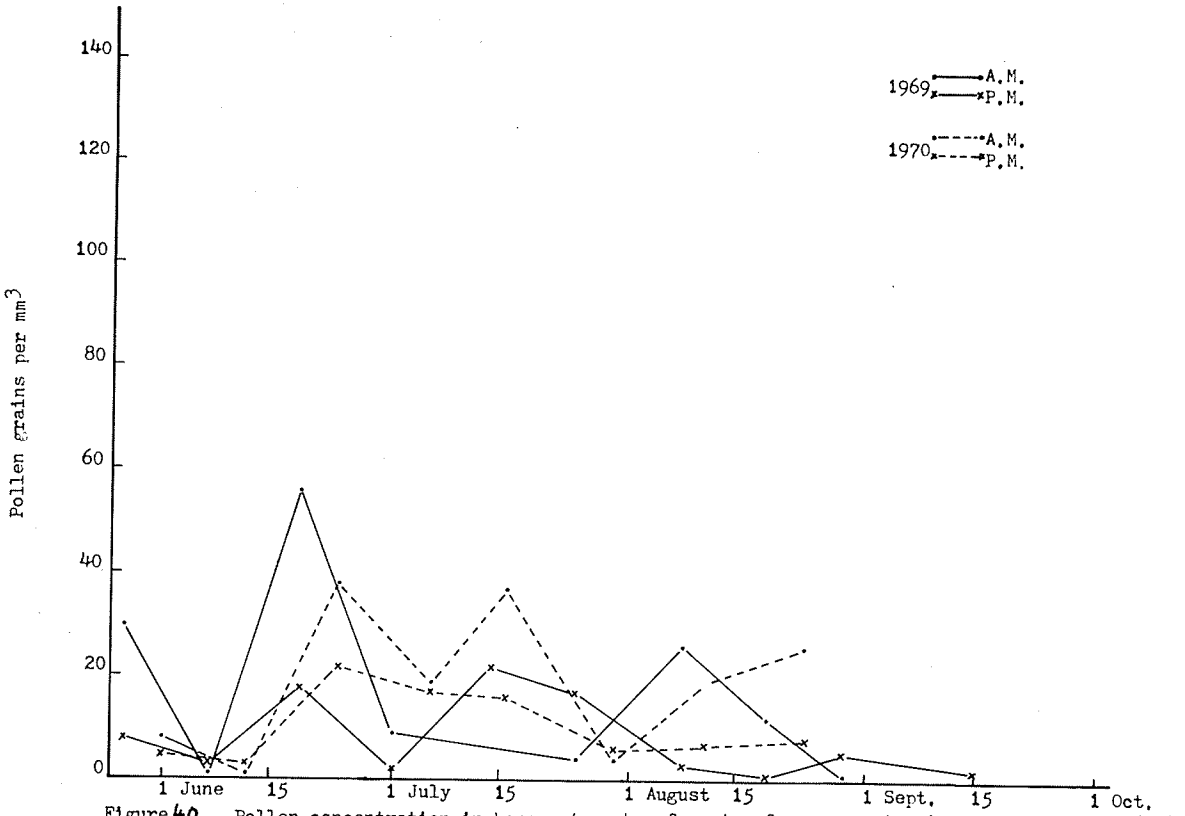

Figure 40. Pollen concentration in honey stomachs of nectar foragers returning to their hives (FE).

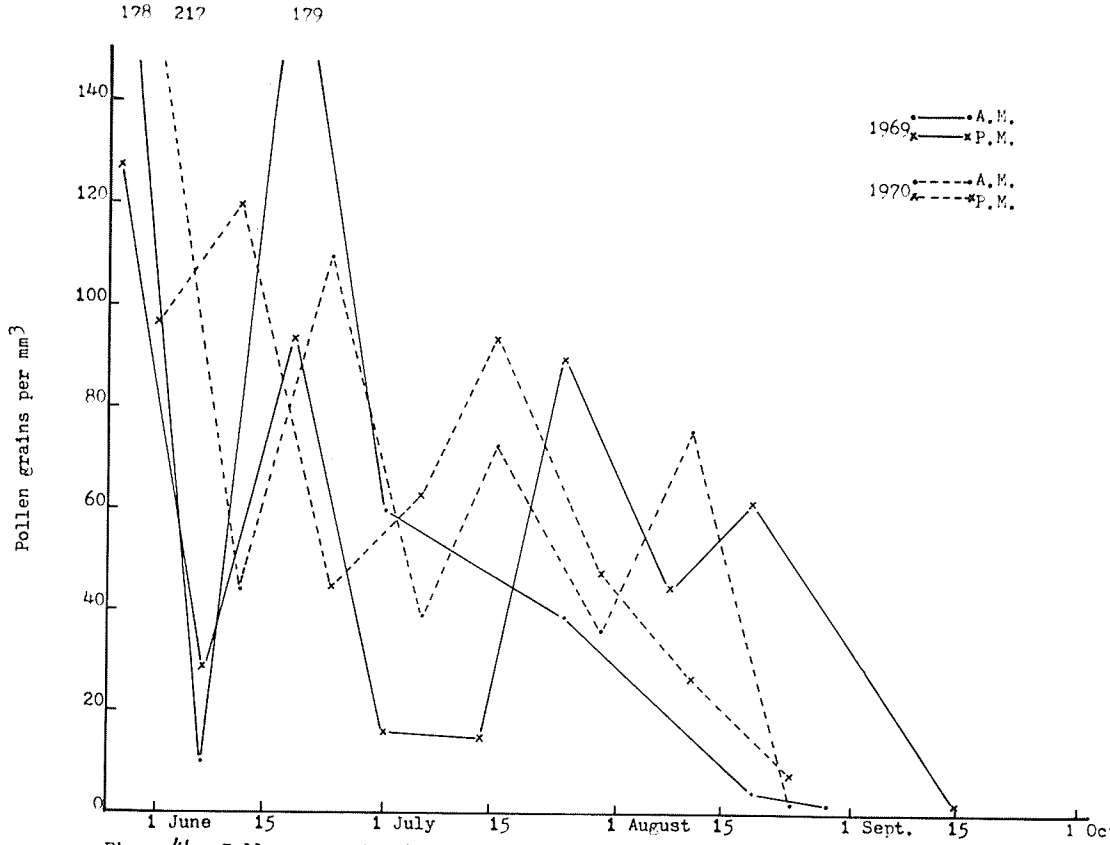

Figure 41 . Pollen concentration in honey stomachs of pollen foragers returning to their hives (PFE).

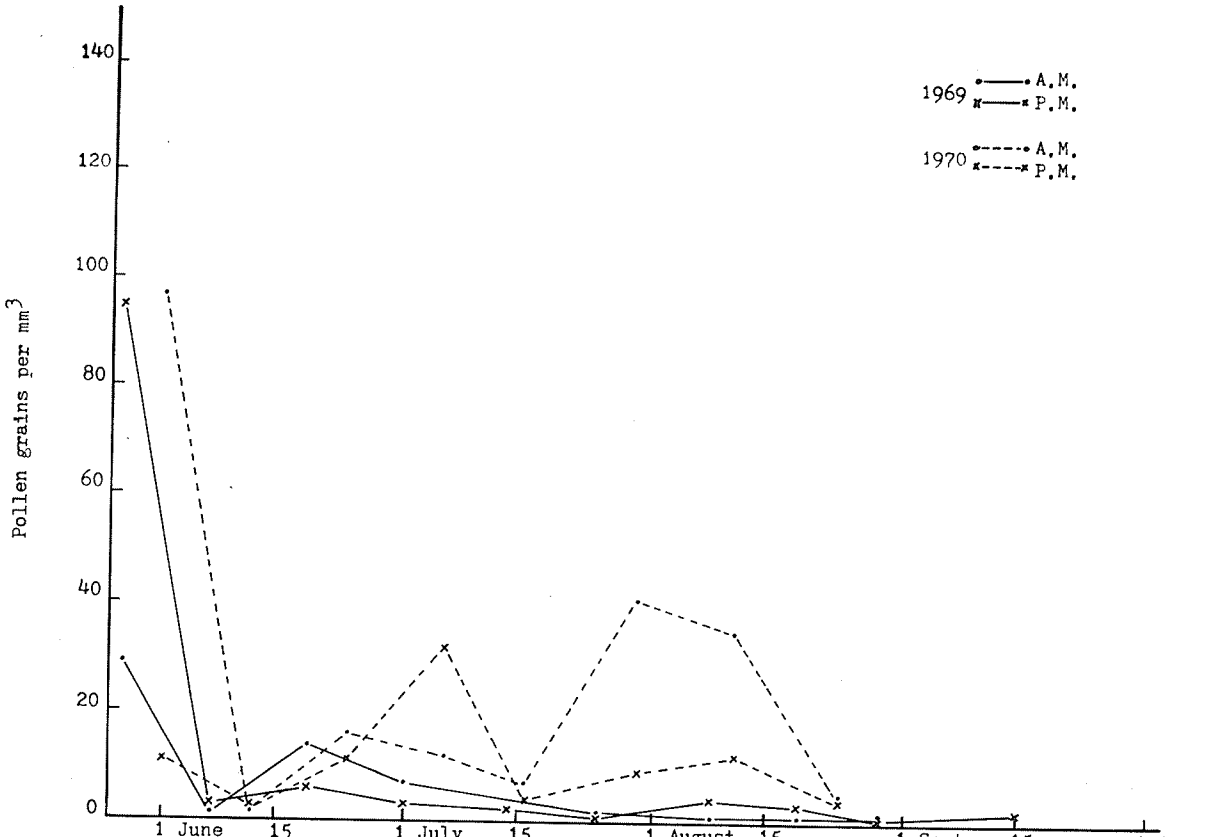

Figure 42. Pollen concentration in honey stomachs of foragers leaving their hives (FL).

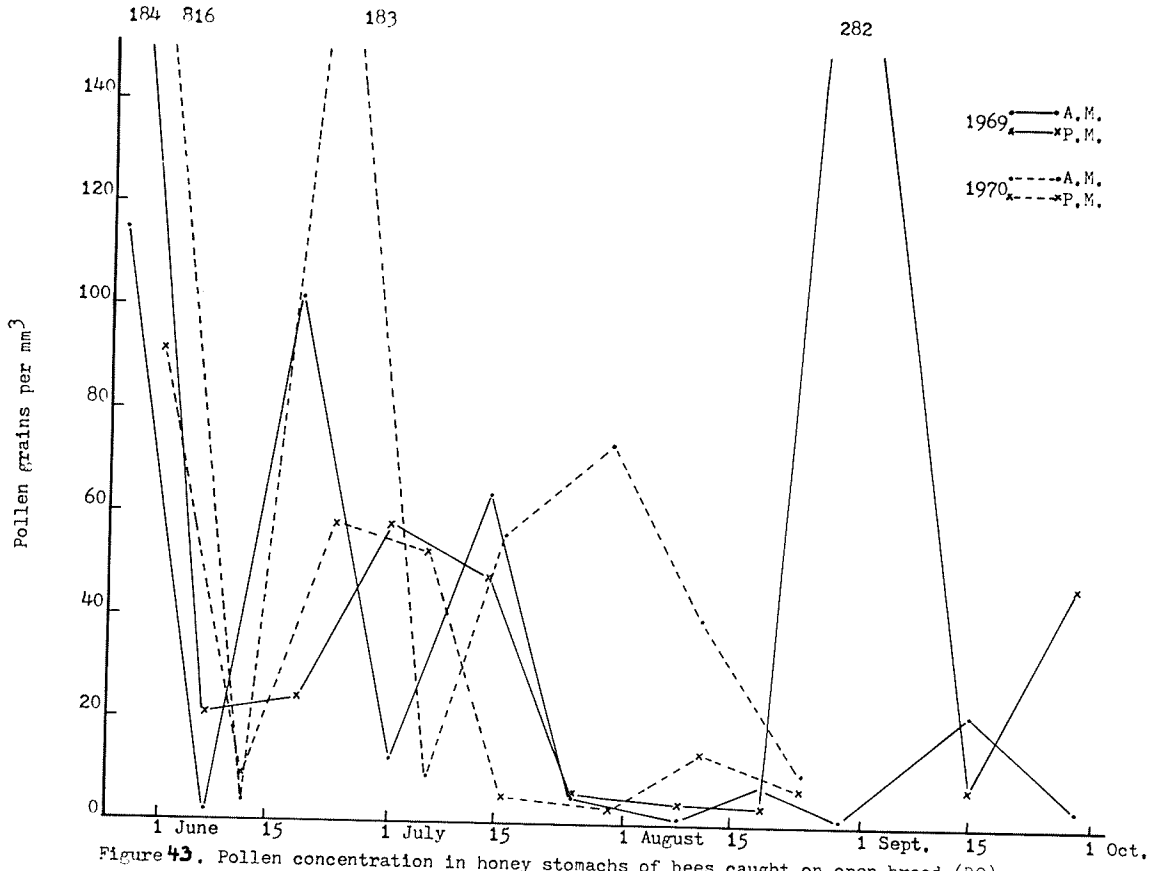

Figure 43. Pollen concentration in honey stomachs of bees caught on open brood (BO).

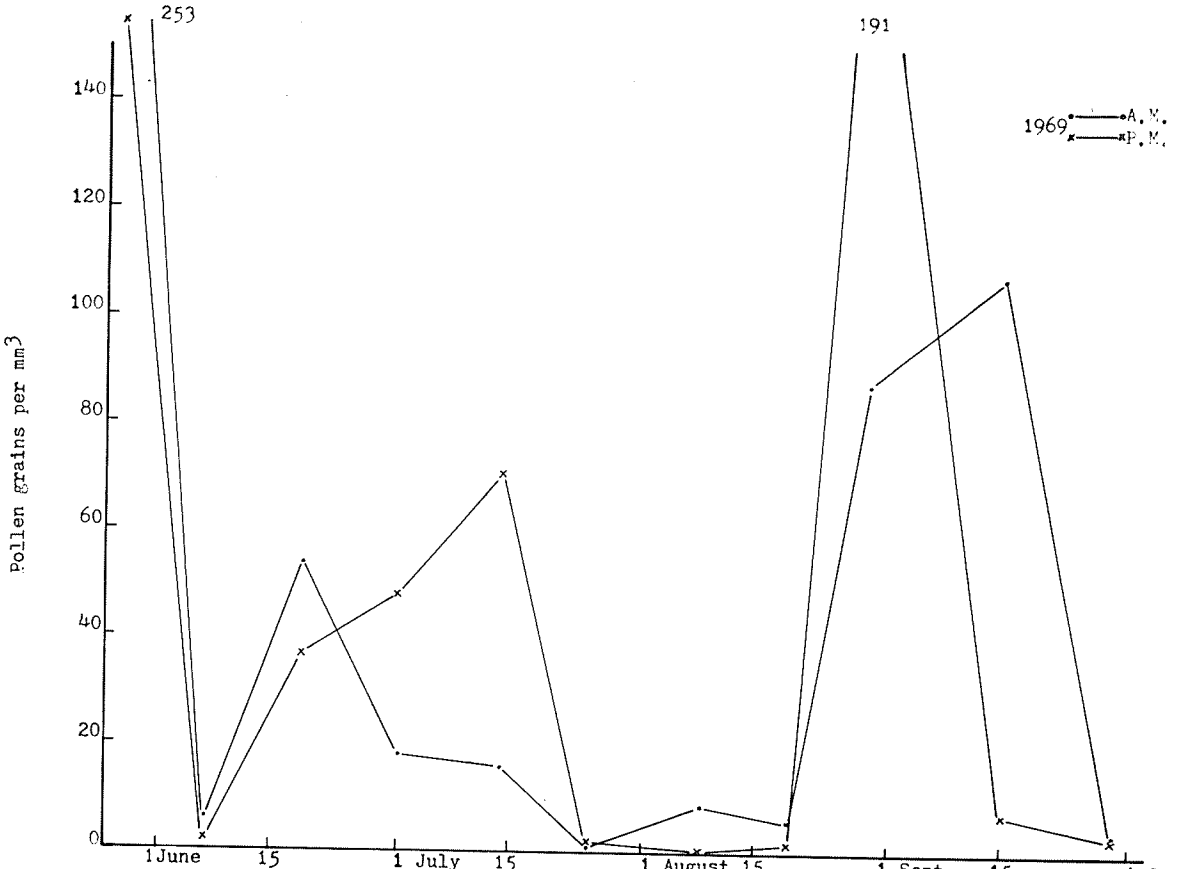

Figure 44. Pollen concentration in honey stomachs of bees caught on sealed brood (BS).

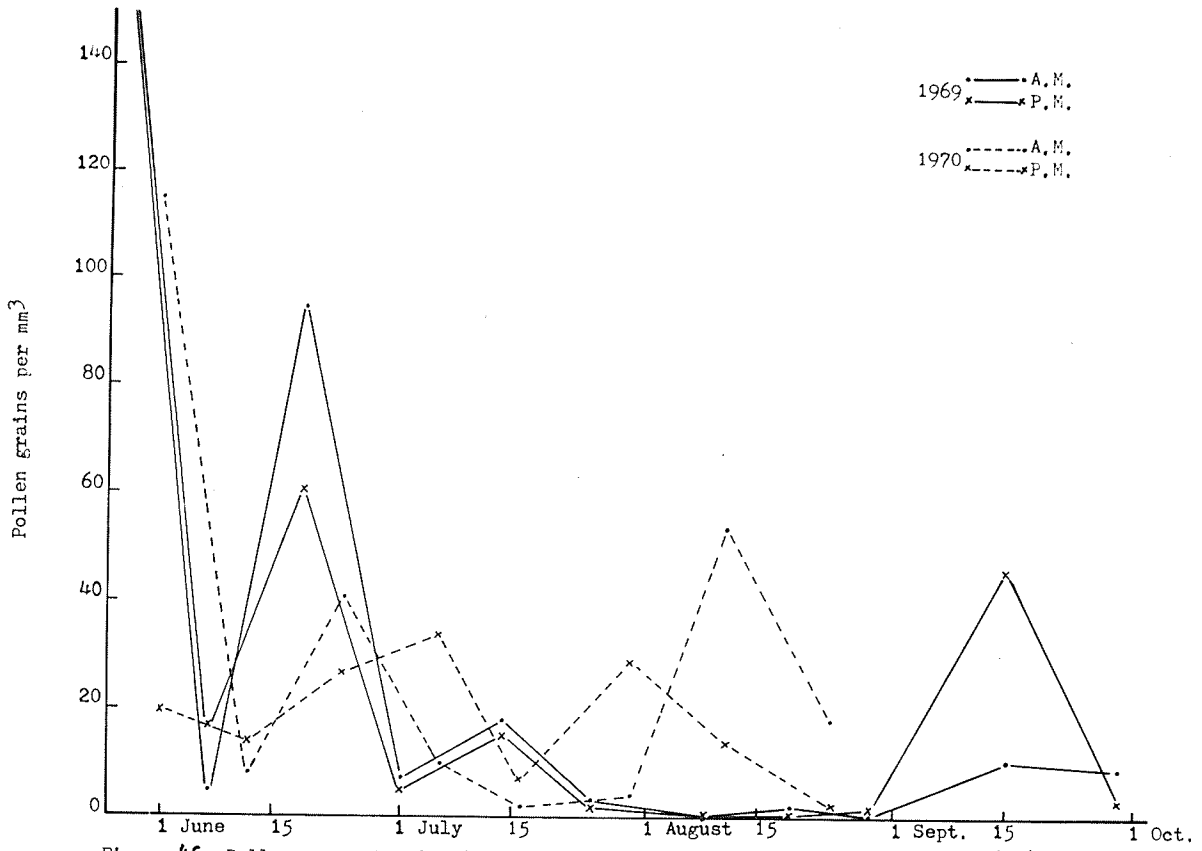

Figure 45. Pollen concentration in honey stomachs of bees caught on open honey (HO).

	FE				PFE				FL				BO				HO			
	1969		1970		1969		1970		1969		1970		1969		1970		1969		1970	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
June vs July	-	-	-	-	-	-	-	-	-	*+	-	-	-	-	-	-	*+	*+	*+	-
June vs August	-	*+	-	-	*+	-	-	*+	*+	-	-	-	*+	-	-	*+	*+	*+	-	*+
July vs August	-	-	-	*+	*+	-	-	*+	*+	-	-	-	-	-	-	-	-	-	*+	-

Table Xa . Statistical comparison of honey stomach pollen concentration, by month, within each year. Statistic used: student's t-test.

Symbols:
1. FE = Foragers caught entering their hives.
2. PFE = Pollen foragers caught entering their hives.
3. FL = Foragers caught leaving their hives.
4. BO = Worker bees caught on open brood.
5. HO = Worker bees caught on open honey.
6. + = Difference is significant at the assigned level of 5%.
7. - = Difference is not significant at the assigned level of 5%.
8. * = Month in which pollen content was greater: *+ indicates June or July, +* indicates July or August.

	FE				PFE				FL				BO				HO			
	1969		1970		1969		1970		1969		1970		1969		1970		1969		1970	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
June	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
July	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
August	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+

Table Xb . Statistical comparison of honey stomach pollen concentration, by time of day. Statistic used: student's t-test. Symbols: As above. + placed according to time of day at which larger pollen counts were obtained.

nectar foragers returning to their hives, both in 1969 and in 1970. In both years the greatest relative quantities of pollen were brought into the colonies during June and July; a slight reduction in pollen concentration occurred in August and September. Although considerable fluctuation resulted in some overlap, the highest pollen concentrations were generally found in the morning collections. Nevertheless, the differences were not statistically significant (Table X b.). A comparison between years (Table IV) shows that significantly higher pollen concentration occurred only in foragers collected in the mornings of June, 1969.

Although it would have been of interest to determine whether there exists a relationship between the concentration of pollen in the honey stomach contents and the plant species in bloom at the same time through pollen identification, this was considered to be outside the scope of the present project and an analysis of the pollens found in the nectar was not attempted. However, considerable work has been done on this subject, particularly with reference to European plant species (e.g. Maurizio, 1949a; 1955; 1956; 1958; Pritsch, 1957; Maurizio and Louveaux, 1960a; 1960b; 1965).

Pollen foragers caught entering their hives - Figure 41 shows the pollen concentration measured in the honey

stomach contents of pollen foragers caught as they returned to their colonies. Although the seasonal trend shown here is similar to that of the nectar foragers, (i.e. a gradual decrease in pollen concentration over the season) there is a considerable difference in the values obtained. Thus, while the greatest mean concentration obtained from nectar foragers was 56 pollen grains per mm^3 of nectar, that obtained from pollen foragers was 217 pollen grains per mm^3. The other values differ proportionately.

The observed differences are largely due to the foraging behaviour of the bees. Pollen gatherers actively "scrabble" for pollen (Free and Spencer-Booth, 1964), using their mouth parts and forelegs to gather pollen which is then packed into the corbicula. This forces much pollen downward between the stamens and into the nectar. The "pollen enriched" nectar is frequently gathered by the same bees and taken back to the colony.

A monthly comparison (Table Xa) shows that in 1969 and in 1970 the pollen concentration in the honey stomach contents of pollen foragers was higher both in June and July than in August; in 1969 higher concentrations were gathered in the mornings, while in 1970 the afternoon readings gave the higher values.

Foragers caught leaving their hives - The concentration of pollen in the honey stomach contents of foragers

leaving their colonies throughout 1969 and 1970 is shown in Figure 42. With the exception of two relatively high readings, obtained in the afternoon of 26 May, 1969, and in the morning of 1 June, 1970, respectively, the values obtained over both seasons were quite low. This is not unexpected, since foragers about to leave their colonies usually take with them a certain amount of food, obtained either from open cells of stored honey or from other workers. In either case, the food material has been at least partially processed by other bees, and much of the pollen initially present will have been removed through proventricular filtration.

Worker bees are highly flexible in the performance of duties related to the maintenance of the colony, and can, if necessary, revert to the execution of tasks at which they worked when much younger. Thus, at a time when there are insufficient numbers of nurse bees to care for the brood, many of the younger foragers may return to nursing duties, often alternating between foraging trips and the feeding of larvae (Lindauer, 1952; Free, 1967). Such conditions occur most frequently in the spring, when the ratio of adult bees to brood is low. It is likely, therefore, that many of the foragers collected at this time also were engaged in the rearing of brood, at least on a "part-time" basis, and that these nurse bees, which require large quantities of pollen for the production of brood food, account for the high pollen

concentrations found in the honey stomach contents in early June.

Because in a good honey flow large quantities of nectar must often be processed by the workers within a short time, nectar is frequently stored in the combs before it is properly ripened (Park, 1925). As a result, less pollen is filtered from it, resulting in honey with a relatively high concentration of pollen (Chapter V). Foragers leaving the colony therefore would obtain honey with a higher pollen content under conditions such as were encountered in 1970, than under poor honey flow conditions, as occurred in 1969.

A comparison between years (Table IV) shows that significantly higher concentrations of pollen were found in the honey stomach contents of foragers (FL) caught in the afternoons of July, and in the mornings of August, in 1970, than were found in 1969 at the same time.

Table Xa shows that in 1969 the overall seasonal trend was one of reduction in pollen concentration, while in 1970, no significant differences were observed.

Worker bees caught on open brood - Pollen supplies most of the proteins, vitamins and minerals required by worker bees for the production of brood food (Haydak, 1935; 1970; Svoboda, 1940; Standifer, 1967), and considerable quantities of it are consumed by workers actively engaged in the care and feeding of larvae (Farrar, 1934; 1968; Todd

and Bishop, 1941; Free, 1968). It is not surprising, therefore that by far the highest concentration of pollen found in the honey stomach contents of any category of bees collected, occurred in workers caught on open brood (Figure 43).

As in the other categories of bees collected, the curves indicate a slight decrease in pollen concentration from spring to autumn, for both years. This seems to be overshadowed by a very high mean concentration of 282 grains per mm^3 of honey stomach contents, obtained from nurse bees collected in the afternoon of 29 August, 1969. This high concentration may have been due to the inclusion among the workers collected of numerous young bees, which normally feed heavily on pollen during the first week of their lives (Maurizio, 1950; 1961; Moeller and Hagedorn, 1967; Haydak, 1970).

Statistical comparison by years shows, however, that the only significant differences occurred between the values obtained from the morning collections in both years (Table IV). Table Xa shows that the mean values obtained in June (A.M.) were significantly higher than those obtained in August (A.M.) in 1969, and that the same relationship holds for the afternoon collections made in June and August of 1970.

Worker bees caught on sealed brood - The graphs

shown in Figure 44 are very similar in configuration to those in Figure 43 . This appears to indicate that considerable mixing and interfeeding between workers on open brood and those on sealed brood takes place.

Worker bees caught on open honey - The curves presented in Figure 45 show the pollen concentration found in the honey stomach contents of worker bees collected on open honey and indicate a seasonal trend resembling that observed in bees collected on open brood. The highest mean pollen concentration was found during June of both years; this was followed by a period of decreasing pollen content, and an increase during August and September of 1969 and 1970, respectively. The main difference between the results obtained from bees collected on open brood (Figure 43) and from those collected on open honey lies in the range of the fluctuations in pollen concentration observed throughout both years. Thus, while the nurse bees contained up to 283 pollen grains per mm^3 of honey stomach contents, bees which were processing nectar, contained 185 pollen grains per mm^3.

The high values obtained in June of both years were probably due to the participation of many of the bees, collected on honey, in activities related to brood rearing. It is assumed that later in the season, as the ratio of adult bees to brood increased, fewer of the workers caught on open

honey had recently been active in feeding larvae, and the mean values of pollen in the honey stomach contents declined. With the approach of the fall period, large numbers of young bees, are known to feed heavily on pollen stored in the cells, and many of these were probably also among the workers collected on open honey, resulting in an increase of the values obtained (See Chapter V).

In general, the similarity between the curves obtained for workers collected on open honey and those collected on open brood, seems to indicate that considerable intermingling between workers on open honey and nurse bees on open brood exists, and to confirm the observations made by Lindauer (1953), Free (1960, 1961, 1968), Furgala and Boch, (1961) and other researchers, that a clear delineation between workers performing different tasks cannot be made.

Table IV shows that significant differences in pollen concentration between years exist only in bees collected in June (P.M.) and those collected in August (A.M.). In 1969 higher concentrations were found to occur in June than in either July or August (Figure Xa), while in 1970, morning collections of bees contained significantly higher concentrations of pollen in June than in July, and in July than in August, and in the afternoon collections the pollen concentration was significantly higher in June than in August.

Drones - As was observed by Mindt (1962), considerable quantities of pollen are often found in the honey stomach contents of drones. The pollen concentrations in drones collected in July, August, and September, are shown in the following table:

Month	No. of Samples	Mean Pollen Concentration
July	4	100 per mm^3
August	8	515
September	16	57

Table XI. Mean pollen concentration of honey stomach contents in drones collected on combs during July, August, and September of 1969.

According to Haydak (1970), drones, like worker bees, require pollen for maturation and growth. Thus, drones were found to increase in weight by 28% within the first four days of their lives. However, relatively little appears to be known as yet about the feeding and nutritional requirements of drones, and much more research is needed in order to be able to evaluate data such as those given above.

Others - The pollen concentrations found in the honey stomach contents of the "minor" categories collected in 1969 are shown in Table XII.

Category	Month	No. of Samples	No. of pollen grains per mm^3
Guards	July	8	13
	August	4	1
Workers "resting" in hive entrance	July	4	15
Wax producing bees caught on foundation	July	8	1
Fanners	August	4	1

Table XII. Pollen concentration of honey stomach contents in "minor" categories of workers collected in 1969.

Because of the small numbers of samples collected, and because so little is known about the food relationships of the above groups, no conclusions can be drawn from the data at the present time.

Pollen load weights - During both 1969 and 1970 the pollen loads, carried by pollen foragers returning to their hives, were carefully removed from the corbiculae and weighed. The mean weights of the "bee loads" each consisting of two pollen pellets, obtained throughout both seasons, are shown in Figure

Under optimal conditions the size of the pollen loads collected appears to be largely dependent on the plant species from which the pollen was gathered by the bees

(Park, 1922; Parker, 1926; Lukoschus, 1957). However, it seems that weather factors also influence the amount of pollen brought back to the colony from any foraging trip; I have frequently observed that under conditions of inclement weather, pollen loads gathered from almost all plant species were considerably smaller than normal. In these studies, the weights of the pollen loads obtained ranged from less than one mg. to 46.5 mg. However, the mean weights obtained during the months of June, July and August of both years varied between 10.7 mg. and 19.0 mg. which is in agreement with the results obtained from previous authors (Gillette, 1897; Park, 1922; Parker, 1926; Maurizio, 1953).

Figure 46 shows the following seasonal trend for both years: Relatively heavy pollen loads were brought into the colonies in early June. This was followed by a period in which the mean weight of pollen loads decreased, and a period of gradual increase in weight throughout July. A decrease in mean weight occurred during August. Although these curves resemble those obtained for honey stomach weights in both 1969 and 1970 (both for FE and PFE), the peaks in pollen load weight followed, rather than coincided with, those obtained for honey stomach weight. A correlation between honey stomach weight and pollen load weight was not apparent.

The statistical comparison between years (Table IV)

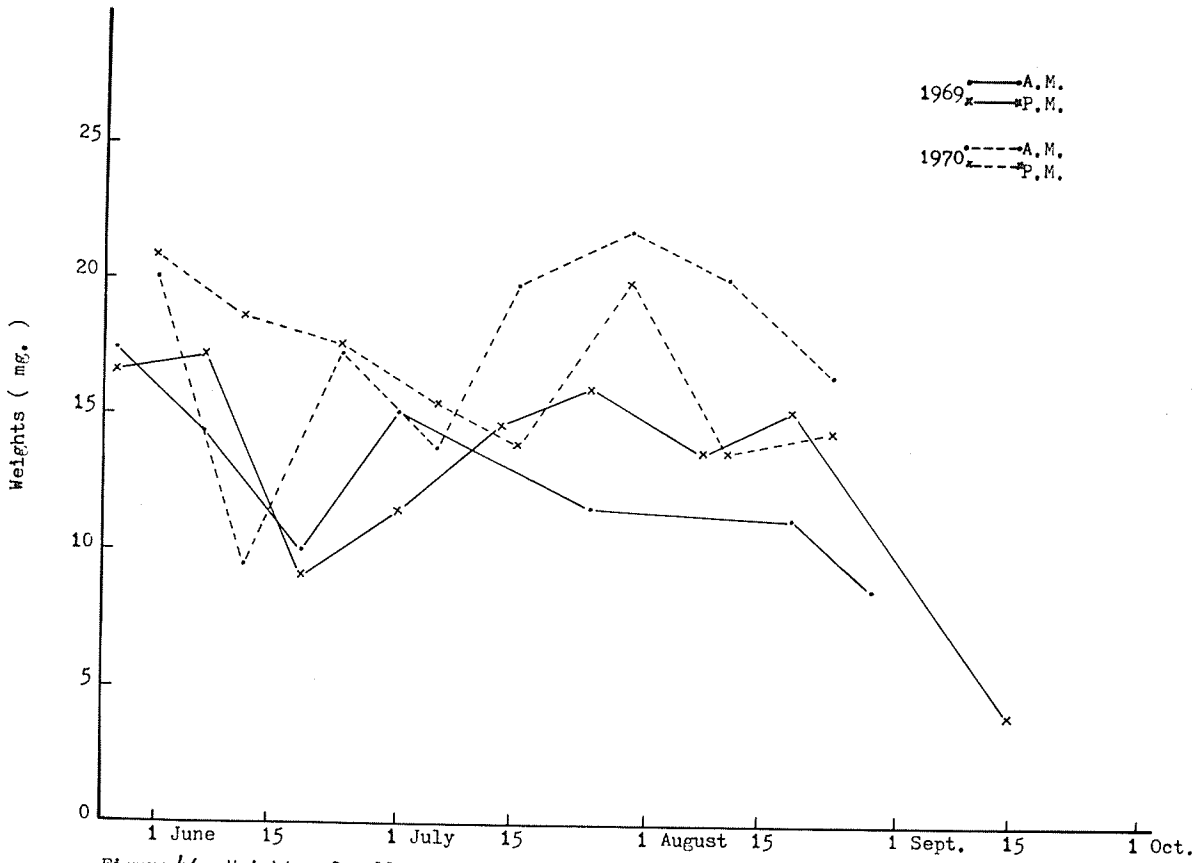

Figure 46. Weights of pollen loads carried by pollen foragers returning to their hives (PFE).

shows that the pollen loads collected in 1970 were heavier for the following months and time of day: June (A.M.), July and August (P.M.). Heavier pollen loads were also collected in the afternoons of August 1969 than in the mornings, while in August of 1970 pollen foragers carried heavier loads in the morning. In June, 1970, the mean pollen load weights were heavier in the afternoons than in the mornings (Table XIII). Table XIII shows that significant differences in pollen load weight were obtained only between June and July, and between June and August, 1970.

	1969	1970
June (A.M.)	-	-
June (P.M.)	-	+
July (A.M.)	-	+
July (P.M.)	-	-
August (A.M.)	-	+
August (P.M.)	-	-

Table XIIIa. Comparison of pollen load weights obtained in 1969 and 1970. Statistic: student's t-test, 5% level of significance. Position of + indicates the time of day and the year in which significantly heavier loads were collected.

Year	Month	Time	Month	Significance (5%)
1969	June	A.M.	July	-
			August	-
	July		August	-
	June	P.M.	July	-
			August	-
	July		August	-
1970	June	A.M.	July	-
			August	-
	July		August	-
	June	P.M.	July	+
			August	+
	July		August	-

Table XIIIb. Statistical comparison of pollen load weights, by month, within each year. Statistic used: student's t-test. + = signifies significance at the assigned level of 5%.

Month	1969 A.M.	1969 P.M.	1970 A.M.	1970 P.M.
June	-	-	-	+
July	-	-	-	-
August	-	+	+	-

Table XIIIc. Statistical comparison of pollen load weights, by time of day. + is placed according to time of day at which heavier pollen loads were collected. Statistic used: as above.

Summary and Conclusions

Nearly all activities of honey bees, both within the colony and in the field, are related either directly or indirectly to the collection, processing and storage of food, which thus serves as the basis for colony cohesion. The constant transfer of food among all members of the colony makes possible the rapid distribution of pheromones emanating from the queen and possibly the brood, and informs each individual of the availability of food in the field, thereby regulating such activities as foraging for water and nectar, brood rearing, wax production and comb construction (Free, 1970). Interfeeding usually starts with the oldest group, the foragers, who bring nectar, water and pollen into the colony. From these the food generally passes through a succession of progressively younger bees to the nurse bees in the brood nest.

In this study, the honey stomach contents of various categories of worker bees, each performing specific duties within the colony, were investigated. For each group the mean honey stomach weights, and mean sugar and pollen concentrations were determined throughout two consecutive seasons, in order to establish the influence of the environment on the quantity and quality of the food retained in the honey stomachs, and to determine, if possible, food relationships existing between the various groups of workers within

the hive. The honey stomach contents of drones collected in July, August and September of 1969 have also been investigated.

In general, the data obtained in this study confirm the trends observed by Feng (1969), on honey stomach weights of worker bees. Thus, workers caught on open honey usually carried the greatest quantity of honey; those caught on open brood contained smaller quantities of food, but still contained more food (in 1969) than did the nectar foragers caught as they entered their colonies; pollen foragers returning from the fields generally carried less nectar in 1969 than did the nectar foragers. The smallest honey stomach weights were obtained from foragers leaving their colonies, under all conditions. In 1970, a very good year for honey production, nectar foragers carried more food than did workers caught on open brood throughout the entire season, and pollen foragers contained greater quantities of nectar than did the nurse bees during the month of July.

Although the 1969 and 1970 seasons differed considerably with respect to nectar flow, the seasonal trends for both years were very similar as to the mean weights, sugar and pollen concentrations of honey stomach contents in each of the five major categories of worker bees collected. In neither year were there consistent differences between the mean honey stomach weights, and the sugar and pollen

concentrations of the honey stomach contents obtained from workers collected in the mornings, and those collected in the afternoons; differences between colonies were not significant at the 5% level.

As is shown in Figures 12 through 17 (Chapter III) the nectar flow in both years began during the first week in July and lasted until the fourth week of August in 1969, and until the second week of August 1970. This is also indicated by an increase in the mean honey stomach weights and the mean sugar concentrations obtained from foragers returning to their hives, and by corresponding decreases as the flows waned. No such trend is apparent, however, in the mean pollen concentrations found in the honey stomach contents, indicating that the bees did not forage extensively on plant species that produced little or no pollen, or on species that produced an excess of it.

A different situation is indicated by the data obtained from the pollen foragers. During the 1969 season, little nectar was gathered by these bees. However, in 1970, the pollen foragers brought in large loads of nectar throughout July and part of August, surpassing in mid-July even the loads brought into the colonies by the nectar foragers at this time. In contrast to that of the nectar foragers, the sugar concentration of the honey stomach contents of pollen foragers remained at a high level (between

approximately 40 and 60%) throughout the season. Although there was a slight decrease in concentration throughout the 1969 season, the sugar concentration remained at more or less the same level (with fluctuations) in 1970. An exception to this was the rise in concentration to approximately 65% in mid-July; this coincided with the peak in the weight of the nectar loads brought into the colonies at this time. The concentration of pollen in the nectar brought in by the pollen foragers was more than four times as high as that found in the nectar gatherers; a steady decrease in pollen concentration was found to occur as the season advanced. The high values observed were presumably due to "scrabbling", a behavioural pattern in which the mouth parts and forelegs are actively used in the collection of pollen, and which tends to force pollen grains downward into the nectar. The high values obtained here, in comparison to those obtained for nectar foragers, lends support to the hypothesis that most of the pollen brought into the hive in nectar is accidentally pushed into the nectar by the activity of the bee itself.

According to Beutler (1936) and von Frisch (1969), foragers leaving their hives take with them sufficient carbohydrate reserves in the honey stomach to meet their metabolic needs on the flight to their foraging area; the amount of honey or nectar taken is proportional to the

amount of energy required to reach the area. The small amounts of food in the honey stomachs of foragers caught as they were leaving their colonies seem to indicate, therefore, that the foraging areas of these bees were relatively close to their colonies; the lack of variation in the quantities carried throughout the season suggests that the same foraging areas were utilized by the foragers over the entire summer of both years, and that these must have contained a good balance in crops in order to be able to hold the workers for that time. This interpretation seems to be substantiated by the presence of large numbers of nectar and pollen yielding plants within a half mile radius of the colonies throughout the season in both years.

Although a resemblance in the curves obtained for the mean honey stomach sugar concentration of foragers leaving their colonies and of pollen foragers returning to them, suggest a common origin of the food carried by both of these groups, a comparison of the pollen concentrations found in the honey stomach contents of both groups does not confirm this. It is possible, however, that the initial quantity of food brought to the field by the pollen foragers is supplemented by nectar taken from plants utilized by these bees, and that this could account for the relatively high sugar concentration recorded for pollen foragers throughout the entire season, as well as for the high concentration of

pollen found in their honey stomach contents.

As was expected, the pollen concentration found in the honey stomach contents of foragers leaving the hives was very low in 1969. However, in 1970, when large quantities of nectar were processed daily, the removal of pollen from the nectar was less efficient and workers leaving for the fields, obtained greater concentrations of pollen with the nectar.

Although differing in magnitude, the honey stomach weights obtained for workers collected on open brood and those collected on open honey show similar seasonal trends, which correspond closely to that of the honey flow. In both groups the lowest honey stomach weights occurred during June; however, with the beginning of the nectar flow in early July, the mean honey stomach weights increased, and remained at a relatively high level until mid-August of both years. Although generally carrying the largest quantity of food, the workers which had been collected on open honey also showed the greatest fluctuation in mean honey stomach weight throughout the season. These fluctuations were not unexpected, since most of the workers caught on open honey presumably were processing nectar received from the foragers returning from the fields, and may therefore have been more sensitive to changing conditions outside of the hive than were those workers which were feeding brood.

With reference to mean sugar concentration of honey stomach contents, both groups were also very similar, in that the sugar concentration increased until approximately mid-July, and for the rest of the season remained at a level varying between 50% and 70%, and between 60% and 70% for workers caught on open brood and those collected on open honey, respectively. The greater fluctuations in mean sugar concentration were found in workers caught on open brood. Since considerable quantities of water are utilized by worker bees in the brood area, it is assumed that the fluctuations observed were due to variations in the amount of water in the honey stomach contents of these bees, and these, in turn, depend on conditions occurring in the brood nest at the time.

Large differences in the relative quantities of pollen in the honey stomach contents of both groups were observed. Since workers feeding brood are known to consume pollen heavily, the high concentration of pollen found in the honey stomach contents of nurse bees is not surprising. The honey stomach contents of workers caught on open honey, however, contained unexpectedly high concentrations of pollen. Because relatively low pollen concentrations were found to occur in the foragers entering their colonies, and very little nectar was brought in by the pollen foragers except during the nectar flow of 1970, it is assumed that

most of the pollen found in the honey stomach contents of workers collected on open honey was derived from workers engaged in brood rearing. If true, this would indicate the occurrence of considerable interfeeding particularly among these two categories of bees. The frequent proximity of the area of open brood to areas of comb in which honey is stored, further supports this conclusion.

Throughout the 1969 season, samples of workers were also collected from areas of sealed brood. These were also investigated for honey stomach weights, sugar concentration of honey stomach contents and pollen concentration. In general, the results obtained for this group are so similar to those obtained for workers collected on open brood, that no separate discussion is presented.

During July, August, and September of 1969, a number of samples of drones, as well as of several "minor" categories, such as guards, foragers resting in the hive entrance, fanners, and workers caught on foundation, were collected. Due to the small numbers of samples obtained, no conclusions can be drawn from the data.

The following generalizations can be made, on the basis of the few samples available. The mean honey stomach weight obtained for drones varied from 4.3 mg. to 6.2 mg. and the mean sugar concentration between 46.2% and 66.7%. In both honey stomach weights and sugar concentrations of

honey stomach contents, the higher values were obtained in August and the lower values in July. Because drones were being driven from the colonies at the time when the final collections were made, the data obtained here indicate that drones are not starved by the workers prior to being driven from the colony, as has been suggested (Grout, 1954). The mean pollen concentrations found in the honey stomach contents varies between 515 pollen grains per mm^3 to as low as 57 grains per mm^3 of honey stomach contents. However, no seasonal trend could be found.

In general, the workers collected outside of the colonies, i.e. guards, "resting" bees, and fanners, contained very little food (less than 6.0 mg.). The only exceptions were the fanners collected in late August; these had a mean honey stomach weight of 21.7 mg. The mean honey stomach weights of workers caught on foundation was 25.2 mg.

With the exception of the last group of fanners collected, whose honey stomach contents had a mean sugar concentration of 65.3%, all of the workers collected in the colony entrances carried honey stomach contents varying in concentration between 44.2% and 32.5%. As was to be expected, the honey stomach contents of workers collected on foundation had a high sugar concentration (66.3%). The pollen concentration of all of the "minor categories" was very low - less than 15 grains per mm^3 of honey stomach

contents.

The size of a colony and the amount of brood cared for by its bees did not appear to influence the mean weights, sugar and pollen concentration of honey stomach contents of workers in any of the categories of bees investigated. Although relatively high concentrations of pollen were frequently found in the honey stomachs of workers collected in June, when the ratio of adult bees to brood in the still growing colonies was small, a statistical comparison of colony A-2/70 (which through swarming had reduced its population to approximately that of the initial package) to the other three experimental colonies for the remainder of the season showed that no differences between colonies existed.

All of the samples of bees collected during both years showed much individual variation in honey stomach contents, in honey stomach weight, sugar concentration, and the amount of pollen present. The variability observed did not seem to follow any definite patterns within the samples, nor did it appear to change considerably with the seasons. The causes underlying the differences found are not known; it appears likely, however, that they are based on inherent differences in the response of individual bees to the same stimuli. A study of the factors underlying variations in the behaviour of individual honey bees, and of means by which the behavioural responses of individuals can be modified

in any desired direction, seems to be a most promising field into which to direct future research in apiculture. Although at present we are able to modify the responses of entire colonies to certain stimuli to a limited degree, it should be possible to greatly increase the efficiency of colonies used in pollination or honey production if means were found to present appropriate stimuli to their individual members.

CHAPTER V

POLLEN FILTRATION

Introduction and Review of Literature

From the results obtained in the field studies, it is apparent that relatively large quantities of pollen often occur in the honey stomach contents of worker bees for all categories of bees in the colony. Yet, despite considerable reduction in volume of the nectar, resulting from the evaporation of water during the processing of nectar - which should lead to an increase in pollen concentration - similar quantities of pollen are rarely found in fully ripened honey (Maurizio, 1955; Demianowicz, 1964).

The decrease in the amount of pollen present in the worker bee honey stomach is primarily due to the activity of the proventriculus, which is located in the anterior end of the ventriculus and protrudes into the honey stomach (Trappmann, 1923; Whitcomb and Wilson, 1929; Bailey, 1951; 1952; Snodgrass, 1956; Dade, 1962). The proventriculus appears to resemble a mouth with four lips which surround a lumen. Within the lumen and along the edges of each lip are fine hairs, each about 150 µ long and spaced about 2.5 µ apart, forming delicate combs, directed posteriorly; longer bristles are located at the tip of each lip. A ventricular pouch is between the bases of the lips (Bailey, 1951; 1952).

Probably the most detailed description of the proventricular action was given by Bailey (1952). While the honey stomach continually writhes and pulsates vigourously, maintaining a homogeneous mixture and an even distribution of the pollen grains within it, (this was not observed by Whitcomb and Wilson, 1929), the proventriculus makes gulping movements, alternately filling with honey stomach contents and forcing the liquid back into the crop. The lips, moving asynchronously, rapidly snap open and close. They appear to permit the pollen suspension to enter the proventriculus during its expansion phase, but seem to guard against the ejection of pollen grains back into the crop.

Pollen accumulates first in the ventricular pouches, and when these are filled, in the lumen of the proventriculus. As the proventriculus becomes increasingly full, the amplitude of its movements decreases, and eventually the whole mass passes as a bolus down the neck of the proventriculus into the ventriculus, where digestion takes place (Trappmann, 1923; Bailey, 1952; Schreiner, 1952). A short, tubular extension of the proventriculus into the ventriculus probably prevents regurgitation of ventricular contents into the honey stomach (Dade, 1962).*

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*Although under most conditions very little nectar passes with the pollen filtered from the honey stomach contents (Whitcomb, and Wilson, 1929; Maurizio, 1949; Schreiner, 1952). Bailey (1952) found that occasionally, if the bees had been starved for long periods of time, i.e. four to five hours, two or three "boluses" of liquid contents would be passed to the ventriculus at once, before any filtering took place. This occurred whether the syrup contained pollen or not.

An accumulation of pollen near the mouth of the proventriculus, as had been described by Whitcomb and Wilson (1929), was never observed by Bailey. He did find, however, that occasionally on dissection a partly full proventriculus collapsed, expelling its contents into the honey stomach. Similar occurrences may have been responsible for the observations made by Whitcomb and Wilson.

Some of the factors influencing the rate at which pollen filtration occurs have been investigated. However, in many cases, the samples used in the experiments were very small, only 2 to 6 bees being used for each sample (Maurizio, 1942; 1949b; Bailey, 1951; 1952; Schreiner, 1952), and frequently the results obtained by various workers were contradictory.

Bailey's findings (1951, 1952), which were confirmed by the results obtained by Whitcomb and Wilson (1929) showed that at an initial concentration of 6,550 per cu. mm., all particles between 3 u and 50 u in size were removed from 0.01 ml. of fluid within 25 to 35 minutes. However, Maurizio (1942, 1949) found that when pollen suspensions, with initial concentrations varying between 450 and 750 grains per cu. mm., were fed,16 to 30 minutes were required to filter out two thirds to three fourths of the pollen in the honey stomach. She also noted that pollen grains were removed most rapidly directly after feeding but was unable to explain the

means by which a relatively large quantity of pollen had been removed from the honey stomach within a very short time.* After the initial reduction, the rate of pollen removal decreased with decreasing concentration in the honey stomach. This is in direct contrast to the results obtained by Bailey (1951, 1952), who found that higher concentrations of pollen were filtered out less efficiently than were lower concentrations, and that small pollens were filtered out more efficiently than were large pollens. These observations were explained by Bailey on the basis of the number of times the ventricular pouches were filled and emptied per unit of time - the process of emptying the pouches apparently resulting in a temporary work stoppage. Demianowicz (1964) stated that large pollen grains stimulate the proventriculus to greater activity than do small ones; nectars containing small pollen grains are "cleaned" to a lesser degree, resulting in honeys with a higher pollen content. A clear-cut discrimination between pollen grains of different sizes in the same suspension was not observed.

From his investigations into the effect of age of the experimental bees and of the environmental temperature

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*The initial high rate of pollen filtration found by Maurizio may have been due, as was suggested by Bailey (1952), to failure to ensure that honey stomachs were completely empty at the time of feeding, and that the apparent pollen reduction, in effect was due to dilution with liquid still in the honey stomach.

as factors influencing the rate of pollen filtration from the honey stomach, Schreiner (1952) concluded that the rate at which pollen passes into the ventriculus is independent of both age and environmental temperature in all but very young bees. In seven hour old bees eight to ten hours were required to clear the honey stomach of all pollen, while older bees required only one hour.

Similarly, the sugar concentration of the pollen suspension did not have any measurable effect on the rate of pollen filtration (Maurizio, 1949b). However, Maurizio tested only concentrations between 10% and 40%; it is conceivable that sugar solutions of higher concentration and higher viscosity might reduce the rate at which pollen is filtered from the liquid contents of the honey stomach.

On investigating the effect of honey flow conditions on the rate of pollen filtration, Demianowicz (1964) found that the greater the volume of nectar which is processed by a given number of bees, the less efficient is the filtration of pollen from it, and concluded that honey produced during a fast flow retains a relatively higher number of pollen grains per unit volume than does honey produced during a slow flow. These observations were supported by the results obtained by Bailey (1952), who found that with different volumes of the same concentration of particles of the same size, the higher volume of liquid will be filtered more slowly.

Thus, while it is clear that a variety of factors influence the rate and efficiency of pollen filtration by the proventriculus of the honey bee, the evidence obtained to date is not conclusive, especially when the small numbers of bees used in the individual samples are considered. The following experiments were done in the expectation that by using larger samples a more precise determination of the effect produced by some of the factors listed, on the rate of pollen filtration, could be obtained.

Methods and Materials

Starline hybrid worker bees (a yellow strain) were permitted to emerge in an incubator. They were marked within 24 hours of emergence, (they were considered to be one day old at this time), and were introduced into full-strength colonies of black Caucasian bees, from where they were collected when they had reached the desired age.

In these experiments, five of the factors which are thought to influence pollen filtration were investigated, including (a) length of time during which filtration proceeds, (b) age of the bees, (c) temperature at which the bees are held, (d) pollen concentration of the mixture fed, and (e) sugar concentration of the pollen suspension fed. Altogether ten experiments were performed; several were used to test more than one factor. The sample size (n=50), age of the bees, and the general technique used, were similar

for all tests; age and technique were varied only as required by the factor under study.

Prior to each test the experimental bees were held at room temperature in a community cage without either food or water, until a small number of the bees showed signs of starvation: i.e. loss of control over leg movements in walking, and inability to fly more than a few inches along a level surface (See Lauffliegen - Beutler, 1936). Preliminary experiments, as well as work done by previous authors (Free, 1957; Feng, 1969) had shown that worker bees of the same age and held under similar conditions, differ greatly in the amount of honey they hold in their crops at any given time, and that the time required by individual bees to starve (even in the same cage) may vary from less than three hours to more than twenty four hours. A standard starvation time, such as was used by Maurizio (1949), was not used in these experiments, since this technique is insufficient to ensure complete removal of all crop contents which could dilute the pollen concentration of the mixture fed and give rise to erroneous results.

In feeding, each bee was held by both wings so that her mouth parts and forelegs could readily reach the tip of the micropipette (Fisherbrand, 100 λ) containing the suspension of pollen (of known concentration) in a 50% sucrose solution.

Because of difficulties encountered in duplicating the pollen concentration, this varied slightly from sample to sample. Throughout each feeding, the pollen was kept in suspension by use of a magnetic stirrer, set at the lowest setting. Stratification of pollen within the pipette was avoided by completely refilling the pipette for each bee fed. The tests were conducted at room temperature, and no attempt was made to regulate the temperature of the pollen suspension.

The bees were permitted to feed freely for up to one minute and fifteen seconds or until they had taken forty λ of the pollen suspension. Most bees took between twenty and thirty λ ; those taking less than twenty λ were discarded. After feeding, the bees were placed individually into vials and were held for a standard time of twenty minutes. The bees were killed by quick-freezing, as in the previous experiments, and were stored in frozen condition until they could be dissected.

In general, readiness to feed from the pipette appeared to depend on the nutritional and physiological condition of each individual bee. Those which were close to but not at the point of starvation, fed most readily. Bees which were still very active when picked up, often fought the pipette, biting and trying to sting it. Whether a bee fought or fed readily seemed to depend both on individual temperament and on previous treatment; workers which had been squeezed, or

held by one wing, usually fought for some time before starting to take syrup from the pipette. On the other hand, those bees which had reached that point of starvation at which they were barely able to crawl, usually took syrup very slowly; such bees sometimes required up to half an hour to recuperate, after which time they usually fed at the normal rate.

For analysis, both pollen counts and sugar concentration measurements were made, as before. The samples were processed in lots of five bees each, resulting in ten pollen counts and ten sugar concentration measurements for each fifty bee sample. The results are shown in Tables through

The tests were carried out as follows:

A) Time:

During a good nectar flow, a given lot of nectar may be actively processed by the bees for only a short time before being placed into a cell. However, when nectar is scarce, it may be held in the honey stomach for a much longer time before being deposited in the comb (Park, 1925; Demianowicz, 1964). In order to test the effect of the length of time a pollen suspension is held in the honey stomach on the removal of pollen from it, three holding times were arbitrarily chosen: (a) 0 minutes - the bees were killed immediately after feeding, (b) 10 minutes - the bees were killed ten minutes after feeding, and (c) 20 minutes - the bees were

killed twenty minutes after feeding. (Table XIV).

B) Age:

Before nectar is completely processed into honey, it passes through several bees, each of which may filter pollen from it. Thus, a nectar forager (which is generally more than fifteen days old) on returning to the colony, distributes its nectar load among two or more of the generally much younger hive bees (Park, 1925; Rösch, 1925; Lindauer, 1952; Free, 1967) which, in turn, may pass part or all of their load to a number of workers of varying ages. To determine the effect of the age of a bee on the rate at which it filters pollen from the nectar in its honey stomach, bees three days old, eleven days old, and twenty five days old were tested. The results are shown in Table XX.

C) Temperature:

In their daily activities adult honey bees often encounter large variations in temperature both within, and outside of, the hive. As in other insects, the temperature of a resting bee approaches that of its environment (Ribbands, 1953). It appears likely, therefore, that the environmental temperature is an important factor in the regulation of the rate at which pollen is filtered out of the honey stomach contents.

In this study, one lot of 50 bees was subjected, after feeding, to a temperature of 92 degrees F. which

approximates the normal brood nest temperature (Dunham, 1929; 1931a; 1931b; Ribbands, 1953). Another lot of 50 bees was held at 60 degrees F., which approaches the temperature at which honey bees begin to form a heat conserving cluster (Ribbands, 1953). Although the bees were starved at room temperature, they were held after feeding in preheated (or prechilled) vials, in the incubator, for twenty minutes. The results are shown in Table XVI.

D) Pollen Concentration:

In the honey stomach contents of bees taken from normal colonies, considerable differences in the amount of pollen per cubic millimeter of liquid were noted. In this test, the effect of two concentrations of pollen (463 grains/mm^3, and 240 grains/mm^3) in 50% sugar syrup, on the rate of pollen filtration was studied. Table XVII shows the results obtained.

E) Sugar Concentration:

Pollen may be found not only in nectar at widely differing concentrations, which may vary from as low as 2.1% to as high as 76.6% (Beutler and Schöntag, 1940; Beutler, 1953) but also in honey and its intermediary products (Todd and Vansell, 1942; Maurizio, 1949a; 1955; 1956; 1958; Berner, 1952; Pritsch, 1957). In order to determine the effect of sugar concentration on the rate of pollen filtration, pollen suspensions, made up from three different sugar

solutions (20.0%, 50.0%, 71.0%) were fed. Since it was not possible under the present conditions to prevent the crystallization of sucrose in solutions at concentrations greater than 62.0%, honey was used to replace sucrose in preparing the 71.0% solution. See Table XVIII for the results obtained.

Results and Discussion

The results of these experiments show that pollen is actively removed from the honey stomach contents of worker honey bees. This process, which occurs through the action of the proventriculus, appears to be largely independent of the activities in which the bees are engaged. Pollen is filtered out of the honey stomach contents of forager bees, even while they are gathering nectar, and out of the crop contents of hive bees, which process the incoming nectar and perform other routine hive duties (Todd and Vansell, 1942; Maurizio, 1949b). Nevertheless, pollen filtration is influenced by a variety of factors, some of which are inherent in the bees (i.e. age), and others, which are environmental.

In these studies the influence of five factors on the rate of pollen filtration was investigated. It should be noted that in all cases the amount of pollen reduction which occurred was significant at the 1% level.

Time:

Table XIV shows the results obtained when bees which had been fed a pollen suspension of known concentration were

Initial Pollen Concentration	HOLDING TIME 0 Min.	(S.D.)	10 Min.	(S.D.)	20 Min.	(S.D.)	Difference	% Reduction	Significance at 1% level
488.3	424.0	(90.4)					64.3	13	+
471.0			252.0	(73.8)			219.0	46	+
462.7					151.2	(37.1)	311.5	67	+

Table XIV. Effect of length of time during which filtration occurs on the removal of pollen from the honey stomachs of 11 day old worker honey bees.

Initial Pollen Concentration	AGES 3 Days	(S.D.)	11 Days	(S.D.)	26 Days	(S.D.)	Difference	% Reduction	Significance at 1% level
503.0	261.0	(77.8)					242.0	48	+
462.7			151.2	(37.1)			311.5	67	+
460.0					175.9	(36.7)	284.1	62	+

Table XV. Effect of worker age on the amount of pollen removed from the honey stomach contents within 20 Min.

Initial Pollen Concentration	60 deg. F.	(S.D.)	90 deg. F.	(S.D.)	Difference	% Reduction	Significance at 1% level
529.0	361.8	(77.7)			167.2	32	+
529.0			164.4	(73.5)	364.6	69	+

Table XVI. Effect of temperature on the amount of pollen removed from the honey stomach contents of 12 day old worker honey bees within 20 minutes.

Initial Pollen Concentration	Reading (20 min)	(S.D.)	Difference	% Reduction	Significance at 1% level
462.7 (High)	151.2	(37.1)	311.5	67	+
240.0 (Low)	73.1	(24.4)	166.9	70	+

Table XVII. Effect of initial pollen concentration on the amount of pollen removed from the honey stomachs of 12 day old workers in 20 minutes.

Initial Pollen Concentration	Sugar Concentration	Readings	(S.D.)	Difference	% Reduction	Significance at 1% level
462.7	50%	151.2	(37.1)	311.5	67	+
502.0	20%	182.0	(112.7)	320.0	64	+
462.7	71% (Honey)	382.4	(71.1)	803	17	+

Table XVIII. Effect of sugar concentration on the amount of pollen removed from the honey stomach contents of 12 day old worker bees in 20 minutes.

permitted to retain the pollen-sucrose solution mixture in the honey stomachs for 0, 10, and 20 minutes. The data show that the filtering action of the proventriculus occurs already at the time when a bee is actively feeding. In the one and one quarter minutes required by the bee to obtain its load, the concentration of pollen was reduced from an initial 488.3 grains per mm^3 to 424 grains per mm^3. This represents a reduction of 13.0% (see table XIV). Similar findings were reported by Todd and Vansell (1942), who compared the pollen concentration in honey stomach contents of bees caught while foraging to the pollen content of nectar taken directly from the flowers of the plant species on which the bees had been working. Maurizio (1949b) also observed that pollen is filtered out of the nectar carried by a forager on its return flight to the colony.

In bees held for 10 minutes, the pollen concentration decreased from an initial 471 grains per mm^3 to 252 grains per mm^3, a reduction of 46.0%. The difference between this value and that obtained at 0 minutes was significant at the 1% level. Bees held for 20 minutes reduced the pollen content of the honey stomach by 67.0%, that is, from 462.7 grains per mm^3 to 151.2 grains per mm^3. The difference between this and the previous value also is significant at the 1% level.

The data obtained in this experiment fit an exponential curve. They are in agreement with the findings of Bailey

(1952), whose curves are "less steep than exponential curves at first", but gradually approach the shape of an exponential curve. This was probably due to Bailey's feeding of much higher initial concentrations of pollen in suspension, some at concentrations of one part of pollen to two parts of sugar solution. Maurizio (1949) reported that, after an initial sharp drop, pollen reduction in the crop is gradual and that within the first 16 - 30 minutes of feeding, the pollen content of syrup is reduced to 1/2 or 1/3 (rarely less). All of these findings are in direct opposition to those of Whitcomb and Wilson (1929), who found that pollen rarely remained in the honey stomach for longer than 20 minutes.

Age:

The data obtained in the second experiment suggest that age does influence the rate of pollen filtration (Table XV). Here, three day old bees (a) reduced the pollen concentration of the suspension they were fed by 48.0% within 20 minutes; within the same time eleven (b) and twenty six day old bees (c) reduced the pollen concentration of their honey stomach contents by 67.0% and 62.0%, respectively. The differences are significant as follows: (a) vs (b), $P < 0.01$; (a) vs (c), $P < 0.05$.

Although both Bailey (1952) and Schreiner (1952) observed that the rate at which pollen passes through the ventriculus into the rectum is much greater in foragers than in hive bees, presumably because of the greater activity and

higher body temperature of the older bees (Schreiner, 1952), only Schreiner related age to rate of pollen filtration by the proventriculus. He concluded that, except in bees which were seven hours old or younger, the rate of pollen passage from the honey stomach into the midgut is independent of age. However, with the exception of the seven hour old bees, Schreiner's youngest age group consisted of six day old bees. It is possible that bees of intermediate age might have given different results.

Temperature:

As can be seen from the data presented in Table XVI, the environmental temperature strongly influences the rate at which pollen grains are filtered from the honey stomach contents of worker honey bees. In this experiment, two groups of workers were held at 90 degrees F. and at 60 degrees F. respectively. While the bees held at the high temperature removed nearly 2/3 of the pollen from their honey stomachs in twenty minutes, those held at the low temperature removed only about 1/3 of the pollen in the same time. The difference is significant at the 1% level.

Although no previous work appears to have been done on the effect of temperature on the rate of pollen filtration, the results are not unexpected. Honey bees, when at rest, take on the temperature of their environment (Himmer, 1925). Previous studies have shown that pollen passes from the

ventriculus to the rectum at a greatly reduced rate at low temperatures (Schreiner, 1952; Jordan, 1966). It may be assumed that low temperatures also slow down the activity of the proventriculus.

Pollen Concentration:

At the two concentrations of pollen in 50% sucrose solution used in Experiment 4, no definite effect of pollen concentration on the rate of pollen filtration was found. (Table XVII). Similarly, Maurizio (1949b) found pollen concentration to have little effect on the rate of pollen filtration, when suspensions containing between 450 and 740 pollen grains per mm^3 were fed. Outside of these limits, there was "some" effect. However Bailey (1952), on feeding pollen suspensions of much higher concentration, found pollen concentration to have a significant effect on filtration. According to his findings, the efficiency of filtration is inversely proportional to the concentration.

Sugar Concentration:

The effect of sugar concentration of the pollen suspension on pollen filtration was investigated in Experiment 5 (Table XVIII). At low (20.0%) and intermediate (50.0%) concentrations the pollen was reduced by 64.0% and 67.0% respectively; the difference is not significant at the 1% level. At the high concentration (71.0%), the rate of pollen filtration was greatly reduced, and only 17.0% of the pollen

was filtered out. The difference between this value and those obtained at the lower concentrations is significant at the 1% level. Similarly, Maurizio (1949b) found no significant difference in the rate of pollen filtration, when pollen was fed in sugar solutions varying in concentration between 10.0 and 40.0%. Sugar solutions of higher concentration were not tested.

The reason for the reduction in the rate of pollen filtration from the 71% sugar solution is not known. Although it is conceivable that honey may exert an effect on the activity of the proventriculus, different from the effect produced by a sucrose solution, this does not appear to be likely. Betts (1927, 1934) suggested the increased viscosity of sucrose solutions above 50% to be the cause of a reduction in the rate of food uptake at those concentrations. It is possible, that the greater viscosity at high concentration also has a retarding effect on the action of the proventriculus.

Throughout all of these experiments, much variation between different 5-bee groups within any given sample was noted. Thus, while some of the bees filtered out relatively large quantities of pollen within a very short time (Experiment 1), others had removed little or no pollen from the honey stomach, even after the standard holding time of twenty minutes. Similar variations among individual bees

were also found by Bailey (1952) and by Maurizio (1949b), who concluded that pollen reduction within the honey stomach depends on influences existing in the individual bee at the moment, and to that extent, is independent of the environmental factors.

It is evident from the data presented in the previous chapter, that pollen normally occurs in the honey stomachs of worker bees in concentration from 0 to approximately 50% of the total honey stomach load. The pollen is removed from the liquid portion of the honey stomach contents through the action of the proventriculus and passes into the ventriculus, where it is digested (Trappmann, 1923; Whitcomb and Wilson, 1929; Bailey, 1952; Schreiner, 1952; Dade, 1962). A variety of factors, including environmental and physiological factors, may influence the rate at which pollen is removed from the honey stomach (Maurizio, 1949; Bailey, 1952; Schreiner, 1952).

In this study five such factors have been investigated. Among them only age appears to have no effect on the rate of pollen filtration - except in the case of very young bees, which filter pollen from the honey stomach contents much more slowly than do older bees under the same conditions (Schreiner, 1952). Similarly, the concentration, at which pollen occurs in the honey stomach, appears to have little or no influence on the rate at which it is removed from the

honey stomach contents. However, this seems to have been due largely to the low concentrations used in these experiments; the results obtained by Bailey (1952) clearly show that the rate at which pollen is filtered from the honey stomach varies considerably with concentration, and that at very high concentrations, the actual number of pollen grains removed per unit of time is high. However, the efficiency of the proventriculus appears to be relatively low because of the number of times filtration must stop in order to pass the accumulating pollen backward into the ventriculus.

It was shown in these studies that the temperature of the environment, at least under some conditions, can exert a considerable influence on the rate of pollen filtration. It may be concluded, therefore, that nurse bees operating under the influence of brood nest temperatures (92 - 93 degrees F.) would show a higher rate of pollen filtration than would bees processing nectar in a cooler part of the hive, or foragers working under field conditions, where they may be subjected to much lower temperatures than in the brood nest. Although individual bees may raise their body temperature considerably above that of their surroundings (Himmer, 1925), the main temperature difference is in the thorax, the site of muscular activity, rather than in the abdomen.

The longer a given lot of nectar is retained in the

honey stomach, the more pollen is filtered from it (Table XIV). Park (1925, 1927, 1928) observed that during a strong nectar flow, when much nectar is brought into the hive within a short time, any given lot of nectar may be processed by the bees only partially before being deposited into cells. Under such conditions the nectar is held in the honey stomachs of the hive bees for a shorter period of time than it would be under poor nectar flow conditions. It is to be expected, therefore, that less pollen would be filtered from nectar at the height of the flow, than under marginal conditions, when only small quantities of nectar are gathered. Similar observations have been made by Demianowicz (1964).

Pollen is filtered out of suspensions containing high concentrations of sugar (71.0%) less readily than it is filtered out of suspensions containing only between 10.0% and 50.0% sugar. Whether there is a gradual reduction in filtration with increasing sugar concentration, or whether the ability of the proventriculus to filter pollen out of suspension is reduced drastically at certain concentration of sugar, has yet to be determined. The data do suggest, however, that highly concentrated nectar may be cleared of pollen to a lesser degree than dilute nectar partly because concentrated nectar requires less "handling time" on the part of the bees, and partly because such nectar would

require less time to reach the concentration at which pollen is filtered out with increased difficulty.

The factors discussed above are only a few of those which may influence the activity of the proventriculus. As was suggested by Maurizio, (1949b), the influence exerted by the physical factors of the environment are sometimes overshadowed by the nutritional and physiological condition of the individual bee. Thus, the effect of changes induced by the feeding of brood, or the lack of brood feeding during the lifetime of a bee (i.e. summer bee vs. winter bee), presence or absence of queen, or the availability or non-availability of pollen in the previous diet of a worker bee, etc., need to be investigated if the activity of the proventriculus and its biological significance are to be fully understood.

Summary

1. Experiments were performed to determine the effect of various factors on the rate at which pollen is filtered out of suspension in the honey stomach contents by the proventriculus of worker honey bees.

2. The length of time which a pollen suspension is retained in the honey stomach and the environmental temperature both significantly affected the rate of pollen filtration. Sugar concentration affected the action of the proventriculus only at a very high (71%) concentration.

3. Pollen concentration did not significantly affect the rate of pollen filtration under the conditions of the experiment; it is suggested, however, that at higher concentrations pollen may exert considerable influence on the activity of the proventriculus.

4. The age of the worker bees had a significant effect on the rate of pollen filtration, at the three ages tested.

5. Biological ramifications of the above results are discussed.

CHAPTER VI

SUMMARY

1. Throughout the summers of 1969 and 1970 30-bee samples of worker honey bees were collected from various locations within four colonies situated on the Campus of the University of Manitoba. The bees were killed immediately by quick-freezing, and were stored in a freezer until they could be dissected.

2. The following data were also collected: (a) nectar flow, (b) pollen income, (c) maximum, minimum temperatures, (d) flowering periods of pollen and nectar yielding plants available to the bees, (e) the amount of brood present in each colony throughout the summer, and (f) the numbers of adult bees in each colony throughout the summer.

3. The honey stomachs of the bees collected during both summers were dissected out and investigated for the following: (a) honey stomach weight, (b) sugar concentration of the honey stomach contents, and (c) pollen concentration of the honey stomach contents. The weights of pollen loads carried by pollen foragers were also determined.

4. In 1969 the following honey stomach weight relationships were obtained: workers caught on open honey> workers caught on open brood> nectar foragers caught entering their colonies> pollen foragers caught entering

their colonies> foragers leaving their hives.

5. In 1970 the relationships were found to be similar, with the exception that nectar foragers carried more food in their honey stomachs than did bees caught on open brood, but less than those caught on open honey. Pollen foragers carried greater quantities of food than did those caught on open brood during the month of July, 1970.

6. In both years the following seasonal trends became apparent: The lowest honey stomach weights in all bees occurred in June. The amount of food carried by field workers returning to their hives increased in the beginning of the nectar flow (first week of July) and decreased when the flow ceased in mid-August. The amount of food retained by hive bees increased at the beginning of the nectar flow and remained at a high level for the remainder of the season. The honey stomach weights of foragers leaving their colonies remained constant throughout the season.

7. The seasonal trends obtained for sugar concentration of honey stomach contents varied with the location from which the bees were collected. In nectar foragers the sugar concentration reached its highest level during the nectar flow, and decreased when the flow ceased; in both pollen foragers and foragers leaving their colonies there was a slight decrease in sugar concentration over the season. In workers caught on open brood and on open honey the sugar

concentration of the honey stomach contents increased in July and remained at a high level for the remainder of the season.

8. For the concentration of pollen in the honey stomach contents a definite seasonal trend was not observed. In general, the pollen concentration was highest in the spring, but tended to fluctuate at lower levels for the remainder of the season. Usually, the highest values were found in bees caught on open brood, followed in descending order by pollen foragers, bees caught on open honey, nectar foragers returning to their colonies, and foragers leaving their hives.

9. From these studies it has been concluded that the honey stomach weight, and the sugar and pollen concentration of honey stomach contents are influenced by the location relative to the colony and by various environmental factors; time of day and size of colony appear to have little effect.

10. The pollen load weights did not show any seasonal effect.

11. Experiments were also performed to determine the effect of various factors on the rate at which pollen is filtered out of suspension in the honey stomach contents by the proventriculus of worker honey bees:

a. The length of time which a pollen suspension is retained in the honey stomach and the environmental

temperature both significantly affected the rate of pollen filtration. Sugar concentration affected the action of the proventriculus only at a very high (71%) concentration.

b. Pollen concentration did not significantly affect the rate of pollen filtration under the conditions of the experiment; it is suggested, however, that at higher concentrations pollen may exert considerable influence on the activity of the proventriculus.

c. The age of the worker bees had a significant effect on the rate of pollen filtration, at the three ages tested.

d. The biological significance of the above results is discussed.

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APPENDIX A (1969)

Colony Category	A - 1 Weight	A - 1 Sugar Conc.	A - 1 Pollen	A - 2 Weight	A - 2 Sugar Conc.	A - 2 Pollen	A - 3 Weight	A - 3 Sugar Conc.	A - 3 Pollen	A - 4 Weight	A - 4 Sugar Conc.	A - 4 Pollen
HO*	11.4mg.	66.5%	8/mm^3	12.9mg.	57.2%	158/mm^3	19.5mg.	64.1%	169/mm^3	9.2mg.	50.5%	335/mm^3
BO	3.7	57.0	138	5.1	48.5	52	8.0	22.0	15	5.4	44.3	255
BS	3.3	54.0	61	7.0	42.1	739	10.8	47.5	16	7.9	46.8	196
FE	7.0	29.5	92	9.1	49.5	7	25.3	56.3	11	18.4	54.0	8
FL	10.0	52.5	13	5.1	50.5	47	5.4	45.3	37	7.0	48.0	20
PFE	4.8	32.3	138	13.6	55.3	135	8.6	55.0	216	7.4	48.5	223
Pol.Ld.	17.5(29)	---	---	21.5(27)	---	---	15.1	----	---	15.3	----	---
HO**	15.6	64.5	184	17.9	52.5	192	14.8	58.0	220	10.2	42.5	145
BO	12.7	49.8	15	3.3	20.5	113	15.4	33.5	83	6.5	37.0	594
BS	6.4	39.5	18	4.9	34.5	207	13.1	34.0	128	4.8	27.3	269
FE	4.5	24.0	12	7.5	45.0	8	13.0	35.5	5	25.5	27.2	15
FL	4.3	42.0	41	5.9	45.5	111	5.1	32.5	177	5.1	37.0	50
PFE	----	----	---	23.3	49.0	110	9.6	38.8	53	19.2	56.3	220
Pol.Ld.	----	----	---	16.5(8)	----	---	13.8(20)	---	---	22.7(29)	---	---

APPENDIX TABLE I a. Analyses of Honey Stomach Contents of Worker Bees Collected on 26 May 1969 and 27 May 1969.
(A.M.* and P.M.**. Symbols: HO = Bees collected on open honey; BO = Bees collected on open brood; BS = Bees collected on sealed brood; FE = Returning forager bees caught entering their hives; FL = Foragers caught leaving their hives; PFE = Pollen foragers caught entering their hives; Pol. Ld. = Average weight of one pollen load. Parenthesis signify the number of bees used to obtain the mean, if less than 30.)

Category	A.M. Weight	A.M. Sugar Conc.	A.M. Pollen	P.M. Weight	P.M. Sugar Conc.	P.M. Pollen
HO	13.3mg.	59.6%	167/mm^3	14.6mg.	54.4%	185/mm^3
BO	5.5	43.0	115	9.5	35.2	234
BS	7.2	47.6	253	7.3	33.8	155
FE	15.0	47.3	30	12.7	32.8	8
FL	6.9	49.1	29	5.1	39.3	95
PFE	8.6	47.8	178	17.4	48.0	128
Pol.Ld.	17.4	----	---	16.7(3)	----	---

APPENDIX TABLE I b. Mean values obtained from (A-1, A-2, A-3, A-4), morning and afternoon. (Symbols as in Table I a. Parenthesis signify the number of samples used to obtain the mean, if less than 4).

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	14.2	16.8	1.0 - 53.0
	Sugar(%)	69.2	---	9.7 - 74.3
	Pollen*	3.1	4.5	0 - 16.0
BO	Weight(mg)	4.8	6.1	1 - 20.5
	Sugar(%)	44.0	---	0.5 - 75.6
	Pollen*	0	0	0 - 0
BS	Weight(mg)	7.4	12.0	1 - 51.5
	Sugar(%)	63.7	---	7.0 - 77.4
	Pollen*	1	1.0	0 - 2.0
FE	Weight(mg)	12.4	12.2	1.0 - 51.5
	Sugar(%)	63.7	---	7.0 - 72.7
	Pollen*	0.6	1	0 - 2.0
FL	Weight(mg)	6.6	7.6	1 - 35.0
	Sugar(%)	66.4	---	3.2 - 73.4
	Pollen*	2.4	3.0	0 - 8.0
PFE	Weight(mg)	2.5	3.0	1 - 13.0
	Sugar(%)	53.2	---	27.2 - 69.4
	Pollen*	26.0	34.0	2.0 - 50.0
Pollen Loads	Weight(mg)	11.2	5.4	1.0 - 23.0

Appendix Table II a. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 7 June, 1969, from colony A - 1.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	7.4	12.6	1.0 - 51.0
	Sugar(%)	44.4	---	0 - 75.5
	Pollen*	10.3	23.0	0 - 62.0
BO	Weight(mg)	7.7	8.5	1.0 - 34.0
	Sugar(%)	61.4	---	16.5 - 72.5
	Pollen*	0	0	0 - 0
BS	Weight(mg)	5.5	5.6	1.0 - 20.5
	Sugar(%)	45.1	---	1.0 - 70.1
	Pollen*	4.0	10.0	0 - 26.0
FE	Weight(mg)	10.0	9.0	1.0 - 34.0
	Sugar(%)	69.0	---	54.0 - 76.0
	Pollen*	0.3	0.7	0 - 2.0
FL	Weight(mg)	5.0	5.7	1.0 - 21.0
	Sugar(%)	53.7	---	12.5 - 70.0
	Pollen*	0.8	1.5	0 - 4.0
PFE	Weight(mg)	5.2	5.3	1.0 - 20.0
	Sugar(%)	28.3	---	4.5 - 39.0
	Pollen*	0	0	0 - 0
Pollen Loads	Weight(mg)	None collected.		

Appendix Table II b. Expanded analysis (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 7 June, 1969, from colony A - 2.

Symbols:
1. Pollen* = number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. BS = Worker bees caught on sealed brood.
5. FE = Nectar foragers caught on returning to their hives.
6. FL = Foragers caught leaving their hives.
7. PFE = Pollen foragers caught returning to their hives.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	9.6	12.2	1.0 - 43.0
	Sugar(%)	63.1	---	1.0 - 74.7
	Pollen*	1.0	1.5	0 - 4.0
BO	Weight(mg)	8.9	13.8	1 - 51.5
	Sugar(%)	68.2	---	1.8 - 76.6
	Pollen*	3.3	1.8	2.0 - 6.0
BS	Weight(mg)	5.6	8.9	1.0 - 44.5
	Sugar(%)	55.0	---	2.0 - 77.8
	Pollen*	12.6	20.7	0 - 54.0
FE	Weight(mg)	19.6	15.3	1.0 - 40.0
	Sugar(%)	16.0	---	0 - 58.8
	Pollen*	2.5	3.2	0 - 10.0
FL	Weight(mg)	5.5	5.1	1.0 - 16.5
	Sugar(%)	66.1	---	32.5 - 72.7
	Pollen*	1.1	3.3	0 - 10
PFE	Weight(mg)	3.6	2.8	1.0 - 12.0
	Sugar(%)	60.0	---	34.5 - 71.2
	Pollen*	5.2	7.6	0 - 18.0
Pollen Loads	Weight(mg)	16.9	6.9	4.0 - 26.0

Appendix Table IIc. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 7 June, 1969, from Colony A - 3.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	10.4	13.7	1.0 - 58.0
	Sugar(%)	54.0	---	0 - 76.2
	Pollen*	3.6	4.3	0 - 14.0
BO	Weight(mg)	3.5	6.3	1 - 32.5
	Sugar(%)	57.2	---	5.0 - 77.7
	Pollen*	5.0	9.2	0 - 16.0
BS	Weight(mg)	2.9	2.5	1.0 - 11.0
	Sugar(%)	42.4	---	25.0 - 70.5
	Pollen*	6.0	8.5	0 - 12.0
FE	Weight(mg)	15.0	11.6	1.0 - 32.5
	Sugar(%)	40.3	---	2.0 - 63.0
	Pollen*	2.3	3.0	0 - 8.0
FL	Weight(mg)	4.7	6.5	1.0 - 31.0
	Sugar(%)	61.4	---	26.6 - 74.3
	Pollen*	1.0	1.4	0 - 2.0
PFE	Weight(mg)	1.9	1.4	1.0 - 6.5
	Sugar(%)	58.2	---	48.2 - 69.5
	Pollen*	---	---	--- ---
Pollen Loads	Weight(mg)	15.0	6.3	5.0 - 28.0

Appendix Table IId. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 7 June, 1969, from Colony A - 4.

Symbols:
1. Pollen* = number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. BS = Worker bees caught on sealed brood.
5. FE = Nectar foragers caught on returning to their hives.
6. FL = Foragers caught leaving their hives.
7. PFE = Pollen foragers caught returning to their hives.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	9.9	8.1	1.0 - 23.0
	Sugar(%)	24.8	---	1.0 - 70.8
	Pollen*	17.1	57.9	0 -226.0
BO	Weight(mg)	6.5	6.4	1.0 - 28.0
	Sugar(%)	13.8	---	1.5 - 63.5
	Pollen*	19.8	35.5	0 -106.0
BS	Weight(mg)	3.5	3.2	1.0 - 13.0
	Sugar(%)	34.3	---	2.5 - 67.4
	Pollen*	2.0	2.0	0 - 4.0
FE	Weight(mg)	9.1	9.5	1.0 - 36.5
	Sugar(%)	39.8	---	0 - 62.0
	Pollen*	1.8	2.5	0 - 6.0
FL	Weight(mg)	3.2	3.3	1.0 - 14.0
	Sugar(%)	53.6	---	21.0 - 69.9
	Pollen*	0	0	0 - 0
PFE	Weight(mg)	1.6	1.2	1.0 - 6.5
	Sugar(%)	50.2	---	20.0 - 62.0
	Pollen*	---	---	--- ---
Pollen Loads	Weight(mg)	20.1	7.1	7.0 - 33.0

Appendix Table IIe. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 7 June, 1969, from colony A - 1

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	21.5	15.0	1.0 - 52.0
	Sugar(%)	67.8	---	0.2 - 76.7
	Pollen*	5.4	15.4	0 - 58.0
BO	Weight(mg)	3.5	5.3	1.0 - 26.0
	Sugar(%)	49.8	---	0 - 68.7
	Pollen*	0.5	1.0	0 - 2.0
BS	Weight(mg)	8.0	11.1	1.0 - 46.0
	Sugar(%)	61.6	---	1.0 - 76.5
	Pollen*	6.2	13.6	0.0 - 44.0
FE	Weight(mg)	13.9	11.9	1.0 - 39.0
	Sugar(%)	29.2	---	0 - 71.5
	Pollen*	3.6	4.5	0 - 12.0
FL	Weight(mg)	4.4	5.5	1.0 - 27.5
	Sugar(%)	41.3	---	0.5 - 61.2
	Pollen*	2.0	2.5	0 - 6.0
PFE	Weight(mg)	7.2	8.8	1.0 - 33.0
	Sugar(%)	54.1	---	39.5 - 67.0
	Pollen*	7.6	9.2	0 - 30.0
Pollen Loads	Weight(mg)	15.9	6.9	6.0 - 29.0

Appendix Table II f. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 7 June, 1969, from colony A - 2.

Symbols:

1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. BS = Worker bees caught on sealed brood.
5. FE = Nectar foragers caught on returning to their hives.
6. FL = Foragers caught leaving their hives.
7. PFE = Pollen foragers caught returning to their hives.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	13.7	13.4	1.0 - 31.0
	Sugar(%)	23.3	---	2.7 - 72.0
	Pollen*	5.6	10.2	0 - 34.0
BO	Weight(mg)	7.1	10.5	1.0 - 51.0
	Sugar(%)	44.0	---	1.0 - 80.0
	Pollen*	1.3	2.4	0.0 - 6.0
BS	Weight(mg)	10.6	16.0	0 - 61.0
	Sugar(%)	43.9	---	1.0 - 76.4
	Pollen*	1.8	3.5	0 - 10.0
FE	Weight(mg)	21.5	14.0	1.0 - 50.0
	Sugar(%)	8.7	---	0.0 - 71.0
	Pollen*	13.5	52.2	0 -202.0
FL	Weight(mg)	5.9	5.6	1.0 - 21.5
	Sugar(%)	56.8	---	7.5 - 74.0
	Pollen*	9.3	17.1	0 - 48.0
PFE	Weight(mg)	3.3	3.5	1.0 - 11.0
	Sugar(%)	48.6	---	34.5 - 60.8
	Pollen*	8.0	11.3	0 - 16.0
Pollen Loads	Weight(mg)	13.8	6.5	8.0 - 28.0

Appendix Table II g. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 7 June, 1969, from colony A - 3.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	16.2	14.0	1.0 - 43.5
	Sugar(%)	39.0	---	0.5 - 76.0
	Pollen*	39.7	136.2	0 -530.0
BO	Weight(mg)	7.7	9.7	1.0 - 37.0
	Sugar(%)	59.1	---	0.6 - 77.5
	Pollen*	35.1	96.8	0 -324.0
BS	Weight(mg)	9.5	11.4	1.0 - 43.5
	Sugar(%)	38.3	---	0 - 63.7
	Pollen*	0	0	0 - 0
FE	Weight(mg)	15.1	11.4	1.0 - 54.0
	Sugar(%)	49.2	---	29.0 - 66.6
	Pollen*	1.1	1.7	0 - 6.0
FL	Weight(mg)	4.8	4.4	1.0 - 17.0
	Sugar(%)	45.6	---	1.5 - 63.5
	Pollen*	1.8	1.2	0 - 4.0
PFE	Weight(mg)	4.5	6.1	1.0 - 23.0
	Sugar(%)	59.0	---	43.7 - 73.0
	Pollen*	74.3	174.3	0 -230.0
Pollen Loads	Weight(mg)	17.7	8.0	2.5 - 36.0

Appendix Table II h. Expanded analysis (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 7 June, 1969, from colony A - 4.

Symbols:
1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. BS = Worker bees caught on sealed brood.
5. PE = Nectar foragers caught on returning to their hives.
6. FL = Foragers caught leaving their hives.
7. PFE = Pollen foragers caught returning to their hives.

Category	Weight	A.M. Sugar Conc.	Pollen	Weight	P.M. Sugar Conc.	Pollen
HO	10.4mg.	58.1%	5/mm^3	15.3mg.	39.5%	17/mm^3
BO	6.2	58.2	2	6.2	42.2	21
BS	5.4	52.0	6	7.9	45.0	2
FE	14.3	37.2	1	14.9	32.1	3
FL	5.5	62.4	1	4.6	49.8	3
PFE	3.3	50.4	10	4.2	53.5	29
Pol. Ld.	14.4(3)	---	---	17.2	---	---

Appendix Table II i. Mean values obtained from (A-1, A-2, A-3, A-4), morning and afternoon. (Symbols as in Page 204. Parenthesis signify the number of samples used to obtain the mean, if less than 4.)

Colony Category	A - 1 Weight	A - 1 Sugar Conc.	A - 1 Pollen	A - 2 Weight	A - 2 Sugar Conc.	A - 2 Pollen	A - 3 Weight	A - 3 Sugar Conc.	A - 3 Pollen	A - 4 Weight	A - 4 Sugar Conc.	A - 4 Pollen
HO*	10.4mg.	60.8%	194/mm^3	13.6mg.	66.0%	145/mm^3	13.7mg.	61.5%	28/mm^3	15.6mg.	68.0%	11/mm^3
BO	5.2	66.0	194	9.1	68.0	141	7.8	39.0	12	9.7	70.0	62
BS	6.8	46.5	13	10.7	65.5	49	7.9	62.0	79	6.1	63.0	75
FE	15.3	23.0	76	7.9	54.0	49	9.0	20.3	7	4.9	62.3	93
FL	6.5	52.8	31	3.3	58.3	14	4.4	57.0	3	4.3	56.0	8
PFE	4.2	47.5	229	3.6	53.0	67	3.3	52.0	55	3.8	48.5	365
Pol.Ld.	7.5	----	---	11.2	----	---	9.6	----	---	11.7	----	---
HO**	14.9	58.0	66	27.3	64.8	35	12.2	45.5	44	7.1	39.5	98
BO	2.5	30.5	12	7.0	42.5	24	11.0	53.3	22	4.8	60.0	36
BS	10.4	61.8	27	7.8	55.8	52	5.3	36.4	24	9.1	68.0	45
FE	8.3	13.5	0	10.3	15.3	27	8.1	29.8	43	18.1	6.0	1
FL	4.3	47.5	2	4.9	44.3	7	3.9	44.0	10	4.5	48.0	6
PFE	----	----	---	6.1	50.8	63	7.7	55.0	62	5.0	43.8	157
Pol.Ld.	----	----	---	8.1(29)	---	---	10.1(8)	---	---	9.1	----	---

APPENDIX TABLE IIIa. Analyses of Honey Stomach Contents of Worker Bees Collected on 19 June, 1969. (A.M.* and P.M.**. Symbols: HO = Bees collected on open honey; BO = Bees collected on open brood; BS = Bees collected on sealed brood; FE = Returning forager bees caught entering their hives; FL = Foragers caught leaving their hives; PFE = Pollen foragers caught entering their hives; Pol. Ld. = Average weight of one pollen load.) (Parenthesis signify the number of bees used to obtain the mean, if less than 30.)

Category	A.M. Weight	A.M. Sugar Conc.	A.M. Pollen	P.M. Weight	P.M. Sugar Conc.	P.M. Pollen
HO	13.3mg.	64.1%	95/mm^3	15.4mg.	52.0%	61/mm^3
BO	8.0	60.8	102	6.3	46.6	24
BS	7.9	59.3	54	8.2	55.5	37
FE	9.3	39.9	56	11.2	16.2	18
FL	4.6	56.0	14	4.4	46.0	6
PFE	3.7	50.2	179	6.3	49.9	94
Pol.Ld.	10.0	----	---	9.1(3)	----	---

APPENDIX TABLE IIIb. Mean values obtained from (A-1, A-2, A-3, A-4), morning and afternoon. (Symbols as in Table IIIa. Parenthesis signify the number of samples used to obtain the mean, if less than 4).

Colony Category	A - 1 Weight	A - 1 Sugar Conc.	A - 1 Pollen	A - 2 Weight	A - 2 Sugar Conc.	A - 2 Pollen	A - 3 Weight	A - 3 Sugar Conc.	A - 3 Pollen	A - 4 Weight	A - 4 Sugar Conc.	A - 4 Pollen
HO*	16.4mg.	66.8%	20/mm^3	23.9mg.	69.5%	0/mm^3	5.9mg.	48.8%	8/mm^3	3.7mg.	63.0%	0/mm^3
BO	3.7	54.0	18	11.1	64.5	4	7.9	52.4	22	4.0	50.9	3
BS	5.5	63.0	9	8.2	60.3	0	9.5	47.5	56	4.0	42.9	6
FE	10.2	39.0	11	16.4	22.5	0	16.7	24.3	27	7.1	31.5	0
FL	6.2	51.3	11	5.0	40.8	0	5.0	47.0	7	4.3	34.0	10
PFE	5.0	38.0	165	5.0	42.5	24	3.6	41.0	27	3.5	44.5	25
G	3.0	41.0	7	3.3	41.0	0	19.0	67.8	60	3.4	25.3	2
Pol.Ld.	21.1	----	---	7.2	----	---	17.3	----	---	14.6	----	---
HO**	10.3	62.5	0	25.7	69.5	4	7.2	54.8	15	31.0	66.8	0
BO	6.4	34.5	131	7.9	18.8	1	9.9	24.5	1	26.7	62.0	100
BS	3.8	44.5	36	9.1	45.5	60	10.1	36.0	90	23.6	35.8	5
FE	24.7	10.8	2	11.7	39.5	0	11.3	15.0	4	8.4	20.5	2
FL	4.3	34.5	3	5.2	36.0	0	2.8	26.8	0	2.9	19.5	9
PFE	11.7	43.0	0	4.3	42.0	22	7.1	44.0	24	11.5	32.5	19
G	2.9	38.5	0	3.0	31.5	31	7.7	66.0	0	1.8	42.5	0
Pol.Ld.	7.3	----	---	13.1	----	---	14.0	----	---	11.6	----	---

APPENDIX TABLE IV a. Analyses of Honey Stomach Contents of Worker Bees Collected on 1 July 1969. (A.M.* and P.M.**. Symbols: HO = Bees collected on open honey; BO = Bees collected on open brood; BS = Bees collected on sealed brood; FE = Returning forager bees caught entering their hives; FL = Foragers caught leaving their hives; PFE = Pollen foragers caught entering their hives; G = Guard; Pol. Ld. = Average weight of one pollen load.)

Category	A.M. Weight	A.M. Sugar Conc.	A.M. Pollen	P.M. Weight	P.M. Sugar Conc.	P.M. Pollen
HO	12.5mg.	62.0%	7/mm^3	18.6mg.	63.4%	5/mm^3
BO	6.7	55.5	12	12.7	35.0	58
BS	6.8	53.4	18	11.7	40.5	48
FE	12.6	29.3	9	13.9	26.5	2
FL	5.2	43.3	7	3.8	29.2	3
PFE	4.1	41.5	60	8.6	40.4	16
G	7.2	43.8	17	3.9	44.6	8
Pol.Ld.	15.1	----	---	11.5	----	---

APPENDIX TABLE IV b. Mean values obtained from (A-1, A-2, A-3, A-4), morning and afternoon. (Symbols as in Table IV a.)

Colony Category	A - 1 Weight	A - 1 Sugar Conc.	A - 1 Pollen	A - 2 Weight	A - 2 Sugar Conc.	A - 2 Pollen	A - 3 Weight	A - 3 Sugar Conc.	A - 3 Pollen	A - 4 Weight	A - 4 Sugar Conc.	A - 4 Pollen
HO*	30.3mg.	69.0%	0/mm^3	34.7mg.	72.3%	0/mm^3	16.3mg.	69.5%	66/mm^3	29.9mg.	70.0%	6/mm^3
BO	5.1	68.5	0	23.2	72.0	1	21.9	70.5	181	16.1	62.5	73
BS	1.8	34.5	59	22.4	69.3	4	41.4	72.0	0	15.4	60.0	0
FE	----	----	---	----	----	---	-----	----	---	----	----	---
FL	----	----	---	----	----	---	-----	----	---	----	----	---
PFE	----	----	---	----	----	---	-----	----	---	----	----	---
D	5.4	20.5	0	3.0	56.5	32	5.5	54.3	362	3.5	53.5	5
E	1.7	32.5	48	4.8	45.8	9	2.1	23.5	0	11.3	42.5	1
Pol. Ld.	----	----	---	----	----	---	-----	----	---	----	----	---
HO**	32.0	69.3	3	37.9	72.5	0	35.2	73.0	0	34.5	74.8	56
BO	15.7	61.5	4	1.6	27.5	23	19.9	56.5	49	12.6	55.0	117
BS	3.4	41.0	84	3.7	22.5	0	12.7	75.5	116	18.3	62.5	84
FE	23.7	57.5	22	13.3	58.0	64	17.0	42.5	1	22.4	28.5	0
FL	5.7	31.5	1	6.1	35.5	0	6.7	36.5	0	8.2	35.8	7
PFE	4.6	40.0	13	8.3	35.0	0	5.1	26.5	46	6.1	38.5	0
Pol. Ld.	18.8	----	---	18.4	----	---	10.7	----	---	10.7	----	---

APPENDIX TABLE V a. Analyses of Honey Stomach Contents of Worker Bees Collected on 14 July 1969.

(A.M.* and P.M.**. Symbols: HO = Bees collected on open honey; BO = Bees collected on open brood; BS = Bees collected on sealed brood; FE = Returning forager bees caught entering their hives; FL = Foragers caught leaving their hives; PFE = Pollen foragers caught entering their hives; D = Drone; E = Entrance; Pol. Ld. = Average weight of one pollen load.)

Category	Weight	A.M. Sugar Conc.	Pollen	Weight	P.M. Sugar Conc.	Pollen
HO	27.8mg.	70.2%	18/mm^3	34.9mg.	72.4%	15/mm^3
BO	16.6	68.4	64	12.4	50.1	48
BS	20.3	59.0	16	9.5	50.4	71
FE	----	----	---	19.1	46.6	22
FL	----	----	---	6.7	34.8	2
PFE	----	----	---	6.0	35.0	15
D	4.3	46.2	100	----	----	---
E	5.0	36.1	15	----	----	---
Pol. Ld.	----	----	---	14.7	----	---

APPENDIX TABLE V b. Mean values obtained from (A-1, A-2, A-3, A-4), morning and afternoon. (Symbols as in Table Va.)

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	30.4	23.9	1.0 - 71.0
	Sugar(%)	72.1	---	18.8 - 80.0
	Pollen*	3.2	7.6	0 - 30.0
BO	Weight(mg)	28.5	22.7	1.0 - 77.0
	Sugar(%)	61.6	---	0 - 76.4
	Pollen*	3.6	6.5	0 - 24.0
BS	Weight(mg)	12.7	13.7	1.0 - 36.5
	Sugar(%)	57.5	---	0.5 - 72.2
	Pollen*	3.6	9.2	0 - 36.0
FE	Weight(mg)	15.4	14.3	1.0 - 39.5
	Sugar(%)	23.3	---	0.5 - 56.5
	Pollen*	11.3	26.3	0 - 84.0
FL	Weight(mg)	2.7	1.9	1.0 - 7.5
	Sugar(%)	37.5	---	2.4 - 54.3
	Pollen*	0	0	0 - 0
Fo	Weight(mg)	18.6	20.4	1.0 - 65.0
	Sugar(%)	71.9	---	26.5 - 77.8
	Pollen*	3.3	5.4	0 - 20.0
PFE	Weight(mg)	9.4	10.5	1.0 - 38.5
	Sugar(%)	53.5	---	37.0 - 60.4
	Pollen*	57.3	46.8	2.0 -132.0
Pollen Loads	Weight(mg)	13.15	8.2	1.0 - 30.0

Appendix Table VI a. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 25 July, 1969, from colony A - 1.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	25.0	21.9	1.0 - 65.0
	Sugar(%)	74.1	---	47.5 - 79.1
	Pollen*	3.3	7.1	0 - 28.0
BO	Weight(mg)	20.0	24.9	1.0 - 73.0
	Sugar(%)	72.4	---	45.0 - 78.5
	Pollen*	3.8	12.7	0 - 44.0
BS	Weight(mg)	15.8	21.7	1.0 - 64.0
	Sugar(%)	68.3	---	13.3 - 77.7
	Pollen*	0.5	1.7	0 - 6.0
FE	Weight(mg)	13.7	11.4	1.0 - 45.0
	Sugar(%)	74.1	---	67.0 - 76.4
	Pollen*	0.3	1.0	0 - 4.0
FL	Weight(mg)	9.5	9.1	0 - 34.5
	Sugar(%)	47.6	---	30.0 - 61.5
	Pollen*	4.8	19.0	0 - 72.0
Fo	Weight(mg)	20.3	17.8	1.0 - 56.0
	Sugar(%)	71.5	---	41.5 - 76.5
	Pollen*	0	0	0 - 0
PFE	Weight(mg)	4.0	3.4	1.0 - 12.0
	Sugar(%)	31.8	---	23.5 - 38.5
	Pollen*	0	0	0 - 0
Pollen Loads	Weight(mg)	None collected		

Appendix Table VIb. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 25 July, 1969, from colony A - 2.

Symbols:

1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. BS = Worker bees caught on sealed brood.
5. FE = Nectar foragers caught on returning to their hives.
6. FL = Foragers caught leaving their hives.
7. Fo = Foundation.
8. PFE = Pollen foragers caught returning to their hives.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	19.8	20.8	1.0 - 81.5
	Sugar(%)	71.1	---	32.5 - 76.0
	Pollen*	2.1	4.1	0.0 - 10.0
BO	Weight(mg)	19.7	27.7	1.0 - 84.0
	Sugar(%)	69.7	---	19.0 - 74.5
	Pollen*	10.3	20.5	0.0 - 64.0
BS	Weight(mg)	32.8	22.4	1.5 - 83.0
	Sugar(%)	73.0	---	51.5 - 75.5
	Pollen*	0.0	0.0	0.0 - 0.0
FE	Weight(mg)	15.1	13.1	1.0 - 58.0
	Sugar(%)	51.8	---	22.5 - 61.5
	Pollen*	0.9	2.3	0.0 - 8.0
FL	Weight(mg)	2.5	2.0	1.0 - 8.0
	Sugar(%)	50.1	---	28.0 - 67.0
	Pollen*	---	---	--- ---
Fo	Weight(mg)	25.7	23.8	1.0 - 72.5
	Sugar(%)	70.3	---	2.0 - 78.5
	Pollen*	1.3	1.8	0.0 - 5.0
PFE	Weight(mg)	11.9	10.5	1.0 - 33.0
	Sugar(%)	50.0	---	29.0 - 60.0
	Pollen*	83.6	117.9	0.0 -448.0
Pollen Loads	Weight(mg)	15.4	6.4	2.5 - 30.0

Appendix Table VI c. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 25 July, 1969, from colony A - 3.

Symbols:

1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. BS = Worker bees caught on sealed brood.
5. FE = Nectar foragers caught on returning to their hives.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	34.5	24.7	1.0 - 70.0
	Sugar(%)	72.9	---	33.0 - 75.2
	Pollen*	1.2	2.1	0.0 - 8.0
BO	Weight(mg)	14.0	18.5	1.0 - 66.5
	Sugar(%)	64.1	---	2.5 - 73.8
	Pollen*	3.5	6.3	0.0 - 20.0
BS	Weight(mg)	26.9	19.7	1.0 - 65.0
	Sugar(%)	69.8	---	11.5 - 76.0
	Pollen*	0.3	0.7	0.0 - 2.0
FE	Weight(mg)	18.0	16.2	1.0 - 48.5
	Sugar(%)	37.5	---	0.5 - 55.5
	Pollen*	3.1	6.6	0.0 - 22.0
FL	Weight(mg)	3.3	3.3	1.0 - 18.0
	Sugar(%)	40.4	---	26.5 - 49.0
	Pollen*	0.0	0.0	0.0 - 0.0
Fo	Weight(mg)	18.6	19.6	1.0 - 66.0
	Sugar(%)	68.3	---	7.0 - 79.0
	Pollen*	0.3	1.0	0.0 - 4.0
PFE	Weight(mg)	19.6	9.5	1.0 - 30.0(7)
	Sugar(%)	46.6	---	40.5 - 56.0(7)
	Pollen*	195.2	114.8	0.0 -316.0(7)
Pollen Loads	Weight(mg)	7.1	5.5	60.0 - 16.0(10)

Appendix Table VI d. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 25 July, 1969, from colony A - 4.

6. FL = Foragers caught leaving their hives.
7. Fo = Foundation.
8. PFE = Pollen foragers caught returning to their hives.
9. (X) = Number of bees in sample, if fewer than 15.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	16.8	16.7	1.0 - 54.0
	Sugar(%)	66.3	---	6.0 - 79.6
	Pollen*	3.5	4.3	0.0 - 16.0
BO	Weight(mg)	23.2	22.0	1.5 - 66.0
	Sugar(%)	65.9	---	0.7 - 71.0
	Pollen*	4.7	8.4	0.0 - 22.0
BS	Weight(mg)	7.5	9.9	1.0 - 33.0
	Sugar(%)	36.8	---	0.7 - 77.5
	Pollen*	8.0	13.0	0.0 - 30.0
FE	Weight(mg)	20.5	16.9	1.5 - 56.0
	Sugar(%)	57.8	---	33.8 - 62.5
	Pollen*	34.1	88.6	0.0 -294.0
FL	Weight(mg)	4.5	9.1	1.0 - 49.0
	Sugar(%)	47.8	---	25.7 - 50.0
	Pollen*	1.7	1.5	0.0 - 4.0
Fo	Weight(mg)	30.4	19.2	1.0 - 66.5
	Sugar(%)	67.5	---	0.0 - 79.4
	Pollen*	1.6	3.1	0.0 - 10.0
PFE	Weight(mg)	14.5	14.2	1.5 - 35.0(27)
	Sugar(%)	57.2	---	35.0 - 64.8
	Pollen*	222.6	210.3	0.0 -696.0
Pollen Loads	Weight(mg)	14.7	8.4	5.0 - 27.0

Appendix Table VI e. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 25 July, 1969, from colony A - 1.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	17.5	10.3	1.0 - 39.5
	Sugar(%)	68.3	---	65.0 - 74.5
	Pollen*	0.0	0.0	0.0 - 0.0
BO	Weight(mg)	11.8	7.4	1.5 - 26.5
	Sugar(%)	73.0	---	62.5 - 76.0
	Pollen*	1.7	4.3	0.0 - 16.0
BS	Weight(mg)	6.1	5.1	1.0 - 24.0
	Sugar(%)	34.0	---	20.5 - 39.5
	Pollen*	0.5	2.1	0.0 - 8.0
FE	Weight(mg)	13.3	9.5	1.0 - 34.0
	Sugar(%)	68.9	---	62.0 - 74.5
	Pollen*	1.1	4.1	0.0 - 16.0
FL	Weight(mg)	5.4	4.3	1.0 - 18.5
	Sugar(%)	57.1	---	46.5 - 70.6
	Pollen*	0.0	0.0	0.0 - 0.0
Fo	Weight(mg)	11.4	14.8	1.0 - 55.0
	Sugar(%)	60.7	---	4.5 - 75.0
	Pollen*	0.6	1.5	0.0 - 4.0
PFE	Weight(mg)	8.4	6.6	1.0 - 27.5
	Sugar(%)	55.4	---	46.0 - 61.5
	Pollen*	0.0	0.0	0.0 - 0.0
Pollen Loads	Weight(mg)	---	---	--- ---

Appendix Table VI f. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 25 July, 1969, from colony A - 2.

Symbols:

1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. BS = Worker bees caught on sealed brood.
5. FE = Nectar foragers caught on returning to their hives.
6. FL = Foragers caught leaving their hives.
7. Fo = Foundation
8. PFE = Pollen foragers caught returning to their hives.
9. (X) = Number of bees in sample, if fewer than 15.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	21.4	20.2	1.0 - 79.0
	Sugar(%)	64.7	---	3.0 - 76.8
	Pollen*	0.5	1.2	0.0 - 4.0
BO	Weight(mg)	19.1	23.4	1.0 - 72.5
	Sugar(%)	57.7	---	1.0 - 76.3
	Pollen*	16.3	27.1	0.0 - 70.0
BS	Weight(mg)	8.7	16.8	1.0 - 68.0
	Sugar(%)	59.5	---	0.0 - 74.0
	Pollen*	0.9	1.1	0.0 - 2.0
FE	Weight(mg)	26.0	16.4	1.0 - 51.5
	Sugar(%)	59.9	---	0.0 - 66.7
	Pollen*	28.5	62.4	0.0 - 196.
FL	Weight(mg)	2.4	1.7	1.0 - 7.5
	Sugar(%)	45.2	---	23.0 - 65.0
	Pollen*	29.0	---	---(2)
Fo	Weight(mg)	21.5	19.8	1.0 - 67.0
	Sugar(%)	54.2	---	0.0 - 79.0
	Pollen*	0.5	1.2	0.0 - 4.0
PFE	Weight(mg)	21.8	16.0	3.0 - 49.0
	Sugar(%)	59.9	---	48.0 - 65.5
	Pollen*	106.3	100.6	8.0 -394.0
Pollen Loads	Weight(mg)	17.3	9.6	2.0 - 36.0

Appendix Table VI g. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 25 July, 1969, from colony A - 3.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	20.6	20.5	1.0 - 60.0
	Sugar(%)	57.6	---	0.0 - 76.0
	Pollen*	2.0	2.8	0.0 - 8.0
BO	Weight(mg)	11.4	16.3	1.0 - 48.5
	Sugar(%)	56.8	---	0.0 - 75.6
	Pollen*	13.4	39.6	0.0 -126.0
BS	Weight(mg)	13.8	19.2	1.0 - 64.0
	Sugar(%)	64.4	---	1.0 - 79.0
	Pollen*	2.6	5.1	0.0 - 16.0
FE	Weight(mg)	13.3	10.3	1.0 - 34.0
	Sugar(%)	74.5	---	73.0 - 76.0
	Pollen*	5.6	21.7	0.0 - 84.0
FL	Weight(mg)	3.5	2.8	1.0 - 11.0
	Sugar(%)	24.9	---	8.0 - 42.5
	Pollen*	0	0	0 - 0
Fo	Weight(mg)	22.5	19.7	1.0 - 62.5
	Sugar(%)	62.3	---	11.5 - 74.8
	Pollen*	1.3	2.1	0.0 - 6.0
PFE	Weight(mg)	7.8	6.2	1.0 - 21.0
	Sugar(%)	47.6	---	38.5 - 65.0
	Pollen*	0	0	0 - 0
Pollen Loads	Weight(mg)	---	---	--- ---

Appendix Table VI h. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 25 July, 1969, from colony A - 4.

Symbols:

1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. BS = Worker bees caught on sealed brood.
5. FE = Nectar foragers caught on returning to their hives.
6. FL = Foragers caught leaving their hives.
7. Fo = Foundation
8. PFE = Pollen foragers caught returning to their hives.
9. (X) = Number of bees in sample, if fewer than 15.

Category	Weight	A.M. Sugar Conc.	Pollen	Weight	P.M. Sugar Conc.	Pollen
HO	27.4mg.	73.1%	3/mm^3	19.0mg.	65.0%	2/mm^3
BO	20.6	67.4	5	13.4	64.1	6
BS	21.9	67.7	1	9.0	49.4	2
FE	15.5	49.4	4	19.3	65.7	17
FL	4.3	44.4	2	4.0	44.3	0
Fo	28.8	71.0	1	21.5	61.6	0
PFE	11.2	45.9	39(3)	13.1	55.5	90
Pol. Ld.	11.6(3)	---	---	16.0(2)	---	---

Appendix Table VI i. Mean values obtained from (A-1, A-2, A-3, A-4), morning and afternoon. (Symbols as in page 214. Parenthesis signify the number of samples used to obtain the mean, if less than 4.)

Colony Category	A - 1 Weight	A - 1 Sugar Conc.	A - 1 Pollen	A - 2 Weight	A - 2 Sugar Conc.	A - 2 Pollen	A - 3 Weight	A - 3 Sugar Conc.	A - 3 Pollen	A - 4 Weight	A - 4 Sugar Conc.	A - 4 Pollen
HO*	47.7mg.	74.8%	0/mm^3	32.5mg.	72.5%	0/mm^3	50.9mg.	77.5%	0/mm^3	58.9mg.	77.5%	0/mm^3
BO	24.6	77.0	0	22.8	76.0	0	27.9	74.8	3	45.2	76.5	0
BS	39.0	77.0	2	55.4	76.8	0	49.0	78.0	8	58.6	76.5	27
FE	13.4	23.5	57	13.1	37.5	13	6.2	24.5	32	23.4	61.5	0
FL	6.1	29.0	1	8.9	27.0	2	5.0	20.5	2	5.1	29.3	0
PFE	----	----	---	----	----	---	----	----	----	----	----	---
G	1.3	24.5	0	1.9	23.5	0	1.6	21.5	0	1.3	24.5	4
Pol.Ld.	----	----	---	----	----	---	----	----	----	----	----	---
HO**	45.7	72.8	0	29.4	78.0	0	40.2	78.0	0	52.2	76.8	0
BO	5.8	63.0	0	17.0	69.3	0	57.8	78.0	0	46.9	63.5	17
BS	10.0	55.0	0	35.6	74.5	1	42.9	78.5	0	45.4	76.5	0
FE	26.7	68.5	0	12.2	59.8	11	22.5	57.5	0	30.7	61.3	0
FL	4.4	34.5	6	5.6	26.8	2	6.8	26.5	1	9.0	33.5	7
PFE	3.5	38.5	20	7.2	41.5	0	4.0	35.5	0	8.0	35.5	161
Fa	----	----	---	----	----	---	1.5	24.0	0	----	----	---
Pol.Ld.	13.2	----	---	10.4	----	---	15.0	----	---	16.0	----	---

APPENDIX TABLE VIIa. Analyses of Honey Stomach Contents of Worker Bees Collected on 8 August 1969.

(A.M.* and P.M.**. Symbols: HO = Bees collected on open honey; BO = Bees collected on open brood; BS = Bees collected on sealed brood; FE = Returning forager bees caught entering their hives; FL = Foragers caught leaving their hives; PFE = Pollen foragers caught entering their hives; G = Guard; Fa = Fanning bees; Pol.Ld. = Average weight of one pollen load.)

Category	A.M. Weight	A.M. Sugar Conc.	A.M. Pollen	P.M. Weight	P.M. Sugar Conc.	P.M. Pollen
HO	47.5mg.	75.5%	0/mm^3	41.9mg.	76.4%	0/mm^3
BO	30.1	76.1	1	31.9	68.5	4
BS	50.5	77.1	9	33.5	71.1	0
FE	14.0	36.8	26	23.0	61.8	3
FL	6.3	26.4	1	6.5	30.3	4
PFE	----	----	---	5.7	37.8	45
G	1.5	23.5	1	----	----	---
Fa	----	----	---	1.5(1)	24.0(1)	0
Pol.Ld.	----	----	---	13.7	----	---

APPENDIX TABLE VIIb. Mean values obtained from (A-1, A-2, A-3, A-4), morning and afternoon. (Symbols as in Table VIIa. Parenthesis signify the number of samples used to obtain the mean, if less than 4.)

Colony Category	A - 1 Weight	A - 1 Sugar Conc.	A - 1 Pollen	A - 2 Weight	A - 2 Sugar Conc.	A - 2 Pollen	A - 3 Weight	A - 3 Sugar Conc.	A - 3 Pollen	A - 4 Weight	A - 4 Sugar Conc.	A - 4 Pollen
HO*	38.7mg.	70.5%	0/mm^3	38.9mg.	78.3%	0/mm^3	38.1mg.	69.3%	9/mm^3	40.1mg.	77.0%	0/mm^3
BO	26.2	69.8	0	52.0	----	---	10.5	33.5	20	19.7	68.0	0
BS	16.8	70.5	0	18.9	35.0	0	25.5	65.5	24	19.3	65.5	0
FE	10.6	26.8	46	26.6	38.0	0	22.2	25.5	3	9.7	34.5	0
FL	7.4	38.8	1	2.7	24.8	0	1.9	30.3	2	3.1	27.8	0
PFE	2.7	26.8	10	3.0	29.8	8	3.7	28.5	0	4.3	32.5	0
D	3.9	41.0	606	4.5	56.8	521	3.9	56.5	0	5.0	41.0	879
Pol.Ld.	7.9(17)	----	---	9.6	----	---	16.5	----	---	10.9	----	---
HO**	24.7	77.5	0	20.4	68.8	0	28.6	74.8	0	46.0	71.3	1
BO	15.1	69.8	0	9.5	59.5	10	27.1	69.5	0	28.1	61.0	4
BS	24.7	68.3	0	32.1	70.0	0	11.1	41.3	4	6.4	41.0	2
FE	24.1	58.5	0	3.3	42.8	0	6.6	39.5	0	19.5	41.0	4
FL	5.0	41.5	1	4.7	35.5	0	7.2	35.5	5	5.7	32.0	6
PFE	5.3	47.0	116	4.0	42.5	0	6.0	41.0	33	14.7	45.0	98
D	6.1	54.0	1464	5.2	54.8	98	5.1	54.0	188	5.5	66.8	363
Pol.Ld.	14.5	----	---	15.0	----	---	16.0(27)	----	---	15.4(29)	----	---

APPENDIX TABLE VIIIa. Analysis of Honey Stomach Contents of Worker Bees Collected on 19 August 1969.

(A.M.* and P.M.**. Symbols: HO = Bees collected on open honey; BO = Bees collected on open brood; BS = Bees collected on sealed brood; FE = Returning forager bees caught entering their hives; FL = Foragers caught leaving their hives; PFE = Pollen foragers caught entering their hives; D = Drone; Pol. Ld. = Average weight of one pollen load. Parenthesis signify the number of bees used to obtain the mean, if less than 30.)

Category	Weight	A.M. Sugar Conc.	Pollen	Weight	P.M. Sugar Conc.	Pollen
HO	38.9mg.	73.8%	2/mm^3	29.9mg.	73.1%	0/mm^3
BO	27.1	57.1(3)	7	19.0	65.0	4
BS	20.1	59.1	6	18.6	55.2	2
FE	17.3	31.2	12	14.1	45.5	1
FL	3.8	30.4	1	5.6	36.2	3
PFE	3.4	29.4	5	7.5	43.9	62
D	4.3	48.8	502	5.5	57.4	528
Pol. Ld.	11.2	----	---	15.2	----	---

APPENDIX TABLE VIIb. Mean Values obtained from (A-1, A-2, A-3, A-4), morning and afternoon. (Symbols as in Table VIIIa. Parenthesis signify the number of samples used to obtain the mean, if less than 4.)

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	28.6	20.4	1.0 - 61.5
	Sugar(%)	74.1	---	1.5 - 78.5
	Pollen*	0.1	0.5	0.0 - 2.0
HS	Weight(mg)	13.8	10.7	1.0 - 29.5
	Sugar(%)	70.2	---	60.0 - 75.5
	Pollen*	0	0	0 - 0
BO	Weight(mg)	15.3	8.2	1.0 - 32.0
	Sugar(%)	74.5	---	69.5 - 77.5
	Pollen*	0	0	0 - 0
BS	Weight(mg)	13.7	9.5	1.0 - 38.0
	Sugar(%)	76.3	---	70.0 - 77.5
	Pollen*	0	0	0 - 0
FE	Weight(mg)	15.1	14.2	1.0 - 51.0
	Sugar(%)	22.6	---	6.5 - 53.6
	Pollen*	0.2	0.6	0.0 - 2.0
FL	Weight(mg)	3.9	2.7	1.0 - 14.5
	Sugar(%)	34.4	---	21.0 - 40.0
	Pollen*	0	0	0 - 0
PFE	Weight(mg)	---	---	--- ---
	Sugar(%)	---	---	--- ---
	Pollen*	---	---	--- ---
Pollen Loads	Weight(mg)	---	---	--- ---

Appendix Table IX a. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 29 August, 1969, from colony A - 1.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	36.7	22.6	3.0 - 75.0
	Sugar(%)	74.1	---	49.5 - 78.8
	Pollen*	0	0	0 - 0
HS	Weight(mg)	33.9	28.9	1.0 - 90.0
	Sugar(%)	70.9	---	2.0 - 79.0
	Pollen*	1.2	2.5	0 - 8.0
BO	Weight(mg)	18.1	12.2	1.0 - 48.0
	Sugar(%)	72.6	---	62.0 - 75.0
	Pollen*	0.4	1.1	0.0 - 4.0
BS	Weight(mg)	29.8	19.1	1.0 - 71.5
	Sugar(%)	74.1	---	70.5 - 74.5
	Pollen*	0	0	0 - 0
FE	Weight(mg)	3.7	2.5	1.0 - 9.0
	Sugar(%)	34.6	---	7.5 - 45.5
	Pollen*	0	0	0 - 0
FL	Weight(mg)	4.6	3.7	1.0 - 16.5
	Sugar(%)	33.5	---	9.5 - 45.5
	Pollen*	0	0	0 - 0
PFE	Weight(mg)	10.4	7.1	1.0 - 29.0
	Sugar(%)	27.4	---	17.5 - 32.0
	Pollen*	1.6	2.0	1.0 - 6.0
Pollen Loads	Weight(mg)	8.7	3.2	3.5 - 12.5

Appendix Table IXb. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 29 August, 1969, from colony A - 2.

Symbols:

1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. BS = Worker bees caught on sealed brood.
5. FE = Nectar foragers caught on returning to their hives.
6. HS = Sealed honey.
7. FL = Foragers caught leaving their hives.
8. PFE = Pollen foragers caught returning to their hives.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	26.4	21.5	1.0 - 71.0
	Sugar(%)	74.6	---	26.0 - 77.5
	Pollen*	0.8	2.1	0.0 - 8.0
HS	Weight(mg)	18.0	23.7	1.0 - 78.0
	Sugar(%)	75.5	---	11.0 - 78.4
	Pollen*	4.0	11.5	0.0 - 40.0
BO	Weight(mg)	33.1	24.7	1.0 - 75.5
	Sugar(%)	75.6	---	70.0 - 78.2
	Pollen*	1.2	2.0	0.0 - 6.0
BS	Weight(mg)	23.6	23.6	1.0 - 60.0
	Sugar(%)	74.9	---	0.0 - 77.1
	Pollen*	0.9	1.9	0.0 - 6.0
FE	Weight(mg)	6.5	8.2	1.0 - 27.0
	Sugar(%)	32.8	---	16.0 - 60.1
	Pollen*	1.3	2.7	0.0 - 6.0
FL	Weight(mg)	---	---	--- ---
	Sugar(%)	---	---	--- ---
	Pollen*	---	---	--- ---
PFE	Weight(mg)	---	---	--- ---
	Sugar(%)	---	---	--- ---
	Pollen*	---	---	--- ---
Pollen Loads	Weight(mg)	---	---	--- ---

Appendix Table IX c. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 29 August, 1969, from colony A - 3.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	38.7	25.8	2.0 - 86.0
	Sugar(%)	75.3	---	73.0 - 79.0
	Pollen*	0.8	1.3	0.0 - 4.0
HS	Weight(mg)	36.7	28.2	1.0 - 98.5
	Sugar(%)	75.3	---	64.0 - 78.7
	Pollen*	1.7	2.7	0.0 - 10.0
BO	Weight(mg)	24.2	20.9	1.6 - 68.0
	Sugar(%)	73.1	---	19.0 - 77.6
	Pollen*	3.7	3.7	0.0 - 16.0
BS	Weight(mg)	16.4	19.0	1.0 - 55.0
	Sugar(%)	71.7	---	1.2 - 77.8
	Pollen*	350.4	1355.4	0.0 -5250.
FE	Weight(mg)	9.7	8.6	1.0 - 26.5
	Sugar(%)	17.4	---	8.5 - 50.0
	Pollen*	3.5	5.1	0.0 - 16.0
FL	Weight(mg)	5.0	4.5	1.0 - 19.0
	Sugar(%)	53.9	---	26.5 - 69.5
	Pollen*	2.8	4.7	0.0 - 16.0
PFE	Weight(mg)	---	---	--- ---
	Sugar(%)	---	---	--- ---
	Pollen*	---	---	--- ---
Pollen Loads	Weight(mg)	---	---	--- ---

Appendix Table IX d. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 29 August, 1969, from colony A - 4.

Symbols:

1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. HS = Sealed honey.
4. BO = Worker bees caught on open brood.
5. BS = Worker bees caught on sealed brood.
6. FE = Nectar foragers caught on returning to their hives.
7. FL = Foragers caught leaving their hives.
8. PFE = Pollen foragers caught returning to their hives.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	---	---	---
	Sugar(%)	---	---	---
	Pollen*	---	---	---
HS	Weight(mg)	---	---	---
	Sugar(%)	---	---	---
	Pollen*	---	---	---
BO	Weight(mg)	---	---	---
	Sugar(%)	---	---	---
	Pollen*	---	---	---
BS	Weight(mg)	---	---	---
	Sugar(%)	---	---	---
	Pollen*	---	---	---
FE	Weight(mg)	7.6	7.7	1.0 - 33.0
	Sugar(%)	27.8	---	1.5 - 77.6
	Pollen*	5.7	16.2	0.0 - 64.0
FL	Weight(mg)	5.8	4.8	1.0 - 20.5
	Sugar(%)	41.1	---	3.0 - 71.4
	Pollen*	0.5	1.2	0.0 - 4.0
PFE	Weight(mg)	---	---	---
	Sugar(%)	---	---	---
	Pollen*	---	---	---
Fa	Weight(mg)	---	---	---
	Sugar(%)	---	---	---
	Pollen*	---	---	---
Pollen Loads	Weight(mg)	---	---	---

Appendix Table IX e. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 29 August, 1969, from colony A - 1.

Symbols:

1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. HS = Sealed honey.
4. BO = Worker bees caught on open brood.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	42.2	29.0	1.0 - 93.0
	Sugar(%)	60.3	---	0.0 - 77.4
	Pollen*	2.4	3.1	0.0 - 12.0
HS	Weight(mg)	---	---	---
	Sugar(%)	---	---	---
	Pollen*	---	---	---
BO	Weight(mg)	27.2	28.3	1.0 - 85.0
	Sugar(%)	65.7	---	13.4 - 79.0
	Pollen*	50.0	182.5	0.0 -684.0
BS	Weight(mg)	22.1	22.2	1.0 - 62.0
	Sugar(%)	50.4	---	2.1 - 79.0
	Pollen*	323.3	1227.6	0.0 -4760.0
FE	Weight(mg)	---	---	---
	Sugar(%)	---	---	---
	Pollen*	---	---	---
FL	Weight(mg)	---	---	---
	Sugar(%)	---	---	---
	Pollen*	---	---	---
PFE	Weight(mg)	---	---	---
	Sugar(%)	---	---	---
	Pollen*	---	---	---
Fa	Weight(mg)	27.9	26.5	1.0 - 77.5
	Sugar(%)	56.6	---	2.5 - 79.0
	Pollen*	2.0	4.5	0.0 - 16.0
Pollen Loads	Weight(mg)	---	---	---

Appendix Table IXf. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 29 August, 1969, from colony A - 2.

5. BS = Worker bees caught on sealed brood.
6. FE = Nectar foragers caught on returning to their hives.
7. FL = Foragers caught leaving their hives
8. PFE = Pollen foragers caught returning to their hives.
9. Fa = Fanning

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	34.0	25.7	1.5 - 80.0
	Sugar(%)	73.3	---	21.5 - 77.0
	Pollen*	0.4	0.8	0.0 - 2.0
HS	Weight(mg)	---	---	--- ---
	Sugar(%)	---	---	--- ---
	Pollen*	---	---	--- ---
BO	Weight(mg)	8.4	12.6	1.0 - 43.0
	Sugar(%)	66.7	---	23.0 - 76.0
	Pollen*	1.5	2.8	1.0 - 10.0
BS	Weight(mg)	18.0	16.4	1.0 - 65.5
	Sugar(%)	60.0	---	1.5 - 76.5
	Pollen*	115.6	416.5	0.0 -1620.0
FE	Weight(mg)	---	---	--- ---
	Sugar(%)	---	---	--- ---
	Pollen*	---	---	--- ---
FL	Weight(mg)	---	---	--- ---
	Sugar(%)	---	---	--- ---
	Pollen*	---	---	--- ---
PFE	Weight(mg)	---	---	--- ---
	Sugar(%)	---	---	--- ---
	Pollen*	---	---	--- ---
Fa	Weight(mg)	9.5	9.1	1.0 - 32.0
	Sugar(%)	67.9	---	9.5 - 75.0
	Pollen*	0.0	0.0	0.0 - 0.0
Pollen Loads	Weight(mg)	---	---	--- ---

Appendix Table IX g. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 29 August, 1969, from colony A - 3.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	19.2	17.8	1.0 - 53.5
	Sugar(%)	73.9	---	24.5 - 77.5
	Pollen*	1.1	2.3	0.0 - 6.0
HS	Weight(mg)	---	---	--- ---
	Sugar(%)	---	---	--- ---
	Pollen*	---	---	--- ---
BO	Weight(mg)	---	---	--- ---
	Sugar(%)	---	---	--- ---
	Pollen*	---	---	--- ---
BS	Weight(mg)	---	---	--- ---
	Sugar(%)	---	---	--- ---
	Pollen*	---	---	--- ---
FE	Weight(mg)	---	---	--- ---
	Sugar(%)	---	---	--- ---
	Pollen*	---	---	--- ---
FL	Weight(mg)	---	---	--- ---
	Sugar(%)	---	---	--- ---
	Pollen*	---	---	--- ---
PFE	Weight(mg)	---	---	--- ---
	Sugar(%)	---	---	--- ---
	Pollen*	---	---	--- ---
Fa	Weight(mg)	27.5	23.0	1.0 - 72.0
	Sugar(%)	69.6	---	12.0 - 75.6
	Pollen*	0.9	1.3	0.0 - 2.0
Pollen Loads	Weight(mg)	---	---	--- ---

Appendix Table IX h. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 29 August, 1969, from colony A - 4.

Symbols:

1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. HS = Sealed honey.
4. BO = Worker bees caught on open brood.
5. BS = Worker bees caught on sealed brood.
6. FE = Nectar foragers caught on returning to their hives.
7. FL = Foragers caught leaving their hives.
8. PFE = Pollen foragers caught returning to their hives.
9. Fa = Fanning

Category	Weight	A.M. Sugar Conc.	Pollen	Weight	P.M. Sugar Conc.	Pollen
HO	32.6mg.	75.0%	0/mm^3	31.8mg.(3)	69.7%(3)	1/mm^3(3)
HS	25.6	73.4	2	---	---	---
BO	22.7	74.5	1	17.8(2)	66.7(2)	282(2)
BS	20.9	74.6	88	20.0(2)	55.7(2)	191(2)
FE	8.8	27.4	1	7.6(1)	28.3(1)	5(1)
FL	4.4(3)	41.1(3)	1(3)	5.8(1)	41.6(1)	1(1)
PFE	10.4(1)	27.9(1)	2(1)	---	---	---
Fa	---	---	---	21.6(3)	65.2(3)	1(3)
Pol. Ld.	8.7(1)	---	---	---	---	---

Appendix Table IX i. Mean values obtained from (A-1, A-2, A-3, A-4), morning and afternoon. (Symbols as in page 223. Parenthesis signify the number of samples used to obtain the mean, if less than 4.)

Colony Category	A - 1 Weight	A - 1 Sugar Conc.	A - 1 Pollen	A - 2 Weight	A - 2 Sugar Conc.	A - 2 Pollen	A - 3 Weight	A - 3 Sugar Conc.	A - 3 Pollen	A - 4 Weight	A - 4 Sugar Conc.	A - 4 Pollen
HO*	27.2mg.	72.3%	26/mm^3	39.3mg.	75.3%	8/mm^3	25.4mg.	74.3%	7/mm^3	30.5mg.	75.5%	1/mm^3
HS	12.7	72.3	3	13.9	70.2	1	13.9	73.0	14	18.5	73.5	3
BO	8.8	70.0	4	40.4	73.0	26	22.4	72.0	0	11.7	67.7	59
BS	11.2	73.5	289	21.7	69.3	31	22.2	75.0	110	20.7	70.5	2
FE	----	----	---	----	----	---	----	----	---	----	----	---
FL	----	----	---	----	----	---	----	----	---	----	----	---
PFE	----	----	---	----	----	---	----	----	---	----	----	---
D	5.7	68.1	2	7.5	67.3	7	8.2	65.6	92	7.9	66.2	173
Pol.Ld.	----	----	---	----	----	---	----	----	---	----	----	---
HO**	32.4	58.5	17	33.4	74.0	14	45.0	74.5	0	30.1	71.1	152
HS	28.6	64.5	0	42.9	75.6	0	33.1	69.7	3	32.3	74.5	1
BO	16.1	68.0	0	27.0	73.7	3	34.0	72.1	4	31.7	64.2	21
BS	23.9	71.0	1	27.8	69.5	1	15.1	68.5	28	28.4	75.8	0
FE	14.9	5.1	---	17.4	41.0	3	17.3	28.5	2	13.6	19.0	1
FL	5.3	31.6	1	3.6	42.0	4	----	----	---	2.7	44.5	0
PFE	1.4	49.5	0	6.5	39.5	4	1.3	----	---	----	----	---
D	9.6	70.5	3	10.6	69.5	0	4.9	64.0	150	5.9	62.3	224
Pol.Ld.	5.6(9)	----	---	3.5(6)	----	---	5.9(22)	---	---	----	----	---

APPENDIX TABLE X a. Analyses of Honey Stomach Contents of Worker Bees collected on 15 September 1969.

(A.M.* and P.M.**. Symbols: HO = Bees collected on open honey; HS = Sealed honey; BO = Bees collected on open brood; BS = Bees collected on sealed brood; FE = Returning forager bees caught entering their hives; FL = Foragers caught leaving their hives; PFE = Pollen foragers caught entering their hives; D = Drone; Pol. Ld. = Average weight of one pollen load. Parenthesis signify the number of bees used to obtain the mean, if less than 30.)

Category	Weight	A.M. Sugar Conc.	Pollen	Weight	P.M. Sugar Conc.	Pollen
HO	30.6mg.	74.4%	11/mm^3	35.2mg.	69.5%	46/mm^3
HS	14.8	72.3	5	34.2	71.1	1
BO	20.8	70.7	22	27.2	69.5	7
BS	19.0	72.1	108	23.8	71.2	8
FE	----	----	---	15.8	23.4	2(3)
FL	----	----	---	3.9(3)	39.4(3)	2
PFE	----	----	---	3.1(3)	44.5(2)	2(2)
D	7.3	66.8	69	7.8	66.6	94
Pol. Ld.	----	----	---	5 (3)	----	---

APPENDIX TABLE X b. Mean values obtained from (A-1, A-2, A-3, A-4), morning and afternoon.

(Symbols as in Table X a. Parenthesis signify the number of samples used to obtain the mean, if less than 4.)

Colony Category	A - 1 Weight	A - 1 Sugar Conc.	A - 1 Pollen	A - 2 Weight	A - 2 Sugar Conc.	A - 2 Pollen	A - 3 Weight	A - 3 Sugar Conc.	A - 3 Pollen	A - 4 Weight	A - 4 Sugar Conc.	A - 4 Pollen
HO*	29.2mg.	70.5%	1/mm^3	26.6mg.	71.5%	32/mm^3	28.2mg.	72.7%	2/mm^3	26.3mg.	72.5%	0/mm^3
HS	19.1	70.3	0	42.7	75.3	0	13.5	68.5	2	16.4	69.0	1
BO	6.2	64.9	1	18.3	73.2	0	10.1	65.5	7	10.7	69.0	6
BS	10.9	69.0	0	9.3	----	2	23.4	70.0	9	14.0	69.5	3
FE	----	----	---	----	----	----	----	----	---	----	----	---
FL	----	----	---	----	----	----	----	----	---	----	----	---
PFE	----	----	---	----	----	----	----	----	---	----	----	---
D	3.1	62.5	4	3.3	54.5	16	5.6	60.0	3	5.2	58.7	21
Pol.Ld.	----	----	---	----	----	----	----	----	---	----	----	---
HO**	34.1	73.7	10	39.6	70.5	1	39.0	74.3	0	37.2	75.7	1
HS	44.2	71.5	1	41.6	72.0	0	31.5	67.0	0	21.1	70.5	0
BO	22.6	66.2	39	31.5	70.5	0	19.4	67.0	65	18.9	72.3	84
BS	33.3	70.2	5	26.2	73.5	3	17.9	62.8	1	26.8	74.4	4
FE	----	----	---	----	----	---	----	----	---	----	----	---
FL	----	----	---	----	----	---	----	----	---	----	----	---
PFE	----	----	---	----	----	---	----	----	---	----	----	---
D	4.7	58.5	3	4.8	60.8	117	4.4	61.5	68	7.4	59.5	19
Pol. Ld.	----	----	---	----	----	---	----	----	---	----	----	---

APPENDIX TABLE XI a. Analysis of Honey Stomach Contents of Worker Bees Collected on 29 September 1969.

(A.M.* and P.M.**. Symbols: HO = Bees collected on open honey; HS = Sealed honey; BO = Bees collected on open brood; BS = Bees collected on sealed brood; FE = Returning forager bees caught entering their hives; FL = Foragers caught leaving their hives; PFE = Pollen foragers caught entering their hives; D = Drone; Pol. Ld. = Average weight of one pollen load.)

Category	A.M. Weight	A.M. Sugar Conc.	A.M. Pollen	P.M. Weight	P.M. Sugar Conc.	P.M. Pollen
HO	27.6mg.	71.8%	9/mm^3	37.5mg.	73.6%	3/mm^3
HS	22.9	70.8	1	34.6	70.3	0
BO	11.3	68.2	4	23.1	69.0	47
BS	14.4	69.5(3)	4	26.1	70.3	3
FE	----	----	---	----	----	---
FL	----	----	---	----	----	---
PFE	----	----	---	----	----	---
D	4.3	58.9	11	5.3	60.1	52
Pol. Ld.	----	----	---	----	----	---

APPENDIX TABLE XI b. Mean values obtained from (A-1, A-2, A-3, A-4), morning and afternoon.

(Symbols as in Table XI a. Parenthesis signify the number of samples used to obtain the mean, if less than 4.)

APPENDIX B (1970)

Colony Category	A - 1 Weight	A - 1 Sugar Conc.	A - 1 Pollen	A - 2 Weight	A - 2 Sugar Conc.	A - 2 Pollen	A - 3 Weight	A - 3 Sugar Conc.	A - 3 Pollen	A - 4 Weight	A - 4 Sugar Conc.	A - 4 Pollen
HO*	15.8mg.	68.0%	96/mm^3	28.8mg.	70.0%	20/mm^3	16.4mg.	62.0%	310/mm^3	25.1mg.	60.3%	32/mm^3
BO	17.7	67.0	24	15.7	58.0	1	5.8	58.5	3220	10.4	56.1	19
FE	2.6	39.5	19	9.6	42.3	3	9.8	41.5	7	13.0	20.5	4
FL	4.0	54.0	7	7.6	55.5	4	4.3	51.2	366	5.1	56.1	9
PFE	3.1	49.0	672	4.8	33.0	34	3.7	33.5	73	3.6	46.5	89
Pol.Ld.	21.2	----	---	16.1	----	---	21.5	----	---	21.5	----	---
HO**	22.9	29.0	7	30.0	58.5	27	13.4	47.5	7	23.8(24)	48.6	40
BO	17.8	33.5	50	18.0	49.8	147	18.2	47.5	168	16.0	46.3	1
FE	15.9	45.5	4	27.0	50.2	7	28.0	51.5	5	21.4(19)	30.0	5
FL	3.6	29.5	13	4.5	46.7	4	5.0	44.5	19	3.8	45.0	8
PFE	4.4	51.0	102	4.8	53.1	62	3.9	47.7	170	5.3	50.5	54
Pol.Ld.	21.4	----	---	19.8	----	---	20.6	----	---	22.0	----	---

APPENDIX TABLE XIIa. Analyses of Honey Stomach Contents of Worker Bees Collected on 1 June 1970. (A.M.* and P.M.**. Symbols: HO = Bees collected on open honey; BO = Bees collected on open brood; FE = Returning forager bees caught entering their hives; FL = Foragers caught leaving their hives; PFE = Pollen foragers caught entering their hives; Pol. Ld. = Average weight of one pollen load.) (Parenthesis signify the number of bees used to obtain the mean, if less than 30.)

Category	A.M. Weight	A.M. Sugar Conc.	A.M. Pollen	P.M. Weight	P.M. Sugar Conc.	P.M. Pollen
HO	21.5mg.	65.1%	115/mm^3	22.5mg.	45.9%	20/mm^3
BO	12.4	59.9	816	17.5	44.3	92
FE	8.8	36.0	8	23.1	44.3	5
FL	5.2	54.2	97	4.2	41.4	11
PFE	3.8	40.5	217	4.6	50.6	97
Pol.Ld.	20.1	----	---	20.9	----	---

APPENDIX TABLE XIIb. Mean values obtained from (A-1, A-2, A-3, A-4), morning and afternoon. (Symbols as in Table XIIa.)

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	19.5	17.0	1.0 - 52.5
	Sugar(%)	75.0	---	18.5 - 78.6
	Pollen*	3.1	8.3	0.0 - 32.0
BO	Weight(mg)	16.8	19.0	1.0 - 65.5
	Sugar(%)	74.9	---	50.0 - 77.8
	Pollen*	2.2	3.2	0.0 - 8.0
FE	Weight(mg)	23.4	12.7	1.0 - 42.0
	Sugar(%)	20.3	---	1.6 - 59.0
	Pollen*	0.8	1.3	0.0 - 4.0
FL	Weight(mg)	4.4	5.6	1.0 - 26.0
	Sugar(%)	37.8	---	17.0 - 73.6
	Pollen*	1.7	3.2	0.0 - 8.0(6)
PFE	Weight(mg)	6.9	10.6	1.0 - 40.0
	Sugar(%)	36.5	---	25.0 - 67.7
	Pollen*	3.0	4.8	0.0 - 10.0(4)
Pollen Loads	Weight(mg)	9.1	6.3	1.0 - 18.0

Appendix Table XIIIa. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 12 June, 1970, from colony A - 1.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	27.3	17.5	1.0 - 61.0
	Sugar(%)	72.8	---	51.0 - 75.5
	Pollen*	4.4	7.0	0.0 - 20.0
BO	Weight(mg)	14.1	14.9	1.5 - 50.0
	Sugar(%)	72.5	---	54.8 - 77.0
	Pollen*	2.9	6.1	0.0 - 22.0
FE	Weight(mg)	15.0	13.5	1.0 - 46.0
	Sugar(%)	23.5	---	0.5 - 75.0
	Pollen*	0.3	0.7	0.0 - 2.0
FL	Weight(mg)	---	---	--- ---
	Sugar(%)	---	---	--- ---
	Pollen*	---	---	--- ---
PFE	Weight(mg)	2.9	2.5	1.0 - 8.0
	Sugar(%)	68.2	---	61.0 - 72.0
	Pollen*	9.5	5.4	36.0 - 92.0
Pollen Loads	Weight(mg)	9.1	6.3	1.0 - 27.5

Appendix Table XIIIb. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 12 June, 1970, from colony A - 2.

Symbols:
1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. FE = Nectar foragers caught on returning to their hives.
5. FL = Foragers caught leaving their hives.
6. PFE = Pollen foragers caught returning to their hives.
7. (X) = Number of bees in sample, if fewer than 15.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	21.6	17.3	1.0 - 48.5
	Sugar(%)	73.1	---	28.5 - 78.0
	Pollen*	20.8	69.0	0.0 -240.0
BO	Weight(mg)	2.8	3.3	1.0 - 18.5
	Sugar(%)	51.0	---	1.5 - 62.5
	Pollen*	0.0	0.0	0.0 - 0.0
FE	Weight(mg)	12.2	14.0	1.0 - 45.0
	Sugar(%)	23.4	---	1.5 - 70.8
	Pollen*	1.3	1.8	0.0 - 4.0
FL	Weight(mg)	4.3	5.9	1.0 - 27.5
	Sugar(%)	61.0	---	19.0 - 74.1
	Pollen*	2.0	2.8	0.0 - 4.0(2)
PFE	Weight(mg)	2.8	2.9	1.0 - 11.5
	Sugar(%)	50.9	---	30.0 - 73.2
	Pollen	60.0	59.6	10.0 -126.0(3)
Pollen Loads	Weight(mg)	9.9	6.2	2.0 - 22.0

Appendix Table XIIIc. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 12 June, 1970, from colony A - 3.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	28.6	15.7	2.0 - 50.0
	Sugar(%)	73.1	---	59.2 - 77.7
	Pollen*	3.2	3.4	0.0 - 10.0
BO	Weight(mg)	11.4	11.7	1.0 - 48.5
	Sugar(%)	65.7	---	29.0 - 76.2
	Pollen*	10.6	17.8	0.0 - 58.0
FE	Weight(mg)	24.5	12.5	1.0 - 40.0
	Sugar(%)	24.7	---	16.8 - 60.5
	Pollen*	2.5	6.2	0.0 - 24.0
FL	Weight(mg)	5.6	5.3	1.0 - 19.5
	Sugar(%)	63.0	---	29.2 - 68.8
	Pollen*	3.1	4.1	0.0 - 10.0
PFE	Weight(mg)	6.1	10.0	1.0 - 31.5
	Sugar(%)	34.5	---	15.5 - 75.0
	Pollen*	47.2	52.7	0.0 -128.0(5)
Pollen Loads	Weight(mg)	9.6	5.9	1.0 - 22.0

Appendix Table XIIId. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 12 June, 1970, from colony A - 4.

Symbols:
1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. FE = Nectar foragers caught on returning to their hives.
5. FL = Foragers caught leaving their hives
6. PFE = Pollen foragers caught returning to their hives.
7. (X) = Number of bees in sample, if fewer than 15.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	25.5	19.5	1.5 - 66.5
	Sugar(%)	71.6	---	8.0 - 80.3
	Pollen*	13.8	47.7	0.0 -186.0
BO	Weight(mg)	6.6	7.5	26.0 - 1.0
	Sugar(%)	44.3	---	5.7 - 69.1
	Pollen*	22.2	66.7	0.0 -200.0(9)
FE	Weight(mg)	16.7	15.1	2.0 - 46.0
	Sugar(%)	30.8	---	15.5 - 47.0
	Pollen*	0.4	1.6	0.0 - 6.0
FL	Weight(mg)	7.5	8.4	1.0 - 28.0
	Sugar(%)	35.4	---	20.3 - 74.8
	Pollen*	0.2	0.7	0.0 - 2.0
PFE	Weight(mg)	2.9	3.8	1.0 - 20.5
	Sugar(%)	48.1	---	24.0 - 69.5
	Pollen*	5.3	3.1	2.0 - 8.0
Pollen Loads	Weight(mg)	19.6	5.6	11.0 - 28.5

Appendix Table XIIIe. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 12 June, 1970, from colony A - 1.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	18.2	14.6	2.0 - 43.0
	Sugar(%)	63.3	---	1.1 - 75.0
	Pollen*	34.5	112.1	0.0 -434.0
BO	Weight(mg)	10.2	17.3	1.0 - 72.0
	Sugar(%)	59.8	---	2.8 - 79.8
	Pollen*			
FE	Weight(mg)	18.8	14.2	1.0 - 41.0
	Sugar(%)	17.1	---	0.0 - 62.6
	Pollen*	0.5	0.9	0.0 - 2.0
FL	Weight(mg)	5.4	5.6	1.0 - 18.0
	Sugar(%)	62.5	---	30.0 - 69.5
	Pollen*	4.5	4.5	0.0 - 10.0(8)
PFE	Weight(mg)	2.7	1.8	1.0 - 6.0
	Sugar(%)	62.8	---	39.5 - 71.0
	Pollen*	165.0	---	--- ---
Pollen Loads	Weight(mg)	17.7	7.3	3.0 - 33.0

Appendix Table XIIIf. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 12 June, 1970, from colony A - 2.

Symbols:
1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. FE = Nectar foragers caught on returning to their hives.
5. FL = Foragers caught leaving their hives.
6. PFE = Pollen foragers caught returning to their hives.
7. (X) = Number of bees in sample, if fewer than 15.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	19.8	9.6	9.5 - 45.5
	Sugar(%)	68.8	---	14.1 - 77.7
	Pollen*	4.5	9.6	0.0 - 34.0
BO	Weight(mg)	14.0	14.9	1.5 - 49.0
	Sugar(%)	47.5	---	12.0 - 73.8
	Pollen*	3.3	5.3	0.0 - 16.0
FE	Weight(mg)	19.4	17.0	1.0 - 50.1
	Sugar(%)	17.8	---	1.0 - 64.0
	Pollen*	0.5	1.2	0.0 - 4.0
FL	Weight(mg)	3.4	3.5	1.0 - 15.5
	Sugar(%)	43.0	---	4.5 - 68.8
	Pollen*	0.0	0.0	0.0 - 0.0
PFE	Weight(mg)	2.8	3.3	1.0 - 11.0
	Sugar(%)	56.0	---	23.8 - 67.8
	Pollen*	37.5	59.0	0.0 -124.0(4)
Pollen Loads	Weight(mg)	22.2	6.0	8.5 - 30.5

Appendix Table XIIIg. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 12 June, 1970, from colony A - 3.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	37.9	20.3	1.0 - 72.0
	Sugar(%)	73.6	---	20.5 - 78.9
	Pollen*	3.2	3.8	0.0 - 10.0
BO	Weight(mg)	27.3	15.6	1.0 - 50.5
	Sugar(%)	72.2	---	37.0 - 78.0
	Pollen*	10.8	19.7	0.0 - 80.0
FE	Weight(mg)	15.6	14.9	1.0 - 44.0
	Sugar(%)	34.2	---	3.6 - 70.4
	Pollen*	8.7	15.5	0.0 -100.0
FL	Weight(mg)	4.3	3.9	1.0 - 14.5
	Sugar(%)	35.1	---	0.5 - 75.5
	Pollen*	2.0	2.5	0.0 - 6.0(6)
PFE	Weight(mg)	2.9	2.9	1.0 - 12.0
	Sugar(%)	68.4	---	62.4 - 75.2
	Pollen*	108.0	83.2	44.0 -202.0
Pollen Loads	Weight(mg)	14.9	5.1	6.0 - 26.0

Appendix Table XIIIh. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 12 June, 1970, from colony A - 4.

Symbols:
1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. FE = Nectar foragers caught on returning to their hives.
5. FL = Foragers caught leaving their hives.
6. PFE = Pollen foragers caught returning to their hives.
7. (X) = Number of bees in sample, if fewer than 15.

Category	Weight	A.M. Sugar Conc.	Pollen	Weight	P.M. Sugar Conc.	Pollen
HO	24.3mg.	73.5%	8/mm^3	25.4mg.	69.3%	14/mm^3
BO	11.3	66.0	4	14.5	55.9	9
FE	18.7	23.0	1	17.6	25.0	3
FL	4.8(3)	53.0(3)	2(3)	5.1	46.8	2
PFE	4.7	47.5	44	2.8	58.8	120
Pol. Ld.	9.5	---	---	18.6	---	---

Appendix Table XIIIi. Mean values obtained from (A-1, A-2, A-3, A-4), morning and afternoon. (Symbols as in page 233 . Parenthesis signify the number of samples used to obtain the mean, if less than 4.)

Colony Category	A - 1 Weight	A - 1 Sugar Conc.	A - 1 Pollen	A - 2 Weight	A - 2 Sugar Conc.	A - 2 Pollen	A - 3 Weight	A - 3 Sugar Conc.	A - 3 Pollen	A - 4 Weight	A - 4 Sugar Conc.	A - 4 Pollen
HO*	13.4mg.	70.0%	3/mm^3	26.8mg.	72.0%	64/mm^3	14.1mg.	62.7%	91/mm^3	22.8mg.	73.8%	6/mm^3
BO	23.2	72.3	8	----	----	---	12.5	64.4	409	15.9	71.0	132
FE	14.6	23.8	2	19.5	40.3	102	17.4	15.5	9	21.0	10.5	---
FL	7.4	58.5	31	6.9	40.9	17	5.8	58.4	6	7.7	57.7	11
PFE	12.4	53.0	134	9.6	53.1	87	9.6	55.3	110	2.0	62.0	---
Pol.Ld.	14.3	----	---	15.7	----	---	19.8	----	---	19.4	----	---
HO**	35.0	68.0	2	12.3	61.5	1	10.2	44.5	60	11.5	38.8	44
BO	16.4	62.5	11	----	----	---	6.7	55.3	50	10.2	45.0	112
FE	26.1	34.0	23	19.8	54.6	55	11.1	31.0	1	31.3	20.1	9
FL	4.4	47.4	10	3.7	48.2	16	4.5	50.5	7	6.0	43.5	10
PFE	15.0	54.3	27	14.5	54.0	65	7.5	55.1	53	10.6	45.5	36
Pol.Ld.	17.0	----	---	13.8	----	---	19.1	----	---	20.3	----	---

APPENDIX TABLEXIVa. Analyses of Honey Stomach Contents of Worker Bees Collected on 24 June 1970. (A.M.* and P.M.**. Symbols: HO = Bees collected on open honey; BO = Bees collected on open brood; FE = Returning forager bees caught entering their hives; FL = Foragers caught leaving their hives; PFE = Pollen foragers caught entering their hives; Pol. Ld. = Average weight of one pollen load.)

Category	A.M. Weight	A.M. Sugar Conc.	A.M. Pollen	P.M. Weight	P.M. Sugar Conc.	P.M. Pollen
HO	19.3mg.	69.6%	41/mm^3	17.3mg.	53.2	27/mm^3
BO	17.2(3)	69.2(3)	83(3)	11.1(3)	54.3(3)	58(3)
FE	18.1	22.5	38(3)	22.1	34.9	22
FL	6.9	53.9	16	4.6	47.4	11
PFE	8.4	55.9	110(3)	11.9	52.2	45
Pol.Ld.	17.3	----	---	17.5	----	---

APPENDIX TABLE XIVb. Mean values obtained from (A-1, A-2, A-3, A-4), morning and afternoon. (Symbols as in Table XIVa.) (Parenthesis signify the number of samples used to obtain the mean, if less than 4.)

Colony Category	A - 1 Weight	A - 1 Sugar Conc.	A - 1 Pollen	A - 2 Weight	A - 2 Sugar Conc.	A - 2 Pollen	A - 3 Weight	A - 3 Sugar Conc.	A - 3 Pollen	A - 4 Weight	A - 4 Sugar Conc.	A - 4 Pollen
HO*	31.8mg.	69.0%	6/mm^3	35.2mg.	71.8%	7/mm^3	20.3mg.	70.5%	24/mm^3	37.0mg.	69.0%	2/mm^3
BO	13.1	64.0	9	----	----	---	11.9	65.0	15	19.7	64.2	4
FE	18.8	38.5	1	24.6	42.3	35	14.0(21)	45.5	40	17.8	37.5	1
FL	6.2	43.5	3	2.7	36.9	21	5.8	41.1	3	4.4	44.0	21
PFE	18.6	43.5	30	18.5	42.1	34	22.6	41.0	50	24.8	44.5	40
Pol.Ld.	14.9	----	---	12.2	----	---	9.8	----	---	18.1	----	---
HO**	39.0	64.2	6	48.7	72.8	2	38.8	61.0	4	21.1	60.1	123
BO	9.4	60.0	151	----	----	---	15.5	63.8	4	7.7	33.0	4
FE	23.6	52.9	19	16.1	56.8	20	26.6	37.2	20	18.6(22)	49.3	7
FL	4.6	46.0	17	4.7	39.0	35	4.1	41.5	46	4.2	43.3	31
PFE	20.3	64.0	58	18.3	53.1	55	27.9	60.7	33	31.2	64.3	104
Pol.Ld.	14.5	----	---	12.7	----	---	15.5	----	---	18.9	----	---

APPENDIX TABLE XVa. Analyses of Honey Stomach Contents of Worker Bees Collected on 6 July 1970. (A.M.* and P.M.**. Symbols: HO = Bees collected on open honey; BO = Bees collected on open brood; FE = Returning forager bees caught entering their hives; FL = Foragers caught leaving their hives; PFE = Pollen foragers caught entering their hives; Pol. Ld. = Average weight of one pollen load. Parenthesis signify the number of bees used to obtain the mean, if less than 30.)

Category	A.M. Weight	A.M. Sugar Conc.	A.M. Pollen	P.M. Weight	P.M. Sugar Conc.	P.M. Pollen
HO	31.1mg.	70.1%	10/mm^3	36.9mg.	64.5%	34/mm^3
BO	14.9(3)	64.4(3)	9(3)	10.9(3)	52.3(3)	53(3)
FE	18.8	41.0	19	21.2	49.1	17
FL	4.8	41.4	12	4.4	42.5	32
PFE	21.1	42.8	39	24.4	60.5	63
Pol.Ld.	13.7	----	---	15.4	----	---

APPENDIX TABLE XVb. Mean values obtained from (A-1, A-2, A-3, A-4), morning and afternoon. (Symbols as in Table XV a.) (Parenthesis signify the number of samples used to obtain the mean, if less than 4.)

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	27.0	22.9	1.0 - 71.0
	Sugar(%)	70.3	---	48.8 - 77.6
	Pollen*	1.6	2.2	0.0 - 4.0
BO	Weight(mg)	20.8	23.2	1.0 - 66.5
	Sugar(%)	62.8	---	13.5 - 67.0
	Pollen*	12.5	14.7	0.0 - 38.0(8)
FE	Weight(mg)	31.9	24.9	1.0 - 66.0
	Sugar(%)	57.5	---	31.4 - 64.0
	Pollen*	7.8	17.9	0.0 - 58.0
FL	Weight(mg)	3.8	6.7	1.0 - 37.0
	Sugar(%)	55.1	---	7.0 - 67.0(7)
	Pollen*	0.0	0.0	0.0 - 0.0(2)
PFE	Weight(mg)	27.1	17.1	1.0 - 59.5
	Sugar(%)	60.3	---	---
	Pollen*	66.0	---	---
Pollen Loads	Weight(mg)	22.4	8.0	12.0 - 41.5

Appendix Table XVIa. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 16 July, 1970, from colony A - 1.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	51.1	25.3	4.5 - 76.0
	Sugar(%)	72.6	---	51.5 - 77.7
	Pollen*	3.2	7.7	0.0 - 30.0
BO	Weight(mg)	7.7	16.3	1.0 - 71.0
	Sugar(%)	60.9	---	4.0 - 75.0
	Pollen*	37.0	77.7	0.0 -194.0
FE	Weight(mg)	22.8	20.0	1.5 - 62.5
	Sugar(%)	58.0	---	39.0 - 66.0(14)
	Pollen*	20.5	32.1	0.0 - 90.0(8)
FL	Weight(mg)	3.3	2.0	1.0 - 8.5
	Sugar(%)	40.4	---	21.3 - 53.9(6)
	Pollen*	2.0	2.8	0.0 - 4.0(2)
PFE	Weight(mg)	26.5	18.0	1.0 - 60.0
	Sugar(%)	61.1	---	38.0 - 64.1
	Pollen*	48.5	53.6	4.0 -222.0
Pollen Loads	Weight(mg)	20.7	9.4	3.0 - 38.0

Appendix Table XVIb. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 16 July, 1970, from colony A - 2.

Symbols:
1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. FE = Nectar foragers caught on returning to their hives.
5. FL = Foragers caught leaving their hives.
6. PFE = Pollen foragers caught returning to their hives.
7. (X) = Number of bees in sample, if fewer than 15.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	22.2	22.3	1.5 - 65.5
	Sugar(%)	64.5	---	20.5 - 76.6
	Pollen*	0.9	2.3	0.0 - 8.0
BO	Weight(mg)	10.0	14.0	1.5 - 61.0
	Sugar(%)	60.5	---	10.0 - 68.5(8)
	Pollen*	6.6	8.9	0.0 - 24.0(7)
FE	Weight(mg)	46.2	22.3	1.5 - 75.5
	Sugar(%)	57.0	---	17.0 - 61.6
	Pollen*	2.5	7.7	0.0 - 30.0
FL	Weight(mg)	2.2	3.1	1.5 - 10.0
	Sugar(%)	43.5	---	18.3 - 54.4
	Pollen*	2.0	---	---(1)
PFE	Weight(mg)	29.2	16.0	1.0 - 57.0
	Sugar(%)	55.4	---	35.0 - 60.8
	Pollen*	113.1	105.7	2.0 -222.0
Pollen Loads	Weight(mg)	19.9	8.6	6.0 - 26.0

Appendix Table XVI c. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 16 July, 1970, from colony A - 3.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	49.4	22.6	2.0 - 80.0
	Sugar(%)	67.6	---	3.0 - 78.0
	Pollen*	0.9	2.1	0.0 - 6.0
BO	Weight(mg)	42.2	28.9	1.5 - 86.5
	Sugar(%)	67.9	---	50.5 - 75.0
	Pollen*	0.7	1.7	0.0 - 6.0
FE	Weight(mg)	30.1	17.5	2.0 - 67.0
	Sugar(%)	53.0	---	25.6 - 55.7
	Pollen*	7.7	20.6	0.0 - 80.0
FL	Weight(mg)	4.4	4.5	1.0 - 16.0
	Sugar(%)	49.7	---	32.0 - 68.5
	Pollen*	24.3	31.9	0.0 - 80.0(6)
PFE	Weight(mg)	29.2	16.1	1.0 - 57.0
	Sugar(%)	55.4	---	35.0 - 60.8
	Pollen*	105.7	113.1	2.0 -222.0
Pollen Loads	Weight(mg)	19.9	8.6	6.0 - 26.0

Appendix Table XVI d. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 16 July, 1970, from colony A - 4.

Symbols:
1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. FE = Nectar foragers caught on returning to their hives.
5. FL = Foragers caught leaving their hives.
6. PFE = Pollen foragers caught returning to their hives.
7. (X) = Number of bees in sample, if fewer than 15.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	26.7	22.8	1.0 - 80.5
	Sugar(%)	66.5	---	33.0 - 79.5
	Pollen*	12.0	27.1	0.0 - 84.0
BO	Weight(mg)	14.0	19.4	1.0 - 65.5
	Sugar(%)	63.7	---	2.5 - 72.5
	Pollen*	1.1	1.9	0.0 - 6.0
FE	Weight(mg)	31.8	27.8	1.0 - 70.0
	Sugar(%)	47.5	---	0.0 - 66.6
	Pollen*	0.9	1.8	0.0 - 6.0
FL	Weight(mg)	3.2	3.1	1.0 - 13.5
	Sugar(%)	52.3	---	20.1 - 61.9
	Pollen*	0.0	0.0	0.0 - 0.0
PFE	Weight(mg)	38.0	17.5	1.5 - 63.0
	Sugar(%)	66.8	---	61.8 - 68.2
	Pollen*	96.5	70.8	22.0 -264.0
Pollen Loads	Weight(mg)	14.1	5.9	4.0 - 26.0

Appendix Table XVIe. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 16 July, 1970, from colony A - 1.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	26.5	24.7	1.0 - 70.0
	Sugar(%)	70.6	---	5.6 - 77.7
	Pollen*	8.0	13.5	0.0 - 50.0
BO	Weight(mg)	7.4	11.3	1.5 - 55.0
	Sugar(%)	53.0	---	0.5 - 70.5
	Pollen*	2.3	2.0	0.0 - 6.0(9)
FE	Weight(mg)	33.2	22.5	1.5 - 72.0
	Sugar(%)	59.4	---	21.0 - 64.0
	Pollen*	8.7	11.8	0.0 - 40.0
FL	Weight(mg)	4.9	6.5	1.0 - 34.5
	Sugar(%)	50.0	---	17.2 - 59.8
	Pollen*	5.0	5.0	0.0 - 12.0(4)
PFE	Weight(mg)	34.3	11.9	2.0 - 56.0
	Sugar(%)	64.2	---	61.5 - 66.5
	Pollen*	21.5	6.2	10.0 -128.0
Pollen Loads	Weight(mg)	21.5	6.2	--- ---

Appendix Table XVIf. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 16 July, 1970, from colony A - 2.

Symbols:
1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. FE = Nectar foragers caught on returning to their hives.
5. FL = Foragers caught leaving their hives.
6. PFE = Pollen foragers caught returning to their hives.
7. (X) = Number of bees in sample, if fewer than 15.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	16.9	21.7	1.0 - 64.5
	Sugar(%)	60.5	---	6.5 - 66.8(13)
	Pollen*	0.8	1.4	0.0 - 4.0(10)
BO	Weight(mg)	12.6	19.8	1.0 - 55.0
	Sugar(%)	63.8	---	9.6 - 78.5(13)
	Pollen*	2.3	4.1	0.0 - 10.0(7)
FE	Weight(mg)	41.1	26.8	2.0 - 68.0
	Sugar(%)	61.5	---	4.5 - 67.0
	Pollen*	28.5	45.0	0.0 - 59.0
FL	Weight(mg)	3.9	3.3	1.0 - 15.5
	Sugar(%)	51.2	---	32.5 - 60.9(8)
	Pollen*	3.0	4.2	0.0 - 2.0 (2)
PFE	Weight(mg)	48.3	12.9	19.0 - 60.5
	Sugar(%)	63.9	---	59.8 - 67.6
	Pollen*	78.5	49.4	32.0 -180.0
Pollen Loads	Weight(mg)	6.4	4.9	1.0 - 15.5

Appendix Table XVI g. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 16 July, 1970, from colony A - 3.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	46.5	28.7	1.5 - 82.0
	Sugar(%)	69.8	---	6.4 - 77.0
	Pollen*	7.5	13.8	0.0 - 50.0
BO	Weight(mg)	28.5	30.8	1.0 - 83.0
	Sugar(%)	67.7	---	23.5 - 73.0
	Pollen*	15.9	36.4	0.0 -142.0
FE	Weight(mg)	25.5	25.3	1.0 - 81.0
	Sugar(%)	60.9	---	5.7 - 66.3
	Pollen*	22.0	45.7	0.0 -160.0
FL	Weight(mg)	5.4	3.6	1.0 - 17.5
	Sugar(%)	54.6	---	20.5 - 64.5
	Pollen*	6.0	11.2	0.0 - 26.0(5)
PFE	Weight(mg)	40.4	19.2	1.0 - 71.0
	Sugar(%)	65.7	---	59.2 - 66.6
	Pollen*	146.0	96.0	28.0 -346.0
Pollen Loads	Weight(mg)	13.6	6.6	4.0 - 26.5

Appendix Table XVI h. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 16 July, 1970, from colony A - 4.

Symbols:
1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. FE = Nectar foragers caught on returning to their hives.
5. FL = Foragers caught leaving their hives.
6. PFE = Pollen foragers caught returning to their hives.
7. (X) = Number of bees in sample, if fewer than 15.

Category	Weight	A.M. Sugar Conc.	Pollen	Weight	P.M. Sugar Conc.	Pollen
HO	37.4mg.	68.8%	2/mm^3	29.1mg.	66.8%	7/mm^3
BO	20.2	63.1	56	15.6	62.1	5
FE	32.8	56.5	37	32.9	57.3	16
FL	3.7	47.2	7	4.4	52.1	4
PFE	29.5	57.4	73	40.2	65.2	94
Pol. Ld.	19.8	---	---	13.9	---	---

Appendix Table XVIi. Mean values obtained from (A-1, A-2, A-3, A-4), morning and afternoon. (Symbols as in page 240. Parenthesis signify the number of samples used to obtain the mean, if less than 4.)

Colony Category	A - 1 Weight	A - 1 Sugar Conc.	A - 1 Pollen	A - 2 Weight	A - 2 Sugar Conc.	A - 2 Pollen	A - 3 Weight	A - 3 Sugar Conc.	A - 3 Pollen	A - 4 Weight	A - 4 Sugar Conc.	A - 4 Pollen
HO*	50.9mg.	74.1%	0/mm^3	40.3mg.	73.3%	5/mm^3	35.6mg.	71.2%	9/mm^3	49.0mg.	73.1%	1/mm^3
BO	47.9	74.0	5	18.0	69.5	42	19.5	67.1	14	28.8	69.6	234
FE	13.6	34.2	4	22.3	48.5	5	38.9	34.0	1	21.4	44.6	7
FL	5.7	32.3	---	3.9	44.9	69	5.9	33.6	---	6.4	35.0	13
PFE	7.4	61.5	36	5.6	45.9	46	13.7	41.3	32	18.5	43.6	28
Pol.Ld.	26.6	----	---	25.1	----	---	15.8	----	---	19.9	----	---
HO**	27.1	71.0	9	21.7	59.5	26	29.2	62.5	69	57.2	74.8	12
BO	28.1	67.0	0	15.5	63.9	3	15.1	58.1	6	25.1	68.0	3
FE	15.3(23)	43.0	1	30.7	48.1	1	35.1	53.5	10	21.2	51.0	11
FL	4.8	42.5	---	7.3	41.1	7	6.0	45.0	10	7.0	52.0	---
PFE	16.6	52.6	30	17.0	49.0	35	29.9	54.6	45	28.2	50.0	81
Pol.Ld.	20.0	----	---	19.7	----	---	20.3	----	---	19.5	----	---

APPENDIX TABLE XVIIa. Analyses of Honey Stomach Contents of Worker Bees Collected on 30 July 1970. (A.M.* and P.M.**. Symbols: HO = Bees collected on open honey; BO = Bees collected on open brood; FE = Returning forager bees caught entering their hives; FL = Foragers caught leaving their hives; PFE = Pollen foragers caught entering their hives; Pol. Ld. = Average weight of one pollen load. Parenthesis signify the number of bees used to obtain the mean, if less than 30.)

Category	A.M. Weight	A.M. Sugar Conc.	A.M. Pollen	P.M. Weight	P.M. Sugar Conc.	P.M. Pollen
HO	44.0mg.	72.9%	4/mm^3	33.8mg.	67.0%	29/mm^3
BO	28.6	70.1	74	21.0	64.3	3
FE	24.1	40.3	4	25.6	48.9	6
FL	5.5	36.5	41(2)	6.3	45.2	9(2)
PFE	11.3	48.1	36	22.9	51.6	48
Pol.Ld.	21.9	----	---	19.9	----	---

APPENDIX TABLE XVIIb. Mean values obtained from (A-1, A-2, A-3, A-4), morning and afternoon. (Symbols as in Table XVII a.) (Parenthesis signify the number of samples used to obtain the mean, if less than 4.)

Colony		A - 1			A - 2			A - 3			A - 4	
Category	Weight	Sugar Conc.	Pollen	Weight	Sugar Conc.	Pollen	Weight	Sugar Conc.	Pollen	Weight	Sugar Conc.	Pollen
HO*	14.9mg.	73.6%	66/mm^3	32.2mg.	71.0%	52/mm^3	27.0mg.	74.0	50/mm^3	25.7mg.	74.0%	46/mm^3
BO	38.6	74.6	40	16.2	68.5	70	23.8	72.6	3	28.1	66.0	46
FE	13.0	30.5	34	9.2	49.0	12	32.0	58.5	30	25.8	34.0	0
FL	9.1	59.8	40	5.9	57.0	15	3.7	53.0	32	6.6	65.5	53
PFE	6.2	55.5	103	6.4	57.6	42	5.9	62.1	83	2.5	----	---
Pol.Ld.	20.6	----	---	23.4	----	---	25.1	----	---	11.2	----	---
HO**	24.5	63.1	45	56.7	71.0	2	45.4	64.3	4	37.7	66.0	3
BO	17.0	39.6	28	5.2	59.5	13	22.2	61.0	6	36.2	64.0	7
FE	38.4	61.5	5	44.9	57.0	1	17.4	59.5	20	35.2	63.1	3
FL	4.5	53.0	24	7.5	38.5	---	12.5	48.7	5	10.3	47.7	6
PFE	14.3	61.0	29	13.6	50.6	40	19.7	49.6	20	13.1	58.9	17
Pol.Ld.	12.1	----	---	13.1	----	---	13.0	----	---	16.4	----	---

APPENDIX TABLEXVIIIa. Analyses of Honey Stomach Contents of Worker Bees Collected on 11 August 1970.

(A.M.* and P.M.**. Symbols: HO = Bees collected on open honey; BO = Bees collected on open brood; FE = Returning forager bees caught entering their hives; FL = Foragers caught leaving their hives; PFE = Pollen foragers caught entering their hives; Pol. Ld. = Average weight of one pollen load.)

		A.M.			P.M.	
Category	Weight	Sugar Conc.	Pollen	Weight	Sugar Conc.	Pollen
HO	24.9mg.	73.2%	54/mm^3	41.1mg.	66.1%	14/mm^3
BO	26.7	70.4	40	20.2	56.0	14
FE	20.0	43.0	19	34.0	60.3	7
FL	6.3	58.8	35	8.7	47.0(3)	12
PFE	5.2	58.4(3)	76(3)	15.2	55.0	27
Pol.Ld.	20.1	----	---	13.7	----	---

APPENDIX TABLEXVIIIb. Mean values obtained from (A-1, A-2, A-3, A-4), morning and afternoon. (Symbols as in Table XVIIIa.) (Parenthesis signify the number of samples used to obtain the mean, if less than 4.)

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	29.3	24.5	1.0 - 75.5
	Sugar(%)	70.0	---	2.0 - 78.7
	Pollen*	5.9	15.1	0.0 - 60.0
BO	Weight(mg)	5.2	7.0	1.0 - 33.5
	Sugar(%)	56.3	---	2.0 - 73.3
	Pollen*	0.3	0.8	0.0 - 1.0
FE	Weight(mg)	19.7	16.3	1.0 - 50.0
	Sugar(%)	28.3	---	0.0 - 56.8
	Pollen*	1.7	2.3	0.0 - 6.0
FL	Weight(mg)	5.9	4.2	1.0 - 11.0
	Sugar(%)	55.6	---	30.0 - 66.5
	Pollen*	1.8	2.7	0.0 - 4.0
PFE	Weight(mg)	3.0	3.6	1.0 - 15.0
	Sugar(%)	48.6	---	37.5 - 66.3
	Pollen*	15.1	5.6	0.0 - 1.0(2)
Pollen Loads	Weight(mg)	15.1	5.6	5.0 - 24.0

Appendix Table XIXa. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 24 August, 1970, from colony A - 1.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	24.2	23.4	1.0 - 59.0
	Sugar(%)	69.4	---	2.5 - 78.5
	Pollen*	9.5	29.1	0.0 -114.0
BO	Weight(mg)	10.7	19.8	1.0 - 81.0
	Sugar(%)	64.2	---	1.0 - 78.6
	Pollen*	28.8	81.3	0.0 -230.0
FE	Weight(mg)	13.8	12.4	1.0 - 56.0
	Sugar(%)	45.1	---	3.5 - 67.5
	Pollen*	10.5	19.1	0.0 - 72.0
FL	Weight(mg)	9.7	5.9	1.5 - 24.0
	Sugar(%)	58.7	---	32.0 - 69.1
	Pollen*	5.9	5.8	0.0 - 11.0
PFE	Weight(mg)	2.1	2.8	1.0 - 13.0
	Sugar(%)	46.4	---	27.3 - 58.2(5)
	Pollen*	2.0	---	2.0 - 2.0(2)
Pollen Loads	Weight(mg)	15.3	6.2	6.0 - 26.0

Appendix Table XIXb. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 24 August, 1970, from colony A - 2.

Symbols:
1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. FE = Nectar foragers caught on returning to their hives.
5. FL = Foragers caught leaving their hives.
6. PFE = Pollen foragers caught returning to their hives.
7. (X) = Number of bees in sample, if fewer than 15.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	46.4	32.2	1.0 - 98.0
	Sugar(%)	74.0	---	23.0 - 76.0
	Pollen*	1.7	3.1	0.0 - 12.0
BO	Weight(mg)	20.8	23.2	1.0 - 69.0
	Sugar(%)	72.2	---	17.6 - 76.7
	Pollen*	7.9	6.8	0.0 - 20.0(13)
FE	Weight(mg)	18.4	19.4	1.0 - 55.0
	Sugar(%)	15.5	---	0.0 - 71.5
	Pollen*	88.7	328.5	0.0 -1230.0(14)
FL	Weight(mg)	12.1	9.1	1.0 - 27.5
	Sugar(%)	61.4	---	41.0 - 71.0
	Pollen*	9.2	11.3	0.0 - 42.0
PFE	Weight(mg)	4.6	4.8	1.0 - 20.5
	Sugar(%)	56.9	---	36.6 - 69.0
	Pollen*	2.0	2.3	0.0 - 6.0
Pollen Loads	Weight(mg)	17.6	7.8	1.0 - 29.5

Appendix Table XIX c. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 24 August, 1970, from colony A - 3.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	51.6	24.9	10.5 - 99.0
	Sugar(%)	75.1	---	10.6 - 79.0
	Pollen*	52.9	196.7	0.0 -764.0
BO	Weight(mg)	9.3	12.4	1.0 - 41.0
	Sugar(%)	65.1	---	0.5 - 78.2
	Pollen*	0.5	0.9	0.0 - 2.0(7)
FE	Weight(mg)	17.9	18.1	1.0 - 58.5
	Sugar(%)	20.4	---	0.0 - 68.0
	Pollen*	1.9	4.0	0.0 - 8.0
FL	Weight(mg)	8.4	5.5	1.0 - 19.5
	Sugar(%)	59.3	---	31.5 - 70.0
	Pollen*	4.3	6.3	0.0 - 24.0
PFE	Weight(mg)	3.4	3.5	1.0 - 15.0
	Sugar(%)	47.4	---	27.8 - 65.2
	Pollen*	3.5	2.5	0.0 - 6.0(4)
Pollen Loads	Weight(mg)	18.1	6.5	2.5 - 32.0

Appendix Table XIX d. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the morning of 24 August, 1970, from colony A - 4.

Symbols:
1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. FE = Nectar foragers caught on returning to their hives.
5. FL = Foragers caught leaving their hives.
6. PFE = Pollen foragers caught returning to their hives.
7. (X) = Number of bees in sample, if fewer than 15.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	52.2	22.1	5.0 - 84.5
	Sugar(%)	71.3	---	1.5 - 80.3
	Pollen*	0.4	0.8	0.0 - 2.0
BO	Weight(mg)	28.6	24.7	1.0 - 72.0
	Sugar(%)	72.7	---	5.5 - 80.0
	Pollen*	1.7	2.4	0.0 - 6.0
FE	Weight(mg)	22.9	21.7	1.0 - 64.0
	Sugar(%)	10.4	---	0.0 - 68.5
	Pollen*	2.5	2.3	0.0 - 6.0
FL	Weight(mg)	2.7	2.9	1.0 - 11.0
	Sugar(%)	47.2	---	31.5 - 57.5
	Pollen*	0.0	0.0	0.0 - 0.0(1)
PFE	Weight(mg)	4.5	4.0	1.0 - 13.0
	Sugar(%)	33.5	---	25.0 - 46.4
	Pollen*	20.4	38.0	0.0 - 88.0
Pollen Loads	Weight(mg)	12.4	4.5	5.0 - 21.0

Appendix Table XIXe. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 24 August, 1970, from colony A - 1.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	20.6	22.7	1.0 - 85.5
	Sugar(%)	56.1	---	0.0 - 76.3
	Pollen*	3.3	5.9	0.0 - 20.0
BO	Weight(mg)	9.1	13.1	1.0 - 47.0
	Sugar(%)	51.3	---	0.0 - 77.8
	Pollen*	1.0	1.5	0.0 - 4.0
FE	Weight(mg)	13.6	16.2	1.0 - 44.5
	Sugar(%)	29.0	---	0.0 - 71.0
	Pollen*	8.8	10.1	0.0 - 56.0
FL	Weight(mg)	8.3	6.9	1.0 - 27.0
	Sugar(%)	57.1	---	23.0 - 74.5
	Pollen*	7.1	20.8	0.0 - 82.0
PFE	Weight(mg)	2.1	1.3	1.0 - 5.0
	Sugar(%)	39.4	---	26.1 - 53.4
	Pollen*	---	---	--- ---
Pollen Loads	Weight(mg)	14.5	3.9	6.5 - 20.0

Appendix Table XIXf. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 24 August, 1970, from colony A - 2.

Symbols:
1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. FE = Nectar foragers caught on returning to their hives.
5. FL = Foragers caught leaving their hives.
6. PFE = Pollen foragers caught returning to their hives.
7. (X) = Number of bees in sample, if fewer than 15.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	50.4	26.9	3.0 - 90.0
	Sugar(%)	76.2	---	38.7 - 79.8
	Pollen*	1.2	2.0	0.0 - 6.0
BO	Weight(mg)	9.4	16.5	1.0 - 70.0
	Sugar(%)	51.1	---	1.0 - 77.3
	Pollen*	1.7	3.2	0.0 - 8.0
FE	Weight(mg)	7.4	14.5	1.0 - 76.0
	Sugar(%)	53.3	---	0.0 - 74.0
	Pollen*	0.4	0.9	0.0 - 2.0
FL	Weight(mg)	5.0	4.1	1.0 - 17.0
	Sugar(%)	46.2	---	2.0 - 65.8
	Pollen*	5.8	10.6	0.0 - 30.0
PFE	Weight(mg)	3.3	2.4	1.0 - 10.0
	Sugar(%)	48.4	---	30.4 - 72.0
	Pollen*	1.0	1.4	0.0 - 2.0
Pollen Loads	Weight(mg)	16.7	4.6	8.5 - 28.0

Appendix Table XIX g. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 24 August, 1970, from colony A - 3.

Category	Factor Measured	Mean	S.D.	Range
HO	Weight(mg)	55.6	22.7	1.0 - 80.0
	Sugar(%)	73.8	---	3.0 - 79.6
	Pollen*	3.6	10.2	0.0 - 40.0
BO	Weight(mg)	23.2	24.2	1.0 - 82.5
	Sugar(%)	53.2	---	1.7 - 76.5
	Pollen*	22.3	79.2	0.0 -308.0
FE	Weight(mg)	9.2	14.8	1.0 - 59.0
	Sugar(%)	11.4	---	0.0 - 69.5
	Pollen*	2.8	4.0	0.0 - 12.0(8)
FL	Weight(mg)	4.9	3.5	1.0 - 13.5
	Sugar(%)	40.4	---	12.4 - 64.0
	Pollen*	1.4	1.9	0.0 - 4.0(7)
PFE	Weight(mg)	3.3	5.9	1.0 - 27.0
	Sugar(%)	40.2	---	20.1 - 59.5(5)
	Pollen*	2.7	4.6	3.5 - 23.0(3)
Pollen Loads	Weight(mg)	14.0	4.8	3.5 - 23.0

Appendix Table XIX h. Expanded analyses (see text, page 18) of honey stomach contents obtained from bees collected in the afternoon of 24 August, 1970, from colony A - 4.

Symbols:
1. Pollen* = Number of pollen grains per mm^3 of honey stomach contents.
2. HO = Worker bees caught on open honey.
3. BO = Worker bees caught on open brood.
4. FE = Nectar foragers caught on returning to their hives.
5. FL = Foragers caught leaving their hives.
6. PFE = Pollen foragers caught returning to their hives.
7. (X) = Number of bees in sample, if fewer than 15.

Category	Weight	A.M. Sugar Conc.	Pollen	Weight	P.M. Sugar Conc.	Pollen
HO	37.9mg.	72.1%	18/mm^3	44.7mg.	69.4%	2/mm^3
BO	11.5	64.5	10	17.6	57.1	7
FE	17.5	27.3	26	13.3	26.0	8
FL	9.0	58.8	5	5.2	47.7	4
PFE	3.3	49.8	2	3.3	40.5	8(3)
Pol. Ld.	16.5	---	---	14.4	---	---

Appendix Table XIXi. Mean values obtained from (A-1, A-2, A-3, A-4), morning and afternoon. (Symbols as in page 247. Parenthesis signify the number of samples used to obtain the mean, if less than 4.)