THE DIVISION OF LABOUR WITHIN BUMBLEBEE COLONIES

by

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INTRODUCTION

In the present studies of the division of labour amongst the workers of bumblebee colonies the constancy of workers to household and foraging duties, and the constancy of foragers to the collection of nectar or pollen has been investigated. Experiments have been carried out to determine whether an individual will alter her behaviour in response to the current needs of her colony.

METHODS AND MATERIALS

Some colonies were reared in artificial domiciles in the field and in the laboratory, but the majority were collected from their natural habitat.

The relative sizes of the members of a colony was found either by weighing them individually or by recording their wing measurements. Before the members of a colony were weighed, they were confined in their nest for several hours, so that any differences between the weights of foragers and non-foragers due to variations in the amount of food in their honey-stomachs would be reduced. Bees were given individually distinctive marks. Newly emerged bees were also marked and their relative sizes recorded—usually about 24 hours after they had emerged, when they were strong enough to withstand this treatment.

Colonies were housed in observation nest-boxes. When 2 colonies were observed simultaneously, 1 serving as a control to the other, their nest-boxes were situated within a few yards of each other.

Time is recorded as G. M. T. (1).

(1) Greenwich mean time.

THE DIVISION OF THE MEMBERS OF A COLONY INTO HOUSE-BEES AND FORAGERS

The constancy of worker bumblebees to foraging and non-foraging duties.

In Table 1 bees have been classified as 'constant foragers' if they foraged on more than 70 % of the bee-days of observation, and 'constant house-bees' if they never left their nests. Most bees were either constant foragers or house-bees, but about a third of the members of any colony were inconstant to either duty. A similar division of labour even occurred between the bees of very small colonies.

TABLE 1

The constancy of worker bees to either Household or Foraging duties (includes all bees 4 or more days old)

YEAR	COLONY No.	SPECIES	PERIOD OF OBSERVATION (days)	MEAN PERIOD OF DAILY OBSERVATION (hrs)	No. OF WORKERS PER COLONY	CONSTANT FORAGERS	CONSTANT HOUSE-BEES	INCONSTANT FORAGERS
1952	1	*B. pratorum.*	3	4.6	4	2	1	1 *a*
	2	—	7	4.3	3	1	1	1 *b*
	3	*B. agrorum.*	4	Irregular observation.	4	1	3	0
	4	*B. terrestris.*	12	2.1	10	4	5	1 *b*
	16	*B. sylvarum.*	14	3.8	49	8	18	23
	18	*B. lucorum.*	15	4.6	181	58	14	109
	24	*B. agrorum.*	14	1.9	31	7	19	5
1953	13	*B. pratorum.*	9	1.7	36	10	16	10

a = queen foraged on one day only.
b = queen foraged on first day only.

During the period of observation of the *B. lucorum* colony (18) large numbers of queens and males emerged. The decrease in brood rearing, and the absence of young workers to take the place of dead foragers probably accounts for the relatively small proportion of non-foragers in this colony.

The date at which new workers emerged in 3 colonies was known, and it was found that the larger foragers tended first to leave their nests at an earlier age than the smaller ones—as first noted by Brian (1952).

The larger bees in each of the above colonies foraged on significantly more bee-days of observation than did the smaller ones. This result is in agreement with that of Richards (1946), Cumber (1949) and Brian (1952) who found that the mean size of the foragers of a bumblebee colony is greater than that of the house-bees. A few of the relatively large bees of colonies were never seen to forage however, and, conversely, very small bees sometimes foraged. The smaller foragers tended to forage less consistently than the larger ones (Table 2).

TABLE 2.

The relative amount of foraging undertaken by large and small foragers.

COLONY No.	SPECIES.	PERCENTAGE FORAGERS WHO FORAGED ON OVER HALF OF THE BEE-DAYS OF OBSERVATION.	
		Below mean weight.	Above mean weight
16	*B sylvarum*	30	67
18	*B lucorum*	43	60
24	*B agrorum*	50	80

A colony was formed by confining captured foragers (*B. pratorum*) for 24 hours in a nest-box which contained brood taken from a *B. pratorum* colony. No division of labour on the basis of body size was subsequently apparent amongst the members of this colony. It was thought that those bees which undertook house-hold duties may have only comparatively recently started to forage at the time of capture.

The following experiment was carried out to determine whether there was any correlation between the length of time that a bee had performed a particular duty and her subsequent tendency to perform that duty.

On 21st May 1952 a colony was started by confining a *B. pratorum* queen and 12 captured *B. pratorum* foragers in a nest-box. On 11th June 7 more captured foragers were added to the colony, and on 13th June the entrance to the nest-box was opened so that the bees could fly. The colony was observed for short periods between 13th and 16th June. Weather conditions were bad during much of this time but 5 of the 7 bees added on 11th June foraged and collected 21 nectar loads. Nine of the original 12 bees remained alive throughout the experiment, but only 2 of them foraged and collected only 1 nectar load each. Thus, those bees which has recently been foragers foraged much more often than bees which had not foraged for some time. These results suggest that the longer an individual has been carrying out either household or foraging activities the more 'fixed' she becomes to the duty with which she has been previously concerned.

The interchange of foraging and non-foraging duties.

In August 1951 a *B. lapidarius* colony and 2 *B. agrorum* colonies were used in experiments which resulted in the loss of most of their foragers. Some of the small house-bees took their places, and the queen of the *B. lapidarius* colony also recommenced to forage.

It appeared possible, therefore, that a bee would change her occupation in response to her colony's requirements. Experiments were carried out in order to investigate this:

A.—THE REMOVAL OF FORAGERS FROM COLONIES

Colonies were observed in order to determine the occupation of each of their bees. Some, or all, of the foragers were then removed and the colonies were again observed. The results of these experiments are shown in Table 3. Several of the house-bees foraged after the normal foragers had been removed. On 10th August the foragers that had been removed were returned to Colony 29, and it was observed again 2 days later. Only 2 of the original house-bees foraged during this period—the remainder had reverted to their former duties inside their nest.

TABLE 3.

The effect on the division of labour of the removal of foragers from colonies.

Colony No.	Species.	No. foragers removed.	Before removal of foragers.		After removal of foragers.	
			Period of observation.	No. of bees which had never foraged.	Period of observation.	No. bees foraged which had not previously done so.
29	*B. agrorum.*	24	14th July — 7th Aug. 1953.	10	8th - 10th Aug. 1953.	6
13	*B. pratorum.*	11	19th June — 2nd July 1953.	11	2nd - 7th July 1953.	4 *a*
2	*B. pratorum.*	13	23rd - 26th June 1952.	9	27th - 30th June 1952.	6 *b*

a = 2 recently emerged queens (and 1 bee which had not foraged since 20th June) also foraged.
b = also 2 bees which had not foraged since the 23rd June 1952.

In another experiment, a small *B. pratorum* colony containing 7 foragers was watched for 10 hours on 20th and 21st May 1952. During this time 2 foragers made twice as many foraging trips as the other 5. These

2 foragers were removed on the evening of 21st May and the colony was observed for a further 6 hours on 22nd May during which time the remaining foragers undertook 43 foraging trips as compared with a total of 22 on the previous 2 days. Foragers of a control colony foraged at an approximately constant rate during the course of the experiment.

A final experiment was performed on 2 *B. terrestris* colonies (31 &32) in neither of which were any young bees emerging. The foragers of these colonies were captured on return to their nests and their wing lengths measured. Foragers belonging to Colony 31 were subsequently returned to their nest but foragers belonging to colony 32 were not. The sizes of foragers collected daily from Colony 32 decreased significantly more ($P < 0.02$) than foragers collected from Colony 31 (Table 4) (unfavourable weather conditions prevented foraging from July 28th until August 1st). As stated previously the house-bees of a colony are on the average smaller than the foragers. Since the removal of foragers from Colony 32 resulted in the size of the foragers that were subsequently collected becoming progressively smaller, it is highly probable that some of the original house-bees had undertaken foraging duties.

TABLE 4.

Mean wing length (mm.) of foragers of *B. terrestris* colonies. Foragers removed each day from colony 32.

	July.			*August.*		
	26	27	28	1	2	3
Colony 31	12.9	13.0	13.0	11.2	11.9	12.8
Colony 32	12.5	11.7	11.0	11.1	10.6	9.3

B.—THE REMOVAL OF HOUSE-BEES FROM COLONIES

House-bees were removed from 3 colonies and observations made on the division of labour amongst the remaining bees which has previous lylargely confined their attentions to foraging (Table 5).

TABLE 5.

The effect on the division of labour of the removal of house-bees from colonies.

Colony No	24	27 *a*	27 *b*
Species	*B.agrorum.*	*B. pratorum.*	*B. pratorum.*
No. bees	27	26	32
No. house-bees removed	14	6	39
Before removal of house-bees.			
Period of observation	11-19.8.52	26-30.6.53	26.6-1.7.53
Ratio foragers/house-bees	0.4	2.1	1.6
After removal of house-bees.			
Period of observation	20-21.8.52	1.7.53	2-3.7.53
Ratio foragers/house-bees	1.9	4.0	1.75
After return of house-bees.			
Period of observation	22-27.8.52	2-3.7.53	4.7.53
Ratio foragers/house-bees	0.8 *	2.05	1.4

4 house-bees died in captivity.

Only 3 foragers of colony 24 remained inside their nest on the 2 days during which the house-bees were absent. These 3 bees had previously been inconsistent foragers and 2 of them foraged again when the house-bees had been returned. The brood of this colony consisted of 3 egg clumps, 1 small larval batch and 10 pupae. Since the reduced population present inside the nest when the original house-bees were absent was apparently adequate to perform all necessary nest duties it seems probable that before the start of the experiment more house-bees were present than the colony actually required, and that so long as sufficient food was being brought into the nest these redundant house-bees did not forage.

Colonies 27*a* and 27*b* served as controls for each other (Table 5). All except 1 house-bee were removed from colony 27*a* on the morning of 1st July and in the afternoon there was a large increase in the forager/house-bee ratio; only 3 bees that had previously been 'inconsistent' foragers together, with the remaining house-bee, did not forage. As in the case of colony 24 the forager/house-bee ratio decreased again soon after the house-been were returned.

All but 1 house-bee were removed from colony 27 b on the evening of 1st July. During the next 2 days 10 bees took their place; 4 of these had foraged each previous day, and 6 had foraged on some of the days. The forager/house-bee ratio showed little change. This was probably because the individual bees had more time than in the previous experiment to adapt themselves to the changed circumstances, the forager/house-bee ratio being lower on the second day than on the first (1.2:2.3). When the house-bees were returned, 7 of the bees which had taken over house-duties foraged again.

It is thus apparent that when a dearth of house-bees occurs some of the foragers will carry out household duties.

THE DIVISION OF FORAGERS INTO NECTAR- AND POLLEN-GATHERERS

In the following investigations a forager has been classified as a pollen-gatherer if she carried a pollen load in her corbiculae when she returned to her nest, otherwise she has been assumed to be a nectar-gatherer. This assumption is justified in the vast majority of cases because:

(a) Whenever a returned forager which was not carrying pollen was observed throughout the period that she remained inside her nest between foraging trips she always deposited a load of nectar.

(b) Confirmed foragers behave in a purposeful manner when entering or leaving their nest which is not the case when they enter or leave their nest for the first time (FREE 1955 a).

(c) The lengths of the expeditions from which bees returned without loads of pollen were greater than would have been expected if they had not been foraging.

(d) Bumblebees do not necessarily leave their nests in order to defecate.
(e) Bumblebees have never been recorded collecting water.

A high percentage of the pollen-gatherers recorded had also probably collected nectar (BRIAN 1952). In the present study individual *B. sylvarum* pollen-gatherers deposited nectar as well as pollen on 19 of the 22 occasions when they were observed throughout the time between foraging trips. When a reference is made to a 'pollen load' it will be assumed that in many cases the bee concerned had also collected nectar. The term 'nectar load' will be used only when the bee concerned was not carrying any pollen.

The constancy of foragers to nectar and pollen collection.

In 1952 observations were made on 4 colonies which possessed plenty of developing brood. In these colonies relatively few foragers collected nectar only, or always pollen, throughout the entire period their colonies were observed (Table 6). With a few exceptions, notably some *B. sylvarum* pollen-gatherers, such bees were only recorded foraging for a few trips.

TABLE 6.

Constancy of foragers to the collection of loads of either nectar or pollen throughout the period for which their colonies were observed. Mean no. trips is shown in brackets.

Colony No.	Species.	No. days of observation.	Behaviour of foragers.		
			Collected nectar only.	Always collected pollen.	Collected nectar only on some trips and pollen on others.
15	*B. pratorum.*	10	14 (5.7)	3 (1.0)	25 (13.3)
16	*B. sylvarum.*	14	4 (2.0)	5 (45.4)	20 (35.7)
18	*B. lucorum.*	15	33 (2.9)	16 (2.2)	112 (13.5)
24	*B. agrorum.*	14	3 (11.3)	0	9 (42.5)

The classification of bees in Table 7 as nectar- or pollen-gatherers depended upon the kind of food they collected on the greatest number of consecutive days on which they foraged. (Bees which collected nectar loads and pollen loads on an equal number of consecutive days have been included in both groups.) Individuals showed little constancy to the collection of either nectar only or always pollen on consecutive days. In general the greater number of consecutive days on which a bee foraged the less constant she was to the collection of either type of food.

TABLE 7.

Constancy of foragers to the collection of either loads of nectar or loads of pollen on consecutive days.

Colony No.	Species.	Nectar-gatherers.			Pollen-gatherers.		
		No. bees.	Mean no. consecutive days foraged.	Mean no. consecutive days during which nectar only was collected.	No. bees.	Mean no. consecutive days foraged.	Mean no. consecutive days during which pollen only was collected.
15	*B. pratorum.*	62	3.5	2.1	27	3.4	1.3
16	*B. sylvarum.*	4	4.25	2.0	20	5.2	4.3
18	*B. lucorum.*	105	4.4	2.2	76	4.2	1.8
24	*B. agrorum.*	9	7.3	3.9	5	10.0	3.8

On days when the *B. lucorum* colony (18) and *B. sylvarum* colony (16) were observed continuously for over 14 hours the proportion of pollen loads to nectar loads, which their foragers collected increased during the day. This was due to changes in the occupation of the individual bees as shown in Table 8 in which only the behaviour of bees which foraged both before and after 11.00 hours on the same day is recorded.

TABLE 8.

The change from nectar- to pollen-gathering during the day.

Colony	Species.	Date.	No. of bees collected nectar only.	No. bees collected nectar only on some trips and pollen on others.	No. bees collected pollen on every trip.
18	*B. lucorum.*	22nd, 25th and 28th July 1952.			
		Before 11.00 hrs.	110	32	40
		After 11.00 hrs.	71	55	56
16	*B. sylvarum.*	29th & 31st July 1952.			
		Before 11.00 hrs.	11	7	10
		After 11.00 hrs.	1	11	16

During consecutive trips, however, foragers were highly constant to the collection of either loads of nectar or pollen (Table 9). The number of consecutive trips from which a forager returned with either loads of

nectar or pollen increased directly with the total number of loads of nectar or pollen which she collected during the course of an observation period. Thus, during relatively short periods many foragers were constant to the collection of one or other type of food, but over longer periods they showed little constancy.

TABLE 9.

Constancy of foragers to the collection of either loads of nectar or loads of pollen on consecutive trips.

Colony No.	Species.	Nectar-gatherers.			Pollen-gatherers.		
		No. bees.	Mean no. trips per observation period during which nectar only was collected.	Mean no. *consecutive* trips during which nectar only was collected.	No. bees.	Mean no. trips per observation period during which pollen was collected.	Mean no. *consecutive* trips during which pollen was collected.
15	*B. pratorum.*	100	3.8	3.6	62	3.9	3.6
16	*B. sylvarum.*	40	4.8	4.6	89	6.3	6.0
18	*B. lucorum.*	157	4.9	4.3	105	3.5	3.2
24	*B. agrorum.*	60	5.2	5.0	56	4.1	4.0

The relationship between the size of a bee and pollen collection.

Brian (1952) found that the larger foragers of *B. agrorum* colonies tended to collect a significantly greater proportion of pollen loads to nectar loads than did smaller foragers. In the present work this has also been found to be true in the case of colonies of *B. agrorum*, *B. lucorum*, *B. pratorum*, *B. sylvarum* and *B. terrestris*. However, even very small foragers of these colonies did collect some pollen.

The sequence of foraging duties with age.

Whether or not bees belonging to colonies 16 and 18 collected nectar or pollen during their first day of foraging was recorded. A significantly greater ($P < 0.01$) number of young foragers from colony 18 (*B. lucorum*) collected nectar loads only rather than pollen loads (36: 8). The ratio of nectar to pollen loads collected by these bees during their first few days of foraging was significantly higher ($P < 0.001$) than that of the older bees of the colony during the same period. Twenty-five young

queens of this colony collected nectar only on their first day of foraging although later some of them collected pollen.

In the case of the *B. sylvarum* colony, however, 11 out of 13 bees collected pollen on their first day of foraging.

The relationship between the presence of larvæ in a colony and the collection of pollen by its foragers.

In April 1952 a *B. terrestris* queen was found to have occupied an artificial domicile. On 5th May her brood was in the larval stage and pollen loads had been deposited around it. On 14th and 15th May, by which time the larvae had pupated, the queen was seen to return to her nest 13 times, but on no occasion did she carry pollen although conditions were suitable for its collection, presumably because she no longer had larvae to feed.

Colonies of *B. pratorum* were used in the first experiment. The brood of colony 1 consisted of a group of old larvae, some of which had already spun their cocoons, and a group of young larvae. The young larvae were removed on May 18th 1952 by which time all the older larvae had pupated. During observations on 20th, 21st and 22nd May the foragers of this colony collected *111 nectar loads* but *no pollen loads*. During the same period the foragers of the control colony (colony 2) which contained a single batch of larvae, collected *16 nectar loads* and *8 pollen loads*. Further observations were made on these 2 colonies on 26th and 27th May by which time colony 1 again possessed larvae and Colony 2 contained no larvae, its former larvae having pupated. During these observations bees from Colony 1 collected *37 nectar loads* and *21 pollen loads* and foragers of colony 2 collected *9 nectar loads* and *no pollen loads*.

The presence of larvae in a colony therefore had a highly significant effect ($P < 0.001$) on the relative proportion of pollen to nectar loads which its foragers collected.

In the second experiment a *B. lucorum* colony was divided into 2 parts A and B, of approximately 40 bees each. Both parts contained pupae but, whereas colony A contained larvae and a queen, colony B did not. On 14th and 15th August the foragers of Colony A collected *14 nectar loads* and *15 pollen loads* and the foragers of colony B collected *19 nectar loads* but *no pollen loads*.

On the evening of 15 August the worker bees of colony A were interchanged with those of colony B and the positions of the nest-boxes were also interchanged so that the bees continued to forage from a nest-box in the same position as before but each colony contained the others' brood. During observations on 16th and 18th August the bees of colony A (which was now without larvae) collected *19 nectar loads* and *1 pollen load* and the bees of colony B collected *8 nectar loads* and *2 pollen loads*. The collection of pollen by foragers was thus again related to the presence of larvae in their colonies (Degree of significance $P < 0.02$).

TABLE 10.

Number of nectar and pollen loads collected by foragers of *B. agrorum* colonies with and without larvæ.

PERIOD OF OBSERVATION.		COLONY 29. No. loads collected.		COLONY 33. No. loads collected.		
		Nectar.	Pollen.	Nectar.	Pollen.	
15th, 16th & 17th (a. m.) July 1953.	Larvæ in both colonies.	29	34	27	53	
17th (p. m.), 18th & 19th July 1953.	Larvæ absent in colony 29.	69	23	29	103	Relative increase in nectar collection by colony 29. $P < 0.05$. Relative decrease in pollen collection by colony 29. $P < 0.01$.
19th, 20th & 21st July 1953.	Larvæ absent in colony 29.	57	14	70	87	
22nd, 23rd, & 24th July 1953.	Larvæ absent in both colonies.	83	7	124	23	Relative increase in nectar collection by colony 33. $P < 0.5$. Relative decrease in pollen collection by colony 33. $P < 0.5$.
1st, 2nd & 4th August 1953.	Larvæ in both colonies.	77	30	55	60	
5th & 6th August 1953.	Larvæ absent in colony 33.	54	30	69	22	Relative increase in nectar collection by colony 33. $P < 0.05$. Relative decrease in pollen collection by colony 33. $P < 0.01$.

Two *B. agrorum* colonies both of which contained plenty of larvae were used in the third experiment (Table 10). The removal of larvae on 17th July and on 4th August resulted in the foragers of the experimental colony collecting relatively fewer pollen loads and relatively more nectar loads in comparison with those collected by the foragers of the control colony.

In contrast to the behaviour of pollen-gatherers of pollen-storing species (e.g. *B. lucorum*, *B. pratorum*, *B. terrestris*) which deposit pollen in storage cells, the foragers of *B. agrorum* colonies (pocket-making species) deposit pollen directly into pockets attached to larval groups (Sladen 1912).

When no larval pockets were available pollen-gatherers of colony 29 deposited their pollen loads in empty cocoon cells but the members of colony 33 constructed a tall cylindrical wax cup in which they stored pollen just inside the nest entrance. This cup was later destroyed and a similar one built near to the centre of the nest. Some pollen loads were still deposited in it even when larval pockets again became available.

The requirements of colonies in relation to their stores of food.

A study has been made of the requirements of colonies (as revealed by their foraging activities) in relation to their stores of food.

A. — THE EFFECTS OF ADDING SUGAR SYRUP TO THE FOOD STORES OF COLONIES

In 5 experiments half of the honey-pots of small *B. pratorum* colonies were filled with sugar syrup. The foragers of these colonies were observed to collect *12 pollen loads* and *87 nectar loads* before the addition of the syrup, and *14 pollen loads* but only *6 nectar loads* afterwards. During the same 2 observation periods, the foragers of 5 control colonies collected *3 pollen and 94 nectar loads*, and *13 pollen and 74 nectar loads* respectively. Thus the addition of sugar syrup to the experimental colonies resulted in their foragers collecting relatively less nectar than previously (Degree of significance. $P < 0.001$).

Only 4 of 26 nectar-gatherers which returned to the experimental colony after syrup had been added to their food stores foraged again, whereas 22 of 25 nectar-gatherers which returned to the control colonies during the same period continued to forage (degree of significance. $P < 0.001$).

There was no significant difference between the relative numbers of pollen-gatherers of the experimental and control colonies which remained in their nests or foraged again.

Similar experiments were carried out with 2 large *B. terrestris* colonies. (Table 11). On each of 3 occasions that sugar syrup was added to 1 or

other of these colonies its foragers collected significantly fewer ($P < 0.001$) nectar loads than previously. Only in the first experiment did the addition of sugar syrup to a colony result in its foragers collecting relatively more pollen. The carbohydrate stores of this colony (No. 31) were previously very low and it seems probable that its foragers only collected pollen when the carbohydrate stores had reached a certain minimum level (which condition was attained after the addition of sugar syrup by the experimenter).

TABLE 11.

The effect on the no. of nectar and pollen loads collected of adding sugar syrup to the food stores of colonies of *B. terrestris*.

Period of observation.		Colony 31.		Colony 32.	
		No. loads collected.		No. loads collected.	
		Nectar.	Pollen.	Nectar.	Pollen.
10th, 11th & 13th (a. m.) July 1953.	Syrup added to colony 31.	269	0	125	169
13th (p. m.) 14th & 15th July 1953.		235	93	276	473
14th, 15th & 16th July.	Syrup added to colony 31.	326	173	217	353
17th, 18th & 19th July.		120	181	281	341
18th, 20th & 21st July.	Syrup added to colony 32.	133	215	252	303
23rd, 24th & 25th July.		220	179	196	118

B.—THE EFFECTS OF ADDING POLLEN TO THE FOOD STORES OF COLONIES

In 4 experiments the pollen stores of colonies were artificially supplemented with fresh pollen (trapped from a honeybee colony). All of these colonies contained plenty of developing brood. The results are shown in Table 12.

Experiment 1 was performed on small *B. pratorum* colonies. Four

TABLE 12.

The effect on the number of nectar and pollen loads collected of adding pollen to the food stores of colonies.

EXPERIMENT No.	SPECIES.		BEFORE THE ADDITION OF POLLEN.				AFTER THE ADDITION OF POLLEN.			
			Date.	Period of observation (hrs).	Loads collected.		Date.	Period of observation. (hrs).	Loads collected.	
					Nectar.	Pollen.			Nectar.	Pollen.
1	*B. pratorum.*	Experimental colony 1.	3rd June 1952.	4.5	3	10	4th June 1952.	5.0	4	2
	«	Control colony 2.			28	1			19	4
2	*B. pratorum.*	Experimental colony 13.	19th, 20th, & 22nd, 23rd (a. m.) July 1953.	5.5	28	41	23rd (p. m.) 25th June 1953.	6.5	75	30
	«	Control colony 21.			30	19			45	32
3	*B. agrorum.*	Experimental colony 39.	17th, 18th, & 19th Aug. 1953.	8.0	70	54	20th, 21st & 22nd Adg.1953.	9.0	116	0
	«	Control colony 40.			84	30			66	16
4	*B. terrestris.*	Experimental colony 42.	17th, 18th & 19th Aug. 1953.	8.0	214	68	20th, 21st & 22nd Aug.1953.	8.5	274	40
	B. lucorum.	Control colony 43.			76	9			103	5

empty cocoon cells of Colony 1, 2 of which had been used for pollen storage, were filled with pollen. The foragers of this colony subsequently collected relatively less pollen than previously. (Degree of significance, $P < 0.05$).

Two larger *B. pratorum* colonies were used in the second experiment. After the addition of plenty of pollen to colony 13 its members also collected comparatively less pollen than previously (Degree of significance, $P < 0.05$). However, the change was gradual and no immediate effect was observed.

Colonies of *B. agrorum* were used in Experiment 3. Six balls of pollen, each about 1,0 mm in diameter, were given to colony 39. None of the foragers of this colony collected pollen during the next 3 days of observation, but foragers of the control colony (40) still collected pollen, although at a reduced rate. (Degree of significance, $P < 0.001$). This result was surprising, since *B. agrorum* pollen-gatherers normally deposit pollen directly into larval pockets (as previously described) and it indicated that either the workers of colony 39 had transferred the pollen to the larval pockets with their mandibles or else had fed the larvae with regurgitated food. After the addition of pollen to Colony 29, 21 of the original pollen-gatherers collected nectar, as a result of which this colony showed a comparative increase in the number of nectar loads collected ($P < 0.01$).

In the final experiment pollen was added to a *B. terrestris* colony (42). Unfortunately a proper control was not available and a *B. lucorum* colony (43) which did not contain larvae had to serve this purpose. The foragers of colony 42 collected a smaller proportion of pollen to nectar loads than before the pollen was added, but pollen collection by members of the control colony also decreased and no significant result was obtained.

From the above data it appeared that pollen collection by foragers is voluntary rather than obligatory. In order to verify this a *B. agrorum* colony was placed beside a small patch of red clover and whilst one observer recorded the foragers when they returned to their nest another confirmed their presence on the crop. It was found that during the same period some of these foragers collected nectar only whilst others collected pollen.

DISCUSSION AND CONCLUSIONS

Cumber (1949) suggested that the smaller workers of a bumblebee colony forage when their colony is dying out. Brian (1952) found that house-bees began to forage at about the time of the death of some of the original foragers. In order to determine whether house-bees would alter their behaviour in response to their colony's needs she took away the foragers and gave sugar syrup to a *B. agrorum* colony. The sugar syrup was removed from this colony after 28 hours during which time 1 house-bee had foraged; the next day no house-bees were observed to leave their nest.

The results of 5 experiments, in the present work, in which foragers were removed from their colonies show conclusively that some house-bees will forage in their absence. When these results are considered in conjunction with those of Brian it appears probable that house-bees only forage when the food stores of their colony become low, and that they take some time to adjust themselves to the new conditions. Some foragers also remained inside their nests when the house-bees of colonies were moved, although many of the foragers did not immediately adapt themselves to the changed circumstances. Free (1955b & 1955c) found that foragers which were confined in nest-boxes and provided with ample food laid eggs and 'nursed' the resultant larvae. It is thus apparent that although the majority of the bees of a colony are consistent foragers or consistent house-bees, many will perform either task in accordance with the current requirements of their colony.

In large colonies some bees alternate their household and foraging activities with guard duty at the nest entrance.

Sladen (1912) and Brian (1952) noted that some of the foragers of *B. agrorum* colonies collected pollen when there were no larvae in their nests. In the experiments described above a correlation has been found between the amount of pollen collected by foragers and the presence or absence of larvae. It appears that the presence of larvae releases the pollen collecting behaviour of foragers, although some of them continued to collect pollen after all the larvae have been removed from their nests.

Sladen (1912) found that when he gave food to colonies it tended to make the workers "lazy". Brian (1952) reported that by filling the honeypots of a colony with sugar syrup she induced the foragers to remain inside their nest. During the present observations when sugar syrup was added to the stores of colonies the pollen-gatherers continued to forage, but the majority of the nectar-gatherers ceased to forage for nectar and did not undertake pollen collection instead. These results further illustrate the constancy of foragers to the collection of either nectar or pollen loads throughout relatively short periods.

On most occasions when the pollen stores of colonies were artificially increased relatively less pollen, and in the case of a *B. agrorum* colony relatively more nectar, was collected. The removal of larvae from *B. agrorum* colonies also resulted in increased nectar collection.

From these results it is apparent that the type of food collected is determined to some extent by colony requirements. These requirements depend on the nature and amount of the food stores in a colony and on the age of the brood. Fluctuations in these factors, and in pollen availability in the field, can explain the day to day variations in the kind of food collected by individual foragers.

Summary.

1. Most of the workers of a bumblebee colony are either consistent foragers or house-bees but about a third of the workers are inconsistent to either duty. The longer a worker has been carrying out either household or foraging duties the more 'fixed' it becomes to the duty concerned.

2. Individual workers will change their occupation and perform either household or foraging duties in accordance with the current requirements of their colonies.

3. Foragers show great constancy to the collection of either pollen loads or nectar loads during consecutive trips, but they show little constancy for periods of a day or over.

4. The amount of pollen which the foragers of a colony collect is related to the presence of larvae in their nest.

5. The type of food collected by foragers is also determined to some extent by the nature of their colonies' food-stores.

Résumé.

1. Les ouvriers d'une colonie de bourdons se divisent pour la plupart en deux catégories bien définies, les récolteurs et les travailleurs au nid ; toutefois ils peuvent, pour un tiers, passer d'une catégorie dans l'autre. Ils se spécialisent d'autant plus dans l'une ou l'autre de ces fonctions (travail au nid ou de récolte) qu'ils les assument plus longtemps.

2. Pris séparément, chaque ouvrier change d'occupation et passe du travail au nid à celui de la récolte, ou vice-versa, selon les besoins du moment de la colonie.

3. Pour la durée de quelques voyages consécutifs, les récolteurs se montrent très assidus dans leur recherche, soit de pollen soit de nectar, mais pour de plus longues durées (un jour entier ou plus) ils se montrent très changeants.

4. La quantité de pollen que les récolteurs de la colonie recueillent est proportionnelle au nombre des larves du nid.

5. De plus, le genre de nourriture amassée par les récolteurs dépend, dans une certaine mesure, de la nature des provisions de la colonie.

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