

**THE FORAGING BEHAVIOR OF HONEYBEES
ON HAIRY VETCH**
II. THE FORAGING AREA AND FORAGING SPEED (1)

by

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Honeybees foraging from blossoms of most plant species are rather similar in their methods of work, and careful observations are necessary to discern minor individual differences. Under these circumstances the student of foraging behavior must guard against the unconscious assumption that any one individual is representative of the entire population. This is not true, however, of the student of bees working hairy vetch. The bees differ so widely from one another in their methods and approach to foraging that the individuality of the bees is a most obvious and striking phenomenon, and the student must guard against the anthropomorphic assumptions that could easily follow from ascribing too much individuality to bees.

MATERIALS AND METHODS

In 1953, 1954, and 1955 studies were conducted on the behavior of honeybees (*Apis mellifera* L.) foraging from hairy vetch (*Vicia villosa* Roth.). The technique used in determining the nectar flow, nectar concentration, amount of bloom, and population of foragers have been published (WEAVER, 1956 *a*, 1956 *b*). Most of the detailed studies of foraging behavior were conducted in the same field throughout any one year; this is designated below as the experimental field.

A few bees were marked by RIBBAND'S (1949) technique for repeated observations, but virtually all of the quantitative data were taken on bees found at random in the field, and presumably most of the bees were observed only once.

The length of time bees spent in tripping blossoms and the total time required to forage from them was measured with a stop watch in 1955. The time required to

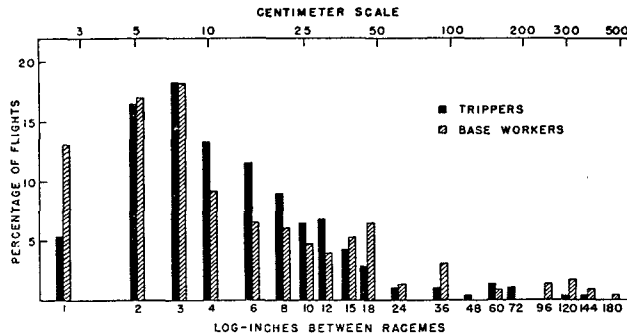


Fig. 1. — Frequency distributions of the estimated distances between successive racemes of hairy vetch visited by tripping and base working honeybees.

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trip a blossom was measured to the nearest 0.1 second from the time the tongue was inserted into the mouth of the blossom until the keel was thrust downward completely free of the sexual column. The time required to forage from a blossom, or the time spent in unsuccessfully attempting to forage, was measured to the nearest second as the time elapsed from the first attempt to insert the tongue into the blossom until the tongue was withdrawn. Data on the time required to forage blossoms that obviously had been tripped previously were recorded separately. For some of these measurements, the first bee that came into view in an area was timed while visiting one, or each of a very few blossoms, her foraging method and the forage she gathered were recorded, and then the observer moved three paces and collected data on the first bee that came into view at the new location. Other bees were timed during visits to many successive blossoms. The analyses of variance which were used in the statistical treatment of these data follow the methods given by SNEDECOR (1946). Only the mean and its standard error were calculated for some of the data.

The over-all foraging speed of bees was determined by counting the number of blossoms foraged over a measured period of time by randomly selected individual bees. In 1953 only the successfully foraged blossoms and their racemes were counted. In 1954 and 1955 the number of blossoms which a bee made a definite unsuccessful attempt to work were recorded separately from the successfully visited blossoms. Hand tally registers were used in keeping the counts. The length of time over which the counts were made was taken with a stop watch and rounded to the nearest 0.1 minute. Data on bees observed for less than 1.5 minutes were discarded. All of this information plus the time of the observation, the forage gathered, the observed foraging area, the general foraging behavior, and the peculiarities of behavior of each bee were recorded.

RESULTS AND DISCUSSION

In a previous communication (WEAVER, 1956 *b*) it was pointed out that the honeybee can reach the nectar from the mouth of the hairy vetch blossom by tripping it, or she can insert her tongue between the petals at the base of the corolla tube and reach the nectar. These non-tripping bees are called base workers, and they gather nectar only. The trippers forage in the mouth of the blossom for pollen only, or they insert the tongue into the blossom to their right or to their left of the sexual column and forage for nectar only or for both nectar and pollen. The number of foragers of each type is variable and some of the variability can be related to the nectar flow. The present communication reports studies of other aspects of foraging behavior.

Foraging Areas. — During the first few hours after colonies began to forage from vetch for the first time, there were always many more foragers near the colonies than farther away. While bees were learning to forage from vetch blossoms they were very nervous and often flew great distances. It is believed that this helped to spread the foragers rather evenly over the field, and that the foraging area may have become fairly well fixed in the locality where the bee finished gathering the first load after the foraging method was learned. Attempts to study the problem by marking bees that were learning to forage were unsuccessful; none of these bees were ever seen again, and it is not known that any of them resumed foraging.

Marked bees with an established foraging method could be found repeatedly, though with some difficulty. These bees were followed during several foraging expeditions to confirm the findings of RIBBANDS (1949) and SINGH (1950) that bees return to the same region on successive trips to the field and forage repeatedly over the same rather ill-defined area. These observations were made near landmarks of various kinds which could have served to orient the foragers, so it is not known how accurately a bee could determine a previous foraging area at a considerable distance from any landmarks other than the vetch itself. Since the vetch vines grow upward in clumps at various places with the surrounding vines being more reclinate, the topography of the field may help to delineate the foraging areas. Bees often foraged from a long narrow area along the side of a road, and it appeared that during a good nectar flow one marked bee foraged an oblong area which followed a series of clumps in the vetch.

When her load was almost complete a bee always visited several blossoms which she made little or no attempt to trip; these appeared to be exploratory visits. The return to the hive usually followed immediately after a number of these visits, though occasionally the bee successfully foraged from one or two blossoms just before leaving the field. During a good nectar flow the explored racemes were always close together, and the bee circled the area before returning to the hive. Presumably the forager was orienting herself for a return visit to the field and was establishing the direction of the colony. During a poor flow the exploratory visits might be scattered over a wide area, and bees sometimes left the field without circling. In these cases the bee flew upward for less than a meter before turning toward the apiary; the approximate direction of the colony would have to be known before flight became level.

RIBBANDS (1949, 1953) emphasized the comparisons which foraging bees continuously make between present yields from blossoms and the memory of past yields. Opportunity for such comparisons between the plants of one species over a short period of time and in a narrow area in the field often can be seen. It was not uncommon for a bee to forage for an extended time in an area much less than a square meter in size, fly three or more meters, and work quickly back to the original area, foraging one or two blossoms on each of several racemes between the two locations. Presumably the yields from the explored areas were not sufficiently better than the yields in the original area to cause the bee to change foraging localities. Often a bee would make several successive long flights with only perfunctor efforts to trip most blossoms, as if dissatisfied with the yields everywhere. One bee that made a definite effort to gather both pollen and nectar from most vetch blossoms alighted on a flower of the sensitive briar, *Neptunia* sp., ran over the anthers, and immediately returned to foraging vetch. Other bees had already gathered the pollen from this and the surrounding *Neptunia* blossoms. Such observations may have been more common if there had been more competing blossoms of different species.

Foragers also compare the yields of nectar on successive days. When,

the nectar flow deteriorated, bees foraged and explored over wider areas flew great distances more often, spent more time exploring, and were less persistent in their efforts to trip many of the blossoms than when the nectar flow was constantly poor or was improving. Differences in the manner of work were so marked that from observations on foraging behavior alone, the gain in weight of a colony of bees as compared to the gain on the preceding day could be accurately predicted. The over-all impressions of foraging behavior were much more useful and accurate than the quantitative data for making predictions. Measurements of the amount of nectar in blossoms in 1955 indicated that the differences in foraging behavior in that year were caused by the amount of nectar available and not by the direct effects of the weather on the bees.

In addition to the elasticity of the foraging area which may cause a bee to discover more attractive vetch at a considerable distance from the point at which she started foraging, bees sometimes change to a foraging area completely removed from the old one. In 1954 the experimental field was among the first in the region to come into bloom, and there was a mean 2.2 foraging bees per square meter of vetch during the first ten days of heavy bloom. The nectar flow was slow, and following several days of inclement weather that reduced the foraging population, the number of foragers in the experimental field fell and remained near 1.1 bees per square meter for the rest of the season. In 1955 the experimental field was among the last to come into bloom, and although there was an apiary in the field there were few bees working the vetch until and an additional colony was brought into the field after the vetch was virtually in full bloom. During the next week there were 0.6 bees per square meter of vetch. The experimental field had more nectar per blossom and nectar of a higher sugar content than at least one nearby field that had come into bloom earlier and had more foragers. During three days of cloudy weather with intermittent showers the foraging population rose sharply and averaged 2.7 bees per square meter during the remainder of the blooming period, with means of more than 4 bees per square meter being common during periods of maximum foraging activity. Both the interruption of foraging and the threat of rain that made it dangerous for the bees to go far from the hive, as well as the greater attractiveness of the vetch in the experimental field, may have made it easier for scout bees to recruit foragers to the new area.

Aggressive Behavior. Competition from other foragers is important in determining the size of the foraging area. This competition may operate by decreasing the amount of nectar available from the blossoms or by the reaction of a bee to the physical presence of competing foragers. Often a bee was observed to collide with a nearby forager in a purposeful manner or to fly threateningly toward another bee without actually touching her. The aggressor in each of these observations continued to forage nearby; the bee that was bumped or threatened sometimes flew several meters

and sometimes continued to forage nearby. When neither bee left the vicinity there was sometimes a prolonged struggle, with contact between the bees every time they were on the wing at the same time, and with one or the other of the bees sometimes being attacked while foraging from a blossom. Some of these bees were always passive but would refuse to leave the area; others would become aggressive on some of the flights so that occasionally both bees attacked the other at the same time. One bee was observed to collide with another forager that was flying past, and then to visit a raceme deep in encircling vines. The bee that was attacked had given no indication of stopping in the area, but she immediately whirled in pursuit of her attacker, bumping into several vines in the recklessness of her pursuit. One bee that was being kept under prolonged observation moved about 2 meters in one flight after being bumped, and then quickly foraged from several racemes on her way back to her original narrow area which she continued to work. Another bee that was under observation flew more than three meters to forage in a new area; soon after beginning to forage she was attacked by another bee already in the vicinity, and moved more than a meter before visiting another blossom; another bee was later observed to behave in the same manner. One bee flew about 3 meters from an area which she had been working for some time and bumped another forager before visiting a blossom at the new location. The bee that was attacked flew away, and the aggressor began to forage in the new area. This aggressive behavior by foraging bees is probably an aid in keeping a foraging area free of too much competition from other bees; and possibly aids bees in moving into new foraging areas. Interestingly, when the competition between foragers became intense and there were over 4 bees per square meter during periods of maximum foraging activity, this aggressive behavior virtually ceased, and bees paid little attention to nearby foragers.

Distance of Flights. It was difficult to keep base workers under observation because of their frequent long flights. The eyes and antennae of the base workers, unlike those of the trippers, were fully exposed while they foraged from blossoms, and the presence of an observer often seemed to disturb them and cause some of the longer flights. They also seemed to be more sensitive than trippers to the presence of competing foragers; base workers were more prone to take evasive action when another forager flew near by, and often moved to a blossom deep in encircling vines, or flew away from the area, after such evasive action. Records of the conditions surrounding over 100 randomly observed flights of more than a meter did not indicate clearly whether or not base workers normally move long distances more often than trippers. By recording only the estimated distance between successive racemes visited by a bee, it was possible for the observer to stay farther from each bee than was possible when the foraging behavior on individual blossoms was being recorded. Each day that this technique was used, base workers and trippers were

observed alternately for an approximately equal length of time in vetch with about 600 racemes per square meter. The nectar flow and concentration fluctuated rather widely during the days in 1954 when these observations were made, and the distances between racemes were determined on days when the nectar flow was equal to, better than, and poorer than on the preceding day.

Estimated distances in inches between racemes visited were recorded on 232 flights by 11 base workers, and on 277 flights by 10 tripping bees. The mean for the estimated distances was 23 cm. for trippers, and 32 cm. for base workers. Since the relatively rare longer flights unduly influence the mean, the frequency distributions of the estimated distance were determined. Figure 1 is a histogram of the percentage of flights plotted against the logarithmically spaced estimated inches between racemes. For ease of conversion, a centimeter scale is also given. It can be seen that base workers were more prone to move to contiguous racemes than trippers. They also sometimes crawled along the stem to racemes more than 5 cm. away; trippers usually flew, even in moving to contiguous racemes. The distribution curves for the two types of foragers are similar, though the differences at some of the shorter distances are greater than would be expected from sampling variation or errors in estimating distances. If the data are grouped so that there are four estimated distances in each of the first three groups, the percentage of flights that falls within each group is:

ESTIMATED.		PERCENTAGE OF FLIGHTS BY :		
<i>Inches.</i>	<i>Centimeters.</i>	<i>Trippers.</i>	<i>Base Workers.</i>	<i>All Bees.</i>
0-5	0-13	53	57	55
5-13	13-33	34	22	28
13-42	33-105	9	16	13
42 <	105 <	4	5	4

Although the divisions between groups fall at points on the curve where maximum accuracy of estimate is expected, the distances obviously were not as precisely estimated as would be implied by the above group limits. These percentages, however, are not greatly affected by the errors in estimating distances that were most likely to have occurred. Thus, if we assume that half of the estimates of each distance were too low, and should be estimated as the next greater distance, the percentage in each group becomes, for trippers, 47, 37, 12 and 4, respectively. The assumption that half of the distances were underestimated, or that half of the distances were randomly mis-estimated to the same degree, results in smaller changes in the original percentages.

Foraging Speed. The foraging method of 300 bees and the time in seconds required for each bee, with few exceptions, to forage from one or

each of several blossoms was determined in 1955. The data on successful visits to previously untripped blossoms were analyzed in an attempt to discover the sources of any nonrandom variation that might have occurred in foraging time. Trippers working to the right and left of the sexual column did not differ significantly in foraging speed, so this classification

TABLE 1. — Mean time in seconds required by 50 honeybees to forage from vetch blossoms on each of 6 occasions in 1955.

Date.	Time Hr.	TRIPPERS.						BASE WORKERS.		ALL BEES.	
		Nectar only.		Nect. and Pol.		Pollen only.		No.	Sec./	Total and Mean.	
		No. Blos.	Sec./ Blos.	No. Blos.	Sec./ Blos.	No. Blos.	Sec./ Blos.	Blos.	Blos.	No. Blos.	Sec./ Blos.
5/5	1100	31	9.0	36	9.4	0	—	3	10.0	70	9.3
5/5	1530	14	10.8	19	9.2	0	—	8	5.8	41	9.1
5/7	0830	23	11.5	19	9.9	2	4.5	5	6.8	49	10.2
5/7	1100	21	10.8	20	10.7	7	5.4	10	12.1	58	10.3
5/12	1300	15	11.8	30	10.3	4	3.7	9	11.1	58	10.4
5/17	1100	7	9.4	29	11.6	2	2.5	34	7.3	72	9.1
Total and Mean ...		111	10.5	153	10.2	15	4.4	69	8.5	348	9.7

is omitted from Table 1, which summarizes the data. The time required to forage blossoms did not vary significantly between the different dates and hours on which observations were made. The differences in mean foraging times of bees classified according to forage gathered were significant beyond the 0.01 level. An examination of the data shows little difference between trippers foraging for nectar only and those gathering both nectar and pollen. This is not surprising since few of the bees that gathered both pollen and nectar foraged specifically for pollen; rather they accumulated the pollen that accidentally clung to them. The bees gathering pollen only and the base workers were strikingly different in foraging speed from these bees and from each other. It took less time for a bee to forage a blossom for pollen than for nectar, but the time required by trippers and base workers to remove nectar was probably approximately equal. Nine bees timed in tripping each of 60 blossoms required a mean of 2.7 ± 0.2 seconds to trip a blossom; no good data was obtained on the length of time required by base workers to insert the tongue into blossoms, but this certainly required less time than tripping.

Records were also made of the number of seconds required for individual bees gathering nectar only or both nectar and pollen to forage successfully from each for 10 or more blossoms. These data are summarized in Table 2.

Because of the findings presented above the time at which the observations were made, the forage gathered, and the direction of entry into blossoms were disregarded and an analysis of variance was run to determine whether or not these twelve bees differed from each other in mean number of seconds required to forage from blossoms. The highly significant F value indicates that they did differ among themselves. The data on bees No. 7 and 8 were taken during a high wind, and these bees sometimes clung to a blossom for up to 46 seconds while the wind buffeted the raceme about. This seemingly accounts for the slow foraging speed of these bees, but if the data on bees 7 and 8 are discarded, the remaining bees differ significantly from each other.

The data on bees observed successfully foraging from less than 10 blossoms are combined and presented in Table 2 as miscellaneous bees. Included in this group are data on unsuccessful visits and visits to previously tripped blossoms by bees whose successful visits are given in Table 1. Observations on the time required for several base workers to forage from blossoms are also grouped and presented in Table 2. The data on base workers in Tables 1 and 2 are not in very good agreement, but this seems to be due to sampling variation.

TABLE 2. — Mean time in seconds required by several bees to forage from blossoms of hairy vetch as trippers or as base workers where indicated.

Bee No.	SUCCESSFUL VISITS.				UNSUCCESSFUL VISITS.	
	Previously Untripped.		Previously Tripped.		No. Bloss.	Sec./Blos.
	No. Bloss.	Sec./Blos.	No. Bloss.	Sec./Blos.		
1	21	8.1	3	5.7	3	4.7
2	23	10.3	3	8.0	8	6.4
3	34	8.0	5	4.0	10	5.0
4	26	10.6	5	4.8	4	4.1
5	10	9.2	4	4.8	4	3.8
6	23	7.5	2	4.5	6	3.2
7	19	13.7	1	5.0	6	5.8
8	15	15.3	3	13.0	2	5.5
9	12	11.2	1	8.0	0	—
10	23	12.3	4	8.2	9	5.9
11	10	12.0	2	6.0	13	4.1
12	11	8.3	2	4.5	4	4.0
Totals and Means 227		10.3	35	6.2	69	5.0
F with 11 and 215 DF		5.4 ***				
Misc. Bees 105		8.2	27	6.4	76	4.8
Base Workers 114		7.7	—	—	17	6.0

*** Probability < 0.001.

Some of the visits to blossoms that the bee did not forage were difficult to classify. A bee sometimes inserted the proboscis in to the mouth of the corolla tube and withdrew it immediately. These visits were considered to be exploratory and were not recorded as unsuccessful attempts to trip, but sometimes there was a brief but perceptible tripping motion, especially after a bee had struggled hard and failed on one or two blossoms, or just before she returned to the hive. Although there was some inconsistency, only the time spent on visits in which there was a definitive efforts to trip the blossoms was recorded and few of the recorded times were less than 3 seconds. These data may, therefore, be biased slightly upward, but it is certain that bees usually spent more time in attempting to trip than in successfully tripping a blossom.

TABLE 3. — Mean number of blossoms which honeybees successfully forager per minute and per inflorescence, and the percentage of blossoms which bees unsuccessfully attempted to forage, while visiting hairy vetch, crimson clover, and hubam clover.

Legume and Year.	Type Forager.	No. Bees.	No. Min.	Blos./ Min.	Blos./ Infl.	% Unsuc.
Vetch 1953.	Trippers :					
	Pollen	4	36.2	5.1	1.8	—
	Pol. and Nect	7	117.7	4.5	1.7	—
	Nectar	9	199.1	3.0	2.7	—
	Base Workers.....	6	41.7	4.6	2.1	—
Vetch 1954.	Trippers :					
	Pollen	3	15.2	3.5	2.5	32
	Pol. and Nect	19	381.7	3.2	1.8	36
	Nectar	2	49.5	2.4	1.9	28
	Base Workers.....	11	132.0	4.8	2.3	9
Vetch 1955.	Trippers :					
	Pollen	2	17.0	9.1	2.4	3
	Pol. and Nect.	19	181.7	4.0	1.8	16
	Nectar	12	99.1	3.8	1.8	16
	Base Workers	5	20.5	4.9	2.1	5
All Vetch.	All Trippers	77	1097.2	3.6	1.9	—
	All Base Workers ...	22	194.2	4.7	2.3	—
Crimson Clover.	Trippers	10	99.2	13.5	2.8	—
Hubam Clover.	Trippers	26	91.2	33.2	5.1	—

Table 3 gives a comparison in the mean over-all foraging speed of bees working on hairy vetch, crimson clover (a variety of *Trifolium incarnatum* L.), and hubam clover (a variety of *Melilotus alba* Desv.). The bees working vetch are classified according to forage gathered and the year the observations were made. The individual bees differed widely from each other in over-all foraging speed and the samples of some types of foragers under different conditions were so small that no detailed statistical treatment of these data was attempted. It will be noted, however, that

there is good agreement in the order of foraging speed of bees gathering the same forage in different years, and in the time required to forage individual blossoms (Table 1).

The speed with which the bees forage from the three legumes is strikingly different. During a good nectar flow when there was little competition between foragers, bees visited a mean of 38.7 hubam clover blossoms per minute and 5.9 blossoms per inflorescence (WEAVER *et. al.*, 1953). During a poorer flow in 1955 when there was much more competition between foragers, bees spent more time on the wing and visited a mean of 29.5 blossoms per minute, and 4.6 blossoms per inflorescence. Blossoms of the clovers are much smaller and more easily tripped and worked than vetch blossoms; bees reach the nectary of hubam clover with ease, and of crimson clover with some difficulty. The hubam clover blossom is foraged so quickly that no attempt was made to determine the length of time required to forage from individual blossoms. According to 79 observations a mean of 3.4 ± 0.2 seconds was required for a bee to forage from a crimson clover blossom. Computations from this figure and the mean number of blossoms foraged per minute indicate that the bees spent 76 per cent of their time foraging from blossoms and the remainder of their time at other activities, mainly in exploring blossoms, packing pollen on the corbiculae, or doing both simultaneously. Similar computations from the data in Tables 1 and 3 indicate that in 1955 the different types of foragers spent means of from 66 to 69 per cent of their time in successfully foraging from vetch blossoms, and the remainder of their time at other activities. Less than 6 per cent of the time was spent in unsuccessfully attempting to forage from blossoms. These data were taken over a fairly homogeneous period in the condition of vetch plants and in the nectar flow. It is doubted that the agreement would have been as close if the data had been taken over more varied conditions, and it is certain that a far smaller percentage of the time is spent in foraging from blossoms during a poor nectar flow.

The trippers gathering nectar only seem to represent two types of foragers. During fast nectar flows when colonies gathered from 6 to 17 kg. of nectar a day, there was little difference in the mean foraging speed of trippers foraging for nectar only and those gathering both nectar and pollen, but after several days with a poor flow the few nectar gathering trippers remaining in the field were invariably highly inefficient workers that visited a mean of at least one fewer blossoms per minute than the mean of the bees gathering both nectar and pollen. It may be that their failure to pack the pollen that clung to their bodies was another expression of their inefficiency. It is believed that after the nectar flow deteriorated most of the efficient and some of the inefficient tripping nectar gatherers ceased to forage, began to gather both pollen and nectar, or became base workers, and that the failure to make a change was a symptom of a general inefficiency.

The slower foragers seemed to be more prone to revisit blossoms that

they had previously tripped than the faster workers, and to be less aware of their surroundings. To keep a bee's performance in clear view it was necessary to get very close to her, and sometimes the observer, while pushing aside entwining vines, shook the raceme being foraged. Of nine bees followed for over 40 minutes, six foraged at less than the mean speed and two at the mean speed, for their own type and year. Prolonged observations on slow bees may have biased the data slightly in favor of the more inefficient foragers, but this was counterbalanced to an unknown extent by the impossibility of prolonged observations on bees that spent most of their time exploring. Many of the highly efficient foragers appeared nervous in their activities, though a few simply went about their tasks in a businesslike way with little lost motion.

Aside from the variation in the speed of work of the bees, there were differences in the ease with which different blossoms were tripped, and some of these differences seem to have been related to the temperature during bud development. The blossoms that developed during cool weather appeared to be slenderer and more difficult to trip than those that developed during warm weather. The average temperature in May 1954 was more than 2°C. cooler than May 1953 and 3°C. cooler than May 1955. Many more of the observations in 1954 followed the cooler weather than in 1953 or 1955. No records were kept in 1954 on the time required for bees to trip or work individual blossoms, but the slow over-all foraging speed of trippers that year appeared to be due to the greater time and effort required by the bees to trip the blossoms, and the larger percentage of blossoms that they were unable to trip. As indicated above, the data on unsuccessful visits depended upon subjective decisions by the observer, and some of these decisions were undoubtedly inconsistent with each other. The percentages of unsuccessful visits in Table 3, however, do indicate the magnitude of difference in 1954 and 1955. Since honeybees are dependable pollinators of alfalfa in parts of California, but not in Manitoba (STEPHEN, 1956), it is suggested that a temperature dependent difference in the ease with which the blossoms are tripped might be partially responsible for this variation.

Some bees spent a great deal of time hovering near, crawling over, and inserting the tongue quickly into blossoms of both vetch and crimson clover. These appeared to be exploratory activities which probably depended upon the sense of smell and the perception of water to locate nectar, and possibly upon tactile and visual senses to distinguish blossoms mature enough to trip easily. These exploratory activities would probably be to the bees' disadvantage when visiting blossoms in which the nectar or pollen is quickly and easily reached, since the time and energy spent in this manner might exceed that required to reach the nectary or anthers, but if exploration resulted in a higher percentage of the blossoms being fruitfully visited, it would be to the bees' advantage on crops that are difficult to forage. Some observations indicated that the ability or inclination to perceive differences in blossoms is not highly developed in all

individuals. Some bees often attempted unsuccessfully to trip older buds; a few bees worked virtually no blossoms that had not previously been tripped; and a few bees often reworked blossoms 1 to 3 times before leaving a raceme, or returned to a previously visited raceme and reworked the blossoms; one base worker and one nectar and pollen gatherer were observed visiting only partially withered blossoms. The more inefficient foragers (as determined by the mean number of blossoms foraged per minute) appeared to spend less time exploring and more time revisiting previously tripped blossoms than the more efficient foragers. In spite of the probable disadvantage to the colony of activities of this kind the ability to locate a likely source of nectar or pollen without contact with it is probably of greater selective advantage to the colony as an aid in finding new forage than in choosing individual blossoms of a species to work.

Some colonies of honeybees are superior to others as nectar gatherers, and the superiority is not fully explained. It is postulated that certain aspects of foraging behavior, and some physiological mechanisms which affect foraging behavior are heritable, and that colonies of bees differ in the mean foraging ability of their workers; all else being equal, the colony with the most efficient foragers will gather the most nectar and pollen.

Summary.

The foraging area of a bee is small during a good nectar flow, but as the nectar flow deteriorates the foraging area becomes larger, the bee begins to explore further from her original area, and is less persistent in her efforts to trip blossoms. If the flow improves again, or remains fairly constant, the bees become more settled in their foraging behavior. An interruption of foraging probably makes it easier for a bee to be recruited to a new area completely removed from the old one. It appears that attack on other bees probably aid in keeping a foraging area free of too much competition from other bees. During a period when the nectar flow fluctuated rather widely, bees moved more than 15 cm. on less than 50 per cent of their flights, and more than 100 cm. on only about 4 per cent of their flights. There were rather minor differences between trippers and base workers in the frequency with which flights of some distances occurred.

Bees gathering the same forage differed from each other in the mean time required to forage from individual blossoms. Of bees gathering different forage, or foraging in different ways, pollen gatherers foraged blossoms the fastest, base workers next, pollen and nectar gatherers next, and tripping nectar gatherers the slowest. The over all foraging speed of the bees fell in the same order, and the data indicated that bees spent approximately 65 to 70 per cent of their time foraging from blossoms, and the remainder of their time at other activities. There was great variation in the over all foraging speed of individual bees, and in the ease with

which different blossoms were tripped. It is proposed that temperature dependent differences in the ease with which blossoms are tripped may account for some of the variability in the value of bees as pollinators of certain crops. During fast nectar flows there was little difference in the foraging speed of tripping nectar gatherers and bees gathering both nectar and pollen, but after several days with a poor nectar flow the few remaining nectar gatherers were inefficient foragers. The inefficient workers were more prone than efficient ones to revisit previously foraged blossoms, and they spent little time exploring. It is proposed that differences in the foraging efficiency of bees help to account for differences in honey production by colonies.

Sommaire.

L'étendue du vol d'une Abeille quand elle va butiner n'est pas grande pendant que le nectar est abondant, mais, quand le nectar devient rare, l'Abeille commence à explorer de plus en plus loin de sa région de butinement originelle et elle est, de plus, moins persistante dans ses efforts de « trip » les fleurs. Si la miellée devient plus grande encore ou si elle reste à peu près constante, l'Abeille devient plus régulière dans la conduite de son butinement. Une interruption de butinement facilite probablement le déplacement de l'Abeille vers une nouvelle région bien éloignée de sa région originelle. Il paraît que les assauts contre les autres Abeilles aident probablement à maintenir une région de butinement libre de trop de concurrence des autres Abeilles. Pendant une période, quand la miellée fluctuait beaucoup, les Abeilles volaient plus de 15 cm sur à peu près 50 p. 100 de leurs vols et plus de 100 cm sur à peu près 4 p. 100 de leurs vols. Il y avait de petites différences entre les Abeilles qui « trip » les fleurs et les ouvrières qui butinent à la base des fleurs en ce qui concerne le nombre de vols de grande étendue.

Les Abeilles butinant dans les mêmes fleurs ne se sont pas accordées sur le temps moyen de butiner dans des fleurs individuelles. En ce qui concerne la vitesse de butiner des Abeilles qui butinent dans des sources de nectar variées, ou de celles dont la façon de butiner varie, celles qui recueillent le pollen butinent le plus vite, puis les ouvrières de base, ensuite celles qui recueillent et le pollen et le nectar, et, enfin, celles qui « trip » sont les moins vites. La vitesse de butiner hors tout des Abeilles est du même ordre, et les données indiquent que les Abeilles passent à peu près 70 p. 100 de leur temps à butiner des fleurs et le reste de leur temps à faire autre chose. Il y avait une grande variation dans la vitesse hors tout d'une Abeille individuelle et dans la facilité de « trip » des fleurs. Il se propose que les différences dépendant de la température dans la facilité de « trip » les fleurs pourraient expliquer en quelque façon la variabilité de la valeur des Abeilles en tant que pollinisateurs de certaines plantes. Pendant les miellées rapides, il y avait peu de différence entre la vitesse de butiner des Abeilles-trippers qui recueillent le nectar et les Abeilles recueillant et le nectar et le pollen ; mais, après

plusieurs jours d'une pauvre miellée, les quelques Abeilles qui continuaient à recueillir le nectar étaient inefficaces dans leur butinement. Les ouvrières inefficaces étaient plus enclines que les efficaces à visiter encore une fois les fleurs préalablement visitées et elles ont passé peu de temps à explorer. Il se propose que les différences dans l'efficacité des Abeilles aident à expliquer les différences dans la production de miel dans les diverses colonies.

Zusammenfassung.

Bei reichlicher Nektartracht ist das Sammelgebiet einer Biene klein, aber wenn die Tracht weniger ergiebig wird, erweitert sich das Gebiet; die Biene unternimmt dann Entdeckungsflüge nach entlegeneren Feldern und ist weniger bestrebt, die Blüten aufzuschnellen. Wenn die Tracht wieder besser wird oder auf gleicher Höhe bleibt, wird die Tätigkeit der Bienen gleichmäßiger. Es ist möglich, daß eine Unterbrechung der Sammel-tätigkeit die Umstellung einer Biene auf ein neues, vom alten völlig getrenntes Sammelgebiet erleichtert. Es scheint, daß Angriffe auf andere Völker dazu beitragen, das Sammelgebiet von einem Übermaß von Konkurrenten freizuhalten. Als die Ergiebigkeit der Tracht stark schwankte, flogen die Bienen weiter als 15 cm bei weniger als 50 v. H. ihrer Flüge, und weiter als 100 cm bei unter 4 v. H. ihrer Flüge. Schnellerinnen und Bodenarbeiterinnen unternahmen ungefähr die gleiche Anzahl von Flügen über größeren Strecken.

Die zum Besuch einer einzelnen Blüte erforderliche Durchschnittszeit schwankte bei Bienen, die die gleichen Nahrungsarten sammelten. Von den Bienen, die verschiedenartige Nahrung, oder die Nahrung auf verschiedenartige Weise sammelten, arbeiteten die Pollensammlerinnen am schnellsten, dann die Bodensammlerinnen, die Pollen- und Nektarsammlerinnen, und schließlich die Schnellerinnen. Die Gesamtbeflugsgeschwindigkeit der Bienen folgten in derselben Reihenfolge, und die Beobachtungsergebnisse zeigen, daß die Bienen ungefähr 70 v. H. ihrer Zeit mit dem Beflug der Blüten zugebracht haben, und den Rest der Zeit mit anderen Tätigkeiten verbracht. Die Gesamtbeflugsgeschwindigkeiten der einzelnen Bienen schwankten stark, und ebenso die Leichtigkeit mit der die verschiedenen Blüten aufgeschnellt wurden. Die Annahme liegt nahe, daß temperaturbedingte Verschiedenheiten in der Leichtigkeit, mit der die einzelnen Blüten aufgeschnellt werden können, der Grund für die verschiedene Leistungsfähigkeit der Bienen als Befruchtungsvermittlerinnen bei den einzelnen Kulturpflanzenarten sind. Bei ergiebiger Nektartracht zeigten sich nur geringe Schwankungen in der Sammelgeschwindigkeit der auf-schnellenden Nektarsammlerinnen und der sowohl Nektar als auch Pollen sammelnden Bienen, aber nach ein paar Tagen mit geringer Nektartracht zeigten die wenigen übriggebliebenen Nektarsammlerinnen einen unrentablen Energieverbrauch. Die « unrentablen » Arbeiterinnen neigten mehr dazu, schon beflogene Blüten wieder zu besuchen, als die wirksam arbei-

tenden Bienen. Erstere wandten auch weniger Zeit auf Entdeckungsflüge an. Es ist anzunehmen, daß die Verschiedenheiten in der Leistungsfähigkeit der Sammelbienen, wenigstens zum Teil, die Verschiedenheiten in der Honigerzeugung bei den verschiedenen Bienenvölkern erklären.

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