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Foraging Range and Distribution of Honey Bees[1] Used for Carrot and Onion Pollination[2]

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ABSTRACT

A magnetic recapture system was used to determine the foraging range and distribution of bees from 389 hives in 29 apiaries (area about 12 km in diameter) to adjacent fields of carrots and onions grown for seed production. Bees from hives around the field perimeters showed intensive, localized foraging activity near their hives (mean flight distance = 266 m). Species diversity requirements were indicated when subpopulations bypassed profitable foraging areas and foraged on different crops at greater distances.

Significant bee populations were attracted from distant apiaries, e.g., 3700 m. The mean flight distance to carrots (1663 m) indicated a greater attraction than for onions to bees from distant apiaries (557 m). The frequencies of pollen foragers were 7 and 66% for onions and carrots, respectively. Nectar sugar concentration was similar (ca 37%) for carrots and onions. Strategies are discussed for enhancing the isolation of nearby fields when interfield pollination is undesirable. Concepts are discussed concerning (a) differential flight range for pollen vs. nectar collectors, and (b) determination of relative plant attraction to honey bees.

Insect pollination is required for commercial production of onion and carrot seeds, and honey bees, *Apis mellifera* L., are used extensively for this purpose. Pollinating effectiveness of honey bees is related to the size of populations that are actively foraging in the crop area. Potential foraging bee populations are determined by controlling the numbers of hives per acre and distributing them in appropriate locations in an effort to achieve uniformity of foraging activity throughout the crop area. Homogeneity of foraging bee distribution is difficult to evaluate because of the many variables in the system, for example the shape and area of fields, pattern of distribution of apiaries, variability of the elements within the crop that attract and reward bees, distribution and abundance of competing flora, and weather factors.

Previous research on the onion-pollinating activities of honey bees has been conducted by van Laere and Gillard (1959), Moffett (1965), Walsh (1965), Lederhouse et al. (1968), Bohart et al. (1970), and Nye et al. (1971). Foraging activities of honey bees on carrots have been studied by Hawthorn et al. (1956), Pankratova (1957, 1958), Carlson (1959), Bohart and Nye (1960), and Hawthorn et al. (1960).

This research was undertaken to study the flight range and distribution of honey bees used for pollinating onions and carrots that are grown commercially for seed production. One unusual aspect of this research is that there were multiple onion and carrot fields within the survey area, thus introducing the element of competition between these 2 crops, in addition to the competition from native plants. It is also noteworthy that this was the 1st large-scale-survey study in which a magnetic recapture system was used to document foraging activities under typical field conditions.

Methods and Materials

This study was conducted in the Sacramento Valley in an area of approximately 8 km diam, the center of which was approximately 4 km north of

[1] Hymenoptera: Apidae.

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Dixon, Calif. A map of the experimental area (Fig. 1) shows the distribution of apiaries and onion and carrot fields. All apiaries were on site at least 1 week prior to the initiation of the survey. Both onions and carrots were in maximum bloom.

Emphasis in the survey was placed on the distribution of bees within Area I (Fig. 1, 2), in which there was a large carrot field (17.4 ha) adjacent to a smaller onion field 1.8 ha). The distribution of foraging bees was determined by using a magnetic recapture system (Gary 1971). Foraging bees were captured in Area I at specific sample plots (20× 20 m) (Fig. 2). Immediately after each bee was captured, it was anesthetized by exposure to CO_2 for 5–15 sec, then identified by gluing a color-coded, ferrous metal disc (diam 2.3 mm, thickness 0.25 mm, weight 11 mg) dorsally in the center of the abdomen. The tagged bees were released immediately at the initial capture locations. They returned to their respective hives. Except for 1 apiary, all hives within potential flight range of Area I were equipped with magnetic traps positioned over the entrances. These traps automatically recaptured the tags by pulling them free from the bees as they entered the hives.

On each day of the 5-day survey, samples of 20 bees were captured and tagged each morning and again each afternoon at the 6 sample plots in the carrot field and 4 plots in the onion field (Fig. 2). Throughout the survey totals of 1200 (data lost from 2 plots, reducing total to 1160) bees from carrot plots and 800 bees from onion plots were tagged and released.

Magnetic traps were installed at Apiaries 1–20 on June 5; traps for the remaining apiaries were not available until June 17, at which time they were installed prior to sampling operations on that day. Consequently, recapture data for Apiaries 22–30 were incomplete for bees tagged June 10, 15, and 16, owing to unknown factors such as frequency of mortality and loss of tags prior to magnetic recapture. Apiary 21 was not equipped with traps. All traps were collected from the hives on June 19 and returned to the laboratory for tag removal and data tabulation.

Observations on the frequencies of bees with and without pollen loads were made when the bees were captured initially. Nectar quality and quantity were evaluated by analyzing the honey stomach contents of foraging bees. The sugar concentration was determined by using a low-range (0–60%) Bausch and Lomb hand refractometer; the volume was estimated. These data were recorded to characterize the reward value of the crops to foraging bees.

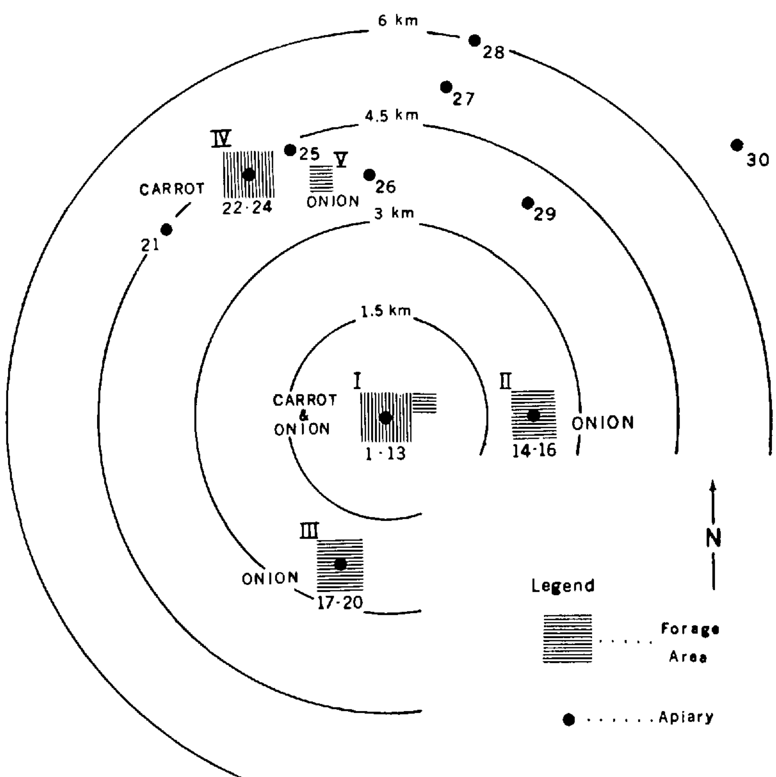

FIG. 1.—Map of apiary and field locations in the experimental area. Apiaries at Areas I–IV were situated around the field peripheries. See Tables 1 and 2 for number of hives in each apiary. Areas (ha) of the respective fields are: I, Carrots ('Red Corded Chantenay') 106; Onions (South Port White Globe) 11: II, Onions (South Port White Globe) 16; III, Onions (South Port White Globe) 16; IV, Carrots (Scarlet Nantes) 49; V, Onions (South Port White Globe) 0.4.

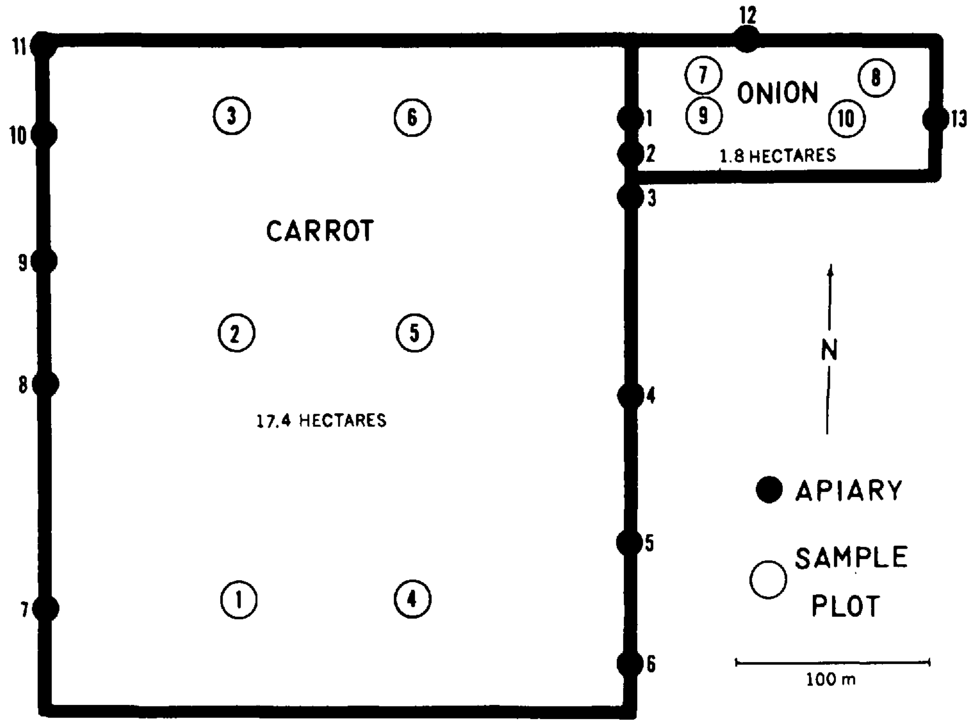

FIG. 2.—Enlarged map of Area I (see Fig. 1). All data are based on recaptured bees that were captured initially at the indicated sample plots at Area I. See Table 1 for numbers of hives in each apiary.

The onion variety in Areas I, II, III, and V was 'South Port White Globe.' In Area I, 4 rows of male-fertile onions were planted alternately with 12 rows of male-sterile inbreds. Rows were spaced 1 m apart.

During the survey, the primary competing flora appeared to be wild morning glory, *Convolvulus arvensis* L., and yellow star thistle, *Centaurea solstitialis* L. Small samples of bees from these species were captured and tagged along the northern perimeter of Area I. Both species were widely and sparsely distributed in the general experimental area.

Owing to ideal weather conditions, bee foraging activities were intensive throughout the experimental period. Temperatures ranged from 19 to 34°C, the sky was generally clear, and variable winds rarely exceeded 12 km/hr.

Results and Discussion

Distribution of Carrot Foragers

Table 1 summarizes data which reveal the distribution of bees from Apiaries 1–13 situated at Area I. A strong tendency to forage near their respective apiaries is evident, i.e., the highest percentage of recaptured tags was recovered from the sample plots nearest the respective apiaries. This was true for 11 of the 13 "local" apiaries; the exceptions were Apiaries 8 and 13. Apiary 8 apparently encountered less competition from Apiary 7 at sample Plot 1, and great competition from Apiary 9 at Plot 2, as indicated by the relative frequency of tag recovery, e.g., 3.3/hive at Apiary 7 and 8.4/hive at Apiary 9. Apparently bees from Apiary 8 responded by developing a foraging pattern biased southerly.

The other exception (Apiary 13), in which the bees did not forage at the nearest carrot plot with greatest frequency, apparently occurred in response to high competition at Plot 6 from Apiaries 1, 2, and 3, as indicated by the numbers of recaptures at those apiaries. Most of the carrot foragers from Apiary 13 apparently were attracted to the area south of Plot 6.

Distribution of Onion Foragers

Foraging bees from the local apiaries (1–13) were distributed similarly in onions, that is, they tended to forage in plots nearest their respective apiaries. For example, 106 recaptures of bees tagged at Plots 7 and 9 were made at Apiaries 1–3, compared with 65 recaptures from Plots 8 and 10. In Apiary 13, 8 bees were recaptured from Plots 7 and 9 compared with 28 recaptures from Plots 8 and 10.

Short Range Distribution at Area I

Data in Table 1 seem to indicate that the short-range distribution of bees from the local apiaries (1–13) at Area I is primarily a function of the competition encountered in a given area, rather than distance per se. The relative localized distribution of bees from any given apiary to either of the crops suggests that (a) colonies compete very effectively within several hundred meters from their hive, thus making the area relatively unattractive to other apiaries, and (b) foraging bees are very sensitive to the areas of less competition and expand foraging activities into these areas. Lee (1961) and Levin (1961) found similar distribution patterns of bees from competing Apiaries. It appears that flight distances of bees from Apiaries 1–13 were primarily a function of the relative locations of sample plots and apiary locations (range 45–695, mean 256 m).

Species Diversity Preference

In Apiaries 1–13 significant populations of bees from any given apiary tended to bypass nearby areas of 1 crop at the time they were foraging on another crop at a greater distance. Yet, the bypassed areas apparently were profitable foraging areas for other colonies from the same apiary, and from other apiaries. For example, 39% of the recaptured foragers originating from Apiary 7 were foraging on carrots in Plots 1 and 2. Yet, all the remaining recaptured foragers (61%) from Apiary 7 were foraging on onions in Sample Plots 7–10, even though Sample Plots 3–6 in carrots were closer to Apiary 7. The same general pattern of bypassing carrots to reach onions was found for Apiaries 7–11. A similar relationship holds for Apiary 13, situated closer to onions than to carrots, in which 35% of the recaptured bees were foraging at carrot plots.

These data seem to document a long-accepted principle that there is such a food diversity requirement within colonies that subpopulations of colonies normally forage on a variety of plant species, if they are available. This kind of foraging behavior might have evolved in response to an increased probability of better nutrition through greater diversity of food sources. If this interpretation is correct, such foraging behavior would seem to be more appropriate for pollen collection than nectar collection, because pollens are much more variable in the quality and quantity of nutrients, compared with nectars that contain primarily sugars.

Distribution of Bees from Distant Apiaries

Most of the recaptured bees from the distant apiaries (14–30) originated from Apiary 26, situated approximately 3700 m north of Area I where all tagging operations were conducted (Fig. 1). Data in Table 2 indicate that foraging bees from the distant apiaries were dispersed uniformly at all sample plots in the carrot field, unlike the localized distribution of bees from hives at Area I. Yet, in the onion plots the foragers from distant apiaries were not uniformly distributed. There is no apparent reason why the long-range foragers were and were not distributed uniformly in the carrot and onion fields, respectively.

Why did a large population of bees from Apiary 26 forage on carrots at Area I (3700 m) when these foragers could have flown a shorter distance (1932 m) to a large field (49 ha) situated at Area IV (Fig. 1)? Since foragers were not tagged at Area IV the comparative distribution of bees from Apiary 26 to Area IV vs. Area I is not known. However, it appears that the competition from Apiaries 22–25 at Area IV was so significantly intense that it became profitable for large populations of bees from Apiary 26 to forage at Area I. This interpretation is reinforced by the observation that only 1 carrot forager from Apiaries 22–25 was recaptured from Area I.

Controlling Pollination by Isolation

In some crops there is an advantage in isolating fields to prevent undesirable transfer of pollen between varieties in different fields. Possible mechanisms of undesirable interfield pollen transfer are

Table 1.—Distribution of foraging bees originating from local apiaries at Area I.[a]

			% recaptured bees foraging at plots[a]									
			Carrot plots						Onion plots			
Apiary	Hives per apiary	Total recaptures	1	2	3	4	5	6	7	8	9	10
1	10	95	1	3	7	0	3	20	33	12	11	11
2	10	73	4	1	3	1	3	16	14	12	29	16
3	10	103	6	10	2	5	7	16	7	9	26	14
4	10	66	9	8	2	8	12	2	12	11	17	21
5	10	64	3	13	2	22	2	0	8	14	20	17
6	10	40	23	10	0	50	8	3	0	3	0	5
7	7	23	35	4	0	0	0	0	17	4	9	30
8	13	39	21	8	0	0	3	0	10	18	23	18
9	10	84	8	21	0	2	1	2	23	17	11	14
10	12	83	4	4	13	1	0	2	15	25	19	17
11	10	78	1	5	15	4	0	5	21	13	10	26
12	2	38	0	0	3	0	3	8	26	26	26	8
13	10	53	4	6	4	4	15	4	2	11	13	38
Totals	124	839	56	63	39	53	35	62	127	115	143	146
% of total recaptures		100	7	8	5	6	4	7	15	14	17	17

[a] See Fig. 2 for apiary and plot locations.

Table 2.—Distribution of foraging bees originating from distant apiaries.[a]

			% recaptured bees foraging at plots[a]									
			Carrot plots						Onion plots			
Apiary	Hives per apiary	Total recaptures	1	2	3	4	5	6	7	8	9	10
14	14	32	3	9	28	13	25	19	0	0	0	3
15	12	5	40	20	20	20	0	0	0	0	0	0
16	15	16	6	38	6	19	31	0	0	0	0	0
17	7	1	100	0	0	0	0	0	0	0	0	0
18	5	1	0	0	0	0	0	100	0	0	0	0
19	6	6	17	33	0	17	0	33	0	0	0	0
20	6	5	0	0	40	40	0	20	0	0	0	0
21	50[b]	—	—	—	—	—	—	—	—	—	—	—
22	19	1	100	0	0	0	0	0	0	0	0	0
23	15	2	0	0	0	0	0	0	0	50	50	0
24	17	0	0	0	0	0	0	0	0	0	0	0
25	44	0	0	0	0	0	0	0	0	0	0	0
26	30	168	13	11	14	13	12	14	7	11	3	3
27	30	16	19	13	13	19	19	0	0	13	0	6
28	8	6	50	0	33	0	0	17	0	0	0	0
29	17[c]	40	18	20	15	15	10	13	8	0	0	3
30	20	1	100	0	0	0	0	0	0	0	0	0
Totals	315	300	42	41	47	41	40	40	14	21	6	8
% of total recaptures		101[d]	14	14	16	14	13	13	5	7	2	3

[a] See Fig. 1 and 2 for apiary and plot locations.
[b] Nucleus colonies (200 containing 5 standard Langstroth frames each) for queen mating, equivalent to approximately 50 standard hives. These hives did not have magnetic traps.
[c] Only 17 of 33 hives at apiary had magnetic traps.
[d] Total is not exactly 100%, because of rounding.

(a) transfer by individual bees that may forage at both areas on the same foraging trip, and (b) intrahive transfer of pollen between bees that are foraging at both locations. Both mechanisms could be controlled if the foraging activities of apiaries could be restricted to the respective fields where they were situated. Isolation by restricted foraging was observed during the present survey; the recapture data taken at Area I indicated that Apiaries 14–20, situated at Areas II and III, were effectively isolated from the onions at Area I, even though bees from Areas II and III foraged at Area I on carrots (Fig. 1). All except 1 of the 67 bees recaptured at Apiaries 14–20 were foraging on carrots in Sample Plots 1–6 (Table 2). Apparently the population of bees inclined to forage on onions were attracted to the nearest onion fields at Areas II or III. The onion field at Area I was certainly within the potential flight range of Apiaries 14–20, as documented by the attraction of significant bee populations from more distant apiaries, e.g., 21 and 29 (Fig. 1), to the onions at Area I.

These data suggest that more effective isolation of nearby fields containing similar varieties of the same crop may be achieved by placing sufficient hives at each location to provide foraging populations that are adequate to collect all available nectar and pollen. If the respective fields can be saturated in terms of bee populations the food reward value would be reduced until it becomes unprofitable for the foragers from hives distant from the field to fly to an identical field at a significantly greater distance.

Relative Attraction of Carrots and Onions

A comparison of the relative attraction of carrots and onions is based on the following assumptions: (a) the disparity in size of the onion and carrot fields at Area I did not influence the relative attractiveness of these crops to bees, especially those originating from distant apiaries, (b) attraction per se is not necessarily correlated with food quantity or the populations of foragers per unit area, and (c) relative attraction is primarily a function of the distance from the hive that bees are attracted to a food source. Attraction, as affected by food reward or profitability of food sources, has been investigated by Beutler (1950), Boch (1956) and others and is reviewed by von Frisch (1967).

If carrots and onions were equally attractive, the ratio of recaptured bees foraging on carrots and onions should equal the ratio of foragers tagged on these 2 crops, viz., a carrot:onion ratio of 29:20 (30:20 before correcting for lost data). However, 23.2% of the recaptured bees at Apiary 26 were foraging on onions, instead of the expected 40.8% ($P<0.001$), based on an adjusted $\chi^2 = 47.74$ using Yates' correction for continuity (Alder and Roessler 1964). Similar evidence that carrots are more attractive was found in the recapture data at Apiaries 27 and 29 were 23% (N = 16) and 10% (N = 40) onion foragers were recaptured, respectively. Additional supporting evidence was found in the percentage recapture of onion foragers that originated from the local Apiaries (1–13) at Area I. The carrot:onion recapture ratio was 308:531, i.e., significantly more bees from the Apiaries 1–13 were

Table 3.—Recapture frequency of bees released at Area I.[a]

Sample plot	Tagged bees released (total)	Recaptured bees from Apiaries 1–30 (total)	% of recaptured bees from Apiaries 1–13 at Area I
	Carrots		
1	200	98	57.1
2	180[b]	104	60.6
3	200	86	45.3
4	200	94	56.4
5	180[b]	75	46.7
6	200	102	60.8
Total		559	
Mean			55.1
	Onions		
7	200	141	90.1
8	200	136	84.6
9	200	149	96.0
10	200	154	94.8
Total		580	
Mean			91.6
	Yellow star thistle		
11	40	25	76.0
12	40	34	97.1
Total		59	
Mean			88.1
	Wild morning glory		
13	40	20	70.0
14	20	6	67.0
15	20	11	81.8
Total		37	
Mean			73.0

[a] See Fig. 1 and 2 for apiary and sample plot locations.
[b] Lost data for 1 sample.

foraging on onions, viz., 63.2% compared with the expected 40.8% ($P<0.001$). Superficially, these data apparently indicate that the onions were more attractive to the local apiaries placed near the fields for pollination. However, the data actually seem to indicate that carrots are more attractive because more bees were attracted from distant apiaries (Table 5), thus greatly reducing the percent of carrot foragers that originated from the local apiaries.

Data on yellow star thistle and wild morning glory are included to provide an indication of the relative attraction of these competing species with onions and carrots (Table 3). By using the percentage of recaptured bees originating from the Apiaries 1–13 at Area I as an index of attractiveness, the rank of relative attraction, from high to low, is carrots (55.1%), wild morning glory (73.0%), yellow star thistle (88.1%), and onions (91.6%). This ranking is based on the assumption that relative attraction is inversely proportional to the percent of foragers that originated in the local Apiaries (1–13).

Perhaps the greatest significance of these data on relative attraction is to emphasize that interpretation of data on the density and distribution of bee populations in a given area should account for the many variables in the broad, overall foraging area (within a radius of approximately 6 km from the areas and apiaries that are being investigated critically).

Comparative Flight Range of Pollen vs. Nectar Foragers

Evidence gathered in this study seems to indicate the desirability of segregating pollen foragers and nectar foragers into independent populations when foraging-distribution and flight-range studies are made. This segregation is frequently not possible, because bees collect pollen and nectar simultaneously on many species. The primary reasons for segregating these populations is that there are significant differences in pollen vs. nectar when considered in the context of the profitability concept (von Frisch 1967). Generally, this concept holds that foraging bees tend to frequent the most profitable food source, as determined by (a) the inherent stimulus or reward value (quality and quantity) of the food to the colony, and (b) by the various for-

Table 4.—Nectar and pollen collection at Area I.

Date	Sampling time	Nectar (% sugar)[a] Mean	Nectar Range	Pollen[b] n	Pollen % of bees with loads
		Onions			
6/10	AM	37.3	34.0–39.5	80	6.3
	PM	40.4	34.0–43.5	80	11.3
6/15	AM	36.6	31.5–41.0	80	11.3
	PM	37.9	26.0–43.5	80	15.0
6/16	AM	35.3	32.5–40.0	80	1.3
	PM	33.0	28.0–37.0	80	6.3
6/17	AM	38.0	30.5–41.5	80	3.8
	PM	37.0	32.0–41.5	80	11.3
6/18	AM	39.0	26.5–51.5	80	1.3
	PM	42.6	38.0–47.5	80	6.3
Means		37.7	31.3–42.7		7.4
		Carrots			
6/10	AM	55.0	42.5–60.0	120	62.5
	PM	36.3	18.5–42.5	120	52.5
6/15	AM	31.6	17.5–43.0	120	78.3
	PM	43.6	36.0–48.5	120	72.5
6/16	AM	34.9	31.0–43.0	120	81.7
	PM	43.2	21.5–51.0	120	59.2
6/17	AM	42.0	32.5–56.0	120	86.7
	PM	43.2	36.5–54.0	120	53.3
6/18	AM	34.5	22.0–59.5	120	60.0
	PM	44.1	30.5–51.0	120	49.2
Means		39.3	28.9–50.9		65.6
		Yellow star thistle[c]			
6/15	PM	32.7	27.5–41.5	—	—
6/16	PM	28.9	22.0–35.5	20	45.0
6/17	PM	27.9	19.0–40.5	20	50.0
6/18	PM	28.2	24.0–32.0	20	60.0
Means		29.4	23.1–37.3		
		Wild morning glory[c]			
6/15	AM	48.8	44.5–61.0	—	—
6/16	PM	37.6	13.5–51.0	—	—
6/17	PM	48.6	27.5–56.0	20	0
6/18	AM	49.2	45.5–54.0	20	0
Means		45.9	32.8–55.5		

[a] Based on samples containing 10 bees.
[b] Based on the bee samples that were tagged at sample plots.
[c] Samples taken around northern perimeter of Area I.

aging deterrents, e.g., distance, that collectively involve energy expenditures required during the collection and transport of food.

In the present study, the best indicator of pollen-foraging reward value or profitability is the frequency of pollen foragers in the samples of tagged bees. Data in Table 4 indicate that approximately 66% of the bees foraging on carrots had pollen loads, compared with approximately 7% of the onion foragers. The highest frequency of pollen collectors occurred during the morning for carrots and during the afternoon for onions (Table 4).

The nectar reward value was estimated by determining the volume and sugar concentration of nectar loads carried by samples of foraging bees (not the samples that were tagged). Onions and carrots appeared to be equal in reward value in terms of sugar concentration. The mean sugar concentration in nectar samples from bees foraging on onions and carrots was 38 and 39%, respectively (Table 4). The nectar-load volume, estimated as small, medium, or large when the samples were being analyzed for sugar, was consistently higher in the bees foraging on onions. Many bees foraging on carrots had insufficient nectar load volume to permit sugar analysis by the method that was used.

Apparently the bees foraging at Area I were rewarded primarily by pollen from carrots and nectar from onions. Furthermore, it seems significant that the flight range of bees to carrots greatly exceeded the range to onions (Table 5). The correlation of long flight distance to the primary pollen source in this study, coupled with other empirical evidence of long flight ranges to other high-yielding pollen plants (e.g. safflower, *Carthamus tinctorius* L.), leads us to suggest that the distances bees are attracted to pollen sources are potentially greater than the distances bees are attracted to nectar sources, especially in the range exceeding approximately 3 km. This hypothesis is supported by the following considerations which seem to be consistent with the profitability concept. First, pollen probably requires less energy to transport to the hive than nectar, which is heavier because it contains much water. The average weight of pollen loads is 15 mg (Parker 1926). Maurizio (1953) reported that pollen loads ranged from 8.4 to 22 mg, based on 35 different species. The average nectar load is 40 mg (Park 1929). Furthermore, there are data, e.g., Park (1929), indicating that pollen loads can be collected in much less time than nectar loads. Another consideration is that pollen is more valuable on a weight basis to the colony, compared with nectar. The value of pollen at any given time to a colony is also greater because colonies do not store large reserves of pollen, compared with honey. This feature necessitates constant replenishment on a short time scale, which functions to compensate for the high turn-over rate of pollen.

If further research supports the hypothesis that bees usually fly farther to collect pollen, this could affect the strategies in distributing hives for pollinating purposes. Another implication is that more effective strategies for protecting bees from pesticide application could be developed by determining the relative attraction of pollen sources, then increasing the distance between apiaries and treated crops that are shown to produce highly attractive pollen.

Table 5.—Distances flown by bees foraging at Area I and originating from apiaries 1–30.

Crop	No. of sample plots	Total recaptures	Distance (m)[a]	
			Range	Mean
Carrots	6	559	121–6117	1663
Onions	4	580	41–4346	557
Yellow star thistle	2	59	62–4346	705
Wild morning glory	3	37	27–4346	1186

[a] Relative distances are more significant than absolute distances, because apiary and plot locations greatly influence the absolute values.

Frequency of Foraging Activity on "Target" Crops

Growers who rent bees for pollination want the bees to forage on the intended crop (target crop), instead of neighboring farms or other competing plants. In this study, the magnetic retrieval system permitted an assessment of bee distribution in this context. Table 3 summarizes the percent of bees that originated from the rented, local hives (Apiaries 1–13). The percentage distribution is relatively stable, when comparing plots within the same crop. The percent of recaptured bees from Apiaries 1–13 that were foraging on onions is much higher than the percent of bees foraging on carrots, again indicating that onions attracted fewer bees from distant apiaries.

The recapture frequency of bees originating from nearby hives promises to be a very useful statistic in detecting and evaluating genetic effects on the preference of bees for various plant species, as well as assessing various colony treatments intended to influence foraging behavior.

The magnetic recapture system, used on a large scale for the 1st time in this project, was found to be very effective for this type of study. The primary problem in field surveys is capturing and labeling adequate samples of bees at multiple sample plots in widely dispersed locations on a time scale that minimizes temporally associated variables in the dynamic foraging system.

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Influence of Sex Pheromones on Mating Behavior and Populations of Virginia Pine Sawfly[1,2]

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ABSTRACT

Rise and decline in populations of *Neodiprion pratti* (Dyar) have been attributed most frequently to the influence of natural control factors. However, data obtained from 1963 through 1970 indicate that population densities are due to the sex attractiveness of the female sawfly. It was shown that the female emits a potent sex pheromone which was apparently necessary for mating. Unmated females oviposited only 17% of their egg potential, whereas mated females oviposited more than 90% of their total egg complement. Severe tree defoliation occurred when more than 50% of the females mated.

The Virginia pine sawfly, *Neodiprion pratti* (Dyar), was first observed causing noticeable defoliation in pine forest of northern Virginia in 1955, and in central and southern areas of the State in 1957. However, the species had probably persisted at very low population levels for many years previous since Hetrick (1956) collected specimens in the same area about 1940. The sawfly population increased very rapidly into outbreak numbers, and by 1959 defoliation in pine forests was evident over an estimated 3 million acres in Virginia. The outbreak began to subside in 1961, and only persistent reservoir populations were present each year until 1967 when populations again began to increase.

Rise and decline in sawfly populations have been attributed most frequently to the influence of natural control factors. Coyne (1959), however, stated that natural control factors have not been effective in preventing all outbreaks; and Middleton (1922) expressed the opinion that some factor other than parasitism played an important role in the decline of sawfly populations. Morris et al. (1963) presented data to show that some factor, other than natural control agents, contributed to the decline of a sawfly population. I attributed the rapid population decline of *N. pratti* in Virginia to loss of sex attractiveness by the female (Bobb 1964). It had previously been shown that virgin females of sev-

[1] Hymenoptera: Diprionidae.

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