TEMPORAL AND SPATIAL VARIATION IN THE FORAGING BEHAVIOR OF HONEY BEES (HYMENOPTERA: APIDAE) AT CHINESE VIOLETS

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ABSTRACT

This study describes temporal and spatial variation in the foraging behavior of honey bees, *Apis mellifera* L., at the Chinese violet, *Asystasia gangetica* (L.) T. Anderson, in Hawaii. Workers made 3 types of visits: "out" (O-) visits involving nectar robbing through corollar slits made by carpenter bees (*Xylocopa sonorina* (Smith), "in-upright" (IR-) visits involving upright entry along the base of the corolla, and "in-upside down" (ID-) visits involving spiral, upside-down entry along the top of the corolla. In general, individual workers displayed only 1 tactic over 10 successive flower visits and over successive days. Nectar-robbing workers visited more flowers per min but spent less time per flower than workers making IR- or ID-visits. Bees making O- or IR-visits carried similar nectar loads but only very small amounts of pollen, whereas the reverse was true for bees making ID-visits. O- and IR-visits were made throughout the day, but ID-visits were observed only in the morning. Based on inter-site comparisons, the incidence of nectar robbing was influenced by the local density of carpenter bees which made the perforations used by nectar robbing honey bee workers.

Key Words: *Apis mellifera*, nectar robbing, pollination, Hawaii

RESUMEN

Este estudio describe la variación temporal y espacial del comportamiento forrajero de la abeja de miel, *Apis mellifera* L., en la violeta china, *Asystasia gangetica* (L.) T. Anderson, en Hawaii. Las obreras hicieron 3 tipos de visitas: Las visitas "por fuera" (F-) incluyeron el robo de néctar a través de las incisiones hechas previamente a la corola por las abejas carpinteras, *Xylocopa sonorina* (Smith), las visistas "dentro-por arriba" (DA-) incluyeron entradas por encima de la flor, a lo largo de la base de la corola, y las visitas "dentro-volteadas" (DV-) incluyeron entradas en espirtal, volteadas a lo largo del extremo de la corola. En general, las obreras individuales desarrollaron una sola táctica cada 10 visitas sucesivas a las flores, en 10 días sucesivos. Las obreras ladronas de néctar visitaron más flores por minuto pero pasaron menos tiempo por flor que las obreras que efectuaban visitas de los tipos DA- y DV-. Las abejas haciendo visitas de los tipos F- y DA- llevaron cargas de néctar similares pero sólo pequeñas cantidades de polen, mientras que lo inverso ocurrió en abejas haciendo visitas DV-. Las visitas F- y DA- fueron hechas a lo largo de todo el día, pero las visitas DV- fueron observadas solamente en la mañana. Basada en comparaciones inter-sitios, la incidencia del robo de néctar fue influenciada por la densidad local de las abejas carpinteras, las cuales hacen las perforaciones usadas por las obreras ladronas de la abeja de miel.

Research on the foraging biology of the honey bee, *Apis mellifera* L., has focused primarily on colony performance, and comparatively little attention has been given to

the food-collecting behavior of individual workers (Schmid-Hempel 1991). Available data reveal that workers visiting the same plant species typically specialize on either nectar or pollen collection. In some instances, this distinction is absolute, and individual workers gather either nectar or pollen exclusively (McGregor et al. 1959; Free 1960a,b). Often, however, workers may collect both nectar and pollen, although they may concentrate primarily on one of these resources. For example, among honey bees visiting native cotton, *Gossypium thurberi*, 40% collected pollen only and 60% concentrated on nectar collection but gathered pollen passively as well (Buchmann & Shipman 1990; see also Fell 1986; Weaver 1956).

Nectar foragers may also display variable foraging modes, either obtaining nectar "legitimately" (thereby serving as pollinators) or via nectar theft or robbing (thus avoiding contact with pollen-bearing anthers, sensu Inouye 1980). Though reports of nectar theft and robbing are common for honey bees (Burrill 1925; Hawkins 1961; Helms 1970; Benedek et al. 1973; Barrows 1980), to our knowledge only 1 study presented information on worker specialization regarding legitimate vs. illegitimate nectar collection. In observing honey bees visit hairy vetch (*Vicia villosa* Roth.), Weaver (1956) found that workers reached the nectary by either entering the flower or inserting their tongue through the petals at the base of the corolla. Observations of individual workers over 2-10 consecutive floral visits revealed a high degree of specialization for 1 tactic or the other, and only 10 of the 300 individuals observed used a mixture of foraging tactics.

The present study describes temporal and spatial variation in the foraging behavior of honey bees at the Chinese violet, *Asystasia gangetica* (L.) T. Anderson (Acanthaceae), in Hawaii. Earlier observations (Barrows 1980; Gerling 1982) recorded *Xylocopa sonorina* (Smith) as a primary nectar robber (actually perforating flowers) and *A. mellifera* as a secondary nectar robber (using existing perforations) of this plant species (sensu Inouye 1980). Here, we describe diurnal variation in the incidence of 3 types of floral visits—2 involving corollar entry and 1 involving nectar robbing—and compare body sizes, nectar and pollen loads, rates of floral visitation, and floral handling times among honey bee workers displaying the different foraging tactics. Workers were also individually marked to assess between-day consistency in foraging behavior. Finally, we compared the incidence of nectar robbing at several sites differing in honey bee, carpenter bee, and floral densities.

Materials and Methods

Study Site and Species

A. gangetica, a procumbent or scandent perennial herb, was introduced to Hawaii around 1925 and is now widespread in disturbed lowland areas (Wagner et al. 1990). Flowers are pentamerous, zygomorphic, and vary in color from pale blue to purple (or less commonly, white or yellowish). Corollas vary from approximately 25-35 mm in length (Barrows 1980). Both *A. mellifera* and *X. sonorina* were introduced to Hawaii in the late 1800s (Lieftinck 1956; Barrows 1980).

Most of the field work was conducted during May-June 1993 in a small untended lot (100 m^2) on the campus of Chaminade University, Honolulu, Hawaii. All observations were made under sunny or only slightly overcast skies, and air temperatures ranged between 25-31°C at 15 cm above ground. *A. gangetica* was the most abundant flower within the study area. Patches of *A. gangetica* covered approximately 1/2 the lot, and the rest of the area was covered by various grasses or bare rock surfaces. *A. mellifera* and *X. sonorina* were the only species of bees observed at the study site.

Censuses of Foraging Bees

We recorded the numbers of bees foraging in 4 quadrats located within representative patches of *A. gangetica* during morning (0800-1000 hours) and afternoon (1400-1600 hours) periods on 6 d. Each 1 m^2 quadrat was separated by a minimum of 3 m. On a given census day, 2-3 counts were made during the morning and afternoon study periods, respectively, and successive counts were separated by a minimum of 25 min. Also, on each census day we recorded flower abundance in the 4 quadrats and collected 100 flowers haphazardly from the study site at 1000 hours and examined them in the laboratory for corollar slits or perforations.

As described below, nearly all the honey bees that were observed displayed only 1 type of foraging tactic. Thus, in addition to the estimates of absolute density provided by the quadrat censuses, we recorded the relative density of the different types of foragers by walking a 10 m transect through the study area and noting the behavior (based on a single floral visit) of all honey bees within 1 m of the line. Three surveys were made during morning and afternoon periods, respectively, on 5 d, and successive surveys were separated by at least 30 min.

Behavioral Observations

The type of foraging behavior displayed by individual honey bees was noted during observations of consecutive floral visits. Initially, we included only data for bees observed to visit 25 or more flowers. However, because of the invariant nature of foraging behavior, additional observations were limited to 10 consecutive floral visits per individual honey bee. Morning (0800-1000 hours) and afternoon (1400-1600 hours) observations of foraging behavior were made on 10 d, and during any given morning or afternoon we observed only 10-15 sequences of floral visits to reduce the likelihood of observing the same individual more than once. Also, we attempted to select focal bees randomly by initiating observations on individuals in flight (i.e., whose foraging tactic was unknown to us). Though emphasis was on honey bees, behavioral observations were also made for carpenter bees (2-6 sequences of floral visits were observed during a given morning or afternoon period on 5 d).

Three types of floral visits were distinguished: "out" (O) visits during which bees did not enter the corolla but probed the base of the corolla from the outside (i.e., nectar robbing), "in-upright" (IR) visits during which bees landed on the lower petals and entered the corolla in an upright position, and "in-upside down" (ID) visits during which bees landed on the lower petals in an upright position but then entered the flower while making a spiral path to the top of the corolla, thus assuming an upside-down position. [Perforations were absent on previously bagged flowers visited exclusively by honey bees, and we conclude (as did Barrows 1980) that honey bees used existing slits and did not perforate flowers themselves.] For approximately 1/2 the bees observed, we also recorded the duration of each floral visit (to the nearest 0.1 s with a stopwatch), the total duration of the observations to obtain rates of flower visitation. Also, for bees making either type of in-visit we recorded the number of flowers they approached (operationally defined as 1-3 s hovering immediately in front of a flower) but did not land on and the number of flowers they landed on but did not enter.

Measurement of Nectar and Pollen Loads

Nectar and pollen loads were estimated for a sample of honey bees observed displaying each of the different foraging tactics. Bees were observed over 10 consecutive

floral visits between 0800-1000 hours over 3 consecutive mornings, captured with an aerial net, and immediately transported to the laboratory for dissection. Nectar in the crop was drawn into a 10 ul glass capillary tube. Pollen was scraped off the hindlegs using a dissecting pin, dried at 45°C for 24 h, and weighed to the nearest 0.1 mg on a Mettler AE163 balance. Because the display of nectar robbing may be related to bee size (e.g., Barrow & Pickard 1984), we also measured forewings of these bees (specifically, the length of the medial cross vein) to the nearest 0.1 mm using a dissecting microscope equipped with a disc micrometer.

Between-day Consistency in Individual Behavior

To determine whether individual workers displayed the same foraging tactic over successive days, we uniquely marked individuals with different color combinations of enamel paint on their thorax. Bees were observed for 10 floral visits, captured with an aerial net, and cooled in an ice chest for marking. Following marking, bees were placed in full sunlight, and after 1-2 min of warming the bees took flight and often resumed foraging activity. A total of 70 bees (approximately equal numbers of O-, IR-, and ID-foragers) was marked between 0830-1100 hours in a single morning, and over the next 7 d we monitored the site between 0900-1000 hours and observed the foraging behavior of marked individuals for 10 consecutive floral visits. Additionally, we checked for within-day consistency in behavior by observing marked workers between 1400-1500 hours on the first 2 d following marking.

Inter-site Variation in Foraging Behavior

Honey bee foraging tactics were monitored concurrently at 3 other locations, all of which were infrequently mowed lawns within 5 km of the main study site. *A. gangetica* was the dominant flowering plant at each of these additional sites, and honey bees and carpenter bees were the only floral visitors observed.

Following the above protocol, we recorded bee abundance in 4 quadrats (each 1 m^2) at each of these sites. At a given site, 3 censuses were made between 0800-1000 hours on 4-5 d. In addition, we walked a transect line (10-15 m) at each site and recorded the number of honey bees making 0-, IR-, and ID-visits. At a given site, 4-6 transects were made during a given morning over 4-5 d. We also made 1 count of flowers in the quadrats per census day collected 100 flowers at 1000 hours and examined them in the laboratory for corollar slits or perforations.

Results

Bee and Flower Abundance

Both carpenter bees and honey bees were more abundant in the morning than in the afternoon. Over a total of 60 censuses made in the 4 quadrats at the Chaminade site, the density of carpenter bees averaged 0.33 per m^2 in the morning (SE=0.07; range:0-2) but only 0.08 per m^2 in the afternoon (SE=0.04; range: 0-2). Similarly, the average density of honey bees was 2.08 per m^2 in the morning (SE=0.14; range: 0-5) compared to 1.15 per m^2 in the afternoon. The mean density of *A. gangetica* flowers was 31.2 per m^2 (SE=2.2; range=23-37; n=6 d $\times$ 4 plots=24 censuses). Flower density was relatively constant over the study period and did not differ significantly over the different census days (χ^2=3.9; $P > 0.05$; Kruskal-Wallis test with χ^2 approximation).

Foraging Behavior of Carpenter Bees

Carpenter bees made O-visits exclusively (n=21 and 10 sequences of 10 floral visits for morning and afternoon periods, respectively). Individuals typically approached a flower frontally, landed on the petals, and then walked over the flower to the base of the corolla. Carpenter bees moved rapidly between flowers, spending little time at each. Averaged over all timed observations, carpenter bees visited 16 flowers per min (SE=0.9; range: 12-24) and spent 1.5 s at each flower (SE=0.1; range=0.3-3.4; n=150).

Temporal Variation in Honey Bee Foraging Tactics

During almost all of the floral visitation sequences observed (215/224=96%), individual honey bees made only 1 type of floral visit. However, the incidence of the different types of foragers varied through the day. In the morning, we observed approximately equal numbers of O-foragers (n=60) and I-foragers (I=IR and ID combined; n=57), but in the afternoon nearly 2/3 (59/98) of the bees observed made O-visits. Even more striking, IR- and ID-foragers were equally common during the morning (29 and 28 observations, respectively), but all I-foragers observed in the afternoon were making IR-visits exclusively. The few bees (n=9) that displayed mixed foraging tactics were all observed in the morning and were making a combination of IR- and ID-visits.

Data from the transects showed the same temporal pattern in foraging behavior. On average, we noted 20 honey bees per morning transect (SE=0.9; range: 16-25; n=15) of which 11 (55%), 5 (25%), and 4 (20%) were making O-, IR-, and ID-visits, respectively. Consistent with the census data from the quadrats, fewer honey bees were present in the afternoon transects ($\bar{x}$=12; SE=0.7; range: 6-19; n=15). Of these, an average of 8 individuals (67%) were making O-visits, and 4 individuals were making IR-visits. No honey bees were seen to make ID-visits during any afternoon transect.

Behavioral Differences Among Honey Bee Foraging Tactics

Rates of floral visitation differed significantly among the different foraging modes (H=54.1; $P < 0.001$; Kruskal-Wallis test; no significant difference was found between morning and afternoon visitation rates for bees making O- or IR-visits, and data for each of these tactics were pooled over the 2 periods; Table 1). Floral visits per min were similar between bees making IR- and ID-visits ($P > 0.05$), but these rates were significantly lower than that observed for O-foragers ($P < 0.05$ for both tests; Dunn's rank sum multiple-comparison test following Daniel 1990). Though IR- and ID-foragers had similar floral entry rates, bees making IR-visits both landed on a higher proportion of flowers (after approaching) and entered a higher proportion of flowers (after landing) than bees making ID-visits (U=558 and 660, respectively; $P < 0.001$ in both cases; Mann-Whitney test; Table 1).

Bees utilizing different foraging tactics also exhibited different handling times at individual flowers (H=50.1; $P < 0.001$; Kruskal-Wallis test; handling times did not differ between morning and afternoon for bees making O- or IR-visits, and data for each of these tactics were pooled over the 2 periods; Table 1). Handling times were similar between bees making IR-and ID-visits ($P < 0.05$), but these individuals spent nearly twice as much time at a given flower as O-foragers ($P < 0.05$ in both cases; Dunn's rank sum multiple comparison test following Daniel 1990).

Nectar and Pollen Loads

Both nectar (H=7.0) and pollen (H=24.1) loads varied with foraging tactic ($P < 0.05$ in both cases; Kruskal-Wallis test; Table 1). Bees making O-visits had significantly

TABLE 1. COMPARISONS AMONG BEES MAKING O-, IR-, OR ID-VISITS, RESPECTIVELY. AVERAGE VALUES (SE) ARE PRESENTED. SAMPLE SIZES FOR BEHAVIORAL DATA WERE: O-54, IR-36, AND ID-15 INDIVIDUAL BEES OBSERVED OVER 10 CONSECUTIVE FLORAL VISITS. FOR NECTAR AND POLLEN LOADS AND WING LENGTH, 15 BEES FROM EACH FORAGING TACTIC WERE EXAMINED.

	Foraging Tactic		
	O	IR	ID
Flowers/Min	10.1 (0.7)	6.9 (0.4)	5.9 (0.4)
% Landings		95 (1.6)	73 (3.9)
% Entries		83 (1.5)	58 (3.5)
Time/Flower (s)	4.3 (0.2)	7.6 (0.4)	7.5 (0.5)
Medial Cross Vein (mm)	1.31 (0.01)	1.29 (0.02)	1.31 (0.01)
Nectar Load (ul)	9.7 (1.6)	7.8 (1.3)	3.3 (0.6)
Pollen Load (mg)	0.0 (0)	1.1 (0.5)	5.1 (0.7)

larger nectar loads than either IR- or ID-foragers, and IR-foragers, in turn, carried more nectar than ID-foragers ($P < 0.05$ in all cases; Dunn's rank sum multiple-comparison test following Daniel 1990). Approximately 1/2 of the O- and IR-foragers had at least 8 ul of nectar, whereas none of the ID-foragers carried more than 5 ul. Conversely, ID-foragers had significantly larger pollen loads than O- or IR-foragers ($P < 0.05$ in both cases; Dunn's rank sum multiple-comparison test following Daniel 1990; Table 1). All ID-foragers had pollen loads exceeding 1 mg (dry weight), whereas none of the O-foragers and only 27% (4/15) of the IR-foragers carried measurable amounts of pollen.

Bees displaying different foraging tactics did not differ significantly in body size ($H=0.9$; $P > 0.05$; Kruskal-Wallis test; Table 1). Also, body size was unrelated to the volume of nectar loads ($r_s=0.21$; data pooled over O- and IR-foragers) or to the dry weight of pollen loads ($r_s=0.11$; ID-foragers only; $P > 0.05$ in both cases; Spearman's rank correlation).

Between-Day Consistency in Individual Behavior

Nearly all of the re-sighted individuals displayed a single foraging tactic across days. Of the 70 bees marked, 22 were seen on 1 or more mornings after marking ($\bar{x}=4.3$ d; range=2-6); re-sighting probabilities were similar among the 3 foraging types (29%, 35%, and 34% for O-, IR-, and ID-foragers, respectively). Of the 22 re-sighted bees, only 2 (2/22=9%) were seen displaying 2 different foraging modes. In the first case, the worker made ID-visits for 2 d and then O-visits over the next 4 d, and in the second, the worker made IR-visits on 3 d and then O-visits on 2 d. Over the 2 d when we made morning and afternoon observations, a total of 11 different individuals (all O- or IR-foragers) was seen during both periods of the same day, and all displayed the same foraging behavior at the 2 times.

Inter-site Variation in Foraging Behavior

The relative occurrence of the different foraging tactics varied considerably among the 4 sites (Fig. 1). Most notably, O-visits represented over 50% of all visits at the Wilson

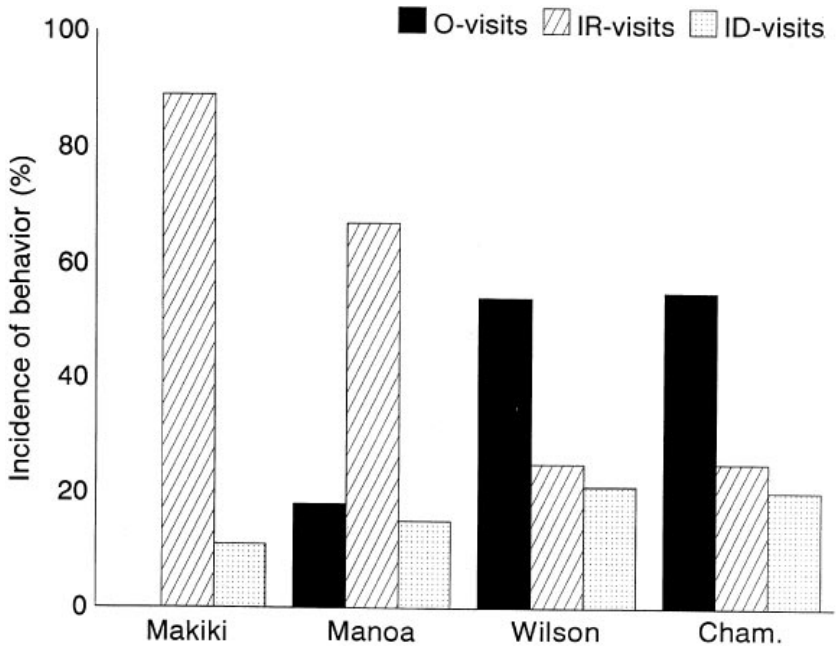

Fig. 1. Average frequencies of the different foraging tactics at the 4 study sites. Average numbers (SE) of honey bees per transect (n=15-21) were: Makiki 12.0 (0.6); Manoa 12.2 (0.4); Wilson 26.4 (1.1); Chaminade 20.0 (0.9).

and Chaminade sites but were relatively rare at Manoa and completely absent at Makiki. Conversely, IR-visits were much more common at Makiki and Manoa than Wilson or Chaminade. The incidence of ID-visits varied only between 11%-21% among the sites.

Though only a few sites were monitored, the incidence of O-visits appeared to be correlated with the abundance of carpenter bees and consequently the frequency of perforated flowers (Table 2). At Makiki, where O-visits were absent, carpenter bees were never recorded from the quadrats, and less than 10% of the flowers had holes or slits. In contrast, carpenter bees and perforated flowers were most common at Wilson and Chaminade, where high proportions of honey bees made O-visits. The density of honey bees was also higher at these latter sites, but since only carpenter bees (and not honey bees) perforated flowers it seems unlikely that the occurrence of O-visits was directly related to the abundance of conspecific foragers (Table 2). Flower density also seemed unimportant as the Makiki site had a flower density nearly 50% higher than the Chaminade site (Table 2).

Discussion

As commonly reported for honey bees (Seeley 1985; Winston 1987), workers at our study sites showed specialization for nectar vs. pollen collection. IR- and ID-foragers gathered both resources, but the former concentrated on nectar and the latter on pollen; workers making O-visits collected nectar exclusively. Also, with respect to nectar harvesting, workers either collected it legitimately (IR- and ID-visits) or via robbing

TABLE 2. BEE AND FLOWER DENSITY AND FREQUENCY OF PERFORATED FLOWERS AT THE 4 STUDY SITES. AVERAGE VALUES (SE) ARE PROVIDED. SEE TEXT FOR SAMPLING METHODS.

Site	Number/m^2			Perforated Flowers (%)
	A. mell.	*X. son.*	*A. gan.*	
Makiki	0.8 (0.1)	0.0	42 (2.2)	8 (1.2)
Manoa	0.6 (0.1)	0.1 (0.05)	25 (1.9)	65 (3.0)
Wilson	2.6 (0.2)	0.4 (0.2)	56 (2.9)	86 (3.8)
Chaminade	2.1 (0.1)	0.3 (0.1)	31 (2.2)	89 (2.2)

through corollar slits made by carpenter bees (O-visits). Consistency in nectar-collecting tactics was evident both within individual trips (see also Weaver 1956) and between trips on the same day or on different days (see Higashi et al. 1988 for similar data on bumble bees).

Nectar robbing appeared to be an opportunistic strategy whose incidence was correlated with the abundance of carpenter bees and corollar perforations. However, it is not known why particular individuals specialized on 1 tactic over another. In the bumble bee *B. pratorum* L., smaller workers were nectar robbers exclusively, whereas larger workers both robbed nectar and collected pollen (Barrow & Pickard 1984; see also Brian 1952). In our study, however, foraging behavior was unrelated to worker size. It also seems unlikely that worker age was important as other studies (Ribbands 1952; Free 1963) found no consistent age-related pattern in honey bee foraging behavior. Based on the observations of Weaver (1956), learning was perhaps an important determinant of foraging specialization, and workers may have become "fixed" to a particular foraging mode that was initially successful. Alternatively, recent studies (Calderone & Page 1988; Robinson & Page 1989) have demonstrated a genetic component to task specialization in *A. mellifera*, and it is possible that inter-individual variation in foraging behavior reflects underlying genetic differences.

In addition to inter-individual variation in behavior, several behavioral differences were evident among the 3 foraging tactics. First, though abundance of all foragers declined in the afternoon, ID-workers were completely absent. Whether ID-foragers remained in the hive or visited another food source is unknown, but based on morning and afternoon sightings of the same individuals, it is unlikely that ID-workers switch to O- or IR-visits at *A. gangetica* in the afternoon. Second, rates of floral visitation varied with foraging mode: O-foragers visited more flowers per min and spent less time per flower than IR- or ID-foragers, which had similar movement rates and handling times. Travel distances between successive floral visits may have also varied with foraging tactic (Zimmerman 1982a), but this hypothesis remains untested. Finally, the degree of floral discrimination appeared to differ between I-tactics. Based on lower probabilities of landing after approach and floral entry after landing, ID-foragers were apparently more selective than IR-foragers. This observation suggests that visual signals associated with pollen availability (Zimmerman 1982b) were more conspicuous and/or reliable than possible visual (Thorp et al. 1975) or odor (Heinrich 1979) cues associated with nectar levels. It is unlikely that scent-marking by previous honey bee visitors was responsible (Wetherwax 1986; Giurfa & Nunez 1992), because unless IR- and ID-foragers leave different odors, a worker would be unable to assess which type of floral visits was made previously.

Description of the different foraging modes raises many questions regarding the economics of food collection. For example, how does the availability of nectar and pollen change through the day? How does the rate of nectar intake compare between workers making O- and IR-visits, respectively? How does this rate vary through the day for these 2 tactics? How does the rate of pollen collection compare between workers making IR- and ID-visits, respectively? Is floral rejection by IR- and ID-workers actually indicative of depleted resources? We intend to address these and related questions in future studies.

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