Diet-selection ecology of tropically and temperately adapted honey bees

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Abstract. Colonies of tropically adapted (Africanized) honey bees had greater numbers and higher percentages of pollen foragers than did temperately adapted (European) honey bees. European colonies had greater overall foraging activity. The number of pollen gatherers in Africanized nests was greater throughout the daily foraging cycle, and was especially high early in the morning when pollen was most abundant. Africanized colonies fielded more pollen collectors even when levels of stimuli which are known to regulate pollen foraging were altered experimentally. Collectively, the foraging patterns resulted in larger stores of pollen in Africanized honey bee nests, while European bee nests typically had larger honey and nectar caches. In mixed nests composed of equal portions of adults of each bee ecotype, foraging patterns were similar for ecotypes within a colony. The behavioural root of differences in resource gathering appears to lie with the nurse bees and foragers of a colony, not with the brood type. Diet selection differences are probably influenced strongly by the climatological constraints which regulate the survival and reproductive capacities of these two bee ecotypes.

When confronted with the significant task of diet selection, an organism should choose to extract resources from a given environment in a manner that maximizes reproductive success. Constraints of different environments might result in different diet-choice strategies. The western honey bee, *Apis mellifera* L., is successful in a variety of habitats, spreading originally from tropical areas to temperate regions, and forming various ecotypes (Louveaux 1969). Diet selection, i.e. colony apportionment of effort into nectar gathering versus pollen gathering, is an important component of this species' foraging strategy (Seeley 1985a), but is a behaviour that is relatively unexplored (Seeley 1985b).

Pollen is the ultimate source of nearly all honey bee nutrition exclusive of carbohydrates. Yet individual foragers, and, by extension, foraging populations, vary greatly in their tendency to collect this resource. Generally, foragers seem to prefer nectar gathering (Ribbands 1953). Free (1967) demonstrated the regulatory effects of several factors within the colony on pollen foraging. The presence of brood and a queen increase pollen collection; eggs and larvae are especially stimulating. Stored pollen within the nest inhibits further collection. Selection for high and low pollen-hoarding bees (Hellmich et al. 1985) has demonstrated that

significant genetic variability exists in this behaviour. The sequence of stimuli that a honey bee forager must encounter before she collects pollen remains unclear. A possible explanation (Free 1967) is that nurse bees search for the pollen they require for brood care, and, if pollen is scarce, they physically or chemically prepare cells to receive pollen loads. Some foragers encountering storage cells are sufficiently stimulated to gather pollen. Additionally, successful foragers may dance to recruit nestmates which were stimulated initially at only low levels by the storage cells (Doull 1971).

The innate tendency for honey bees to collect and hoard nectar is similarly regulated by the presence of a queen and brood (Free 1967; Jaycox 1970), and by the amount of empty comb in the nest (Rinderer & Baxter 1978). Genotypic variability exists, as evidenced by artificial selection for superior honey production. Nectar availability (Lundie 1925) and quality (Butler 1945) also influence foraging.

We compared two honey bee ecotypes to determine whether different selection pressures have led to discernible differences in patterns of diet selection. The study involved two ecotypes having widely divergent evolutionary histories, one in the tropics (Africanized bees, taxonomically a mixture comprised mostly of *A. m. scutellata*) and the other

in temperate zones (European bees, mainly *A. m. ligustica*). All honey bees are exotic to the neotropics. Africanized bees have been tremendously successful in South America, colonizing nearly the entire continent since their introduction 30 years ago. In marked contrast, repeated introduction of European bees during four centuries failed to result in significant feral populations on much of the continent. Differing patterns of diet selection might have contributed to the disparity in colonization successes of these bee ecotypes.

MATERIALS AND METHODS

Investigations took place near Sarare, Venezuela (09° 44′N, 69° 08′W). The area is predominantly dry tropical forest and supports a large feral population of Africanized honey bees. Bee sources were Africanized colonies started from local swarms and European colonies headed by commercially bred queens imported from the United States. All bees used in the experiments were naive to the specific test sites.

Experiment I

During January 1985, 12 colonies with 750 g (7000–8000) of adult worker honey bees each were established for each bee ecotype in five-frame (24 cm depth) Langstroth hives. For each bee ecotype, workers were collected from seven stock colonies, pooled, and held for 24 h before being introduced into the hives.

The colonies were given a controlled level (medium) of pollen-foraging stimuli which consisted of two dark combs holding 470 sq cm of brood (4 days old or younger) and 840 sq cm of stored pollen. A mated queen of the same ecotype as each colony's workers was provided in each hive; she was caged so that foraging stimuli were not altered by increasing brood levels. One empty comb and a comb containing honey sufficient for sustenance were added.

The foraging activity of the colonies was monitored six times daily (every 2 h, beginning at 0700 hours local time) during the 3 test days. The total number of foragers and number of pollen foragers returning during a 5-min interval were recorded; the percentage of pollen foragers was derived from these parameters. Observations were aided by using hive entrances (4 × 1 cm). The change in the

amount of pollen stored in each hive was calculated by measuring the area of cells containing pollen during the evenings preceding and following the experiment. Pollen cell areas were determined with a 2·5-cm-sq grid (25 storage cells/grid square) laid over each side of the combs; partial grid squares were estimated and summed with full squares. The amount of nectar stored in the empty comb that had been provided was calculated as the difference of weights of the comb with nectar and the comb after nectar had been removed by centrifugal extraction.

Experiment II

The colonies established previously were manipulated for 3 consecutive days following experiment I. Half of the colonies of each bee type were given a high foraging stimulus while the others were given a low stimulus. The high stimulus was 930 sq cm of brood and no pollen; the low stimulus was no brood and 690 sq cm of pollen. Foraging and food storage were monitored as in experiment I.

Experiment III

Twelve colonies, each composed of 380 g of dark-yellow Africanized workers and 380 g of light-yellow European workers, were used. This difference in body colour facilitated ecotype discrimination during observations of foragers. Each colony was stocked with about 1400 sq cm of mixed-age brood; half of the colonies were given Africanized brood, half were given European brood. A queen of the same ecotype as the brood was caged in each colony. One comb containing honey and one empty comb were added. No pollen stores were supplied.

Foraging activity from these colonies was observed for 4 days, following the general format used in the two previous experiments. In this test, however, returning foragers were also classified by ecotype. Experiment III took place in February 1985.

Statistical Analyses

Ecotypic responses were evaluated with two-tailed *t*-tests, modified for heterogeneous variances when necessary (Snedecor & Cochran 1980). All daily observations were pooled to produce colony means. Daily foraging trends were based on 12

Table I. Division of foraging efforts and changes in food stores ($\bar{X}\pm$SE) in colonies of tropical ($N=12$) and temperate ($N=12$) honey bee ecotypes during experiment I

Ecotype	Total foragers (bees/5 min)	Pollen foragers (bees/5 min)	% Foragers with pollen	Change in nectar stores (g)	Change in pollen stores (sq cm)
Africanized	51 ± 4	8 ± 1	11 ± 1	382 ± 21	23 ± 18
European	66 ± 3	2 ± 1	3 ± 1	439 ± 41	-63 ± 22
P	0·006*	0·001	0·001	0·240	0·008

Each colony had 750 g of bees and a medium level of foraging stimuli (470 sq cm of brood and 840 sq cm pollen); the experiment lasted 3 days.
* Probability levels for ecotype comparisons are based on *t*-tests.
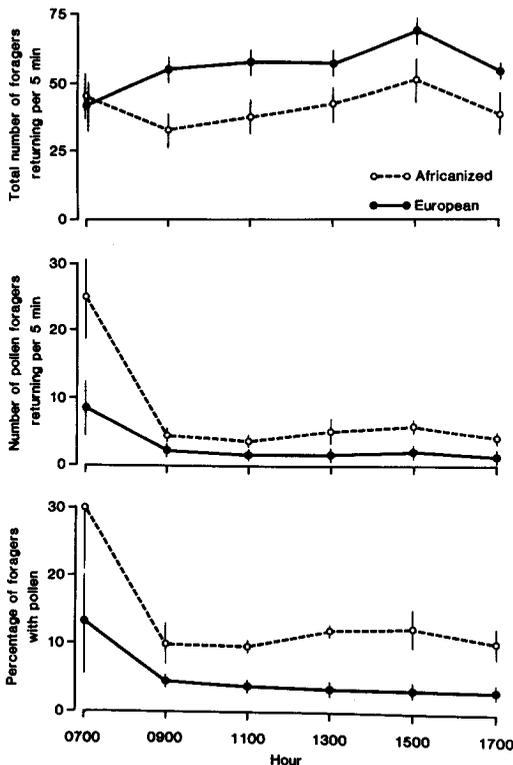
Figure 1. Daily foraging patterns of Africanized and European honey bees when in colonies of their own ecotype (experiment I). Means and 95% confidence intervals are derived from 12 colonies of each ecotype.

(experiment I) or six (experiment III) colony replicates per ecotype. Mean responses of the four ecotype and stimuli-level combinations in experiment II were assessed with analysis of variance, and, when a significant interaction was noted, a least significant difference test.

RESULTS

Experiment I

When established with similar levels of pollen-foraging stimuli and bee populations, European colonies had more total foragers ($P=0·006$, $df=22$; Table I). Africanized colonies had more pollen foragers ($P=0·001$, $df=13$) and a higher percentage of pollen foragers ($P=0·001$, $df=14$). Flight patterns during the course of the day suggest differential diurnal foraging strategies. The total number of foragers was similar at 0700 hours ($P=0·598$, $df=22$), but European colonies consistently fielded more foragers during the remainder of the day ($P\leqslant0·007$, $df=22$; Fig. 1). Africanized colonies had greater numbers and percentages of pollen collectors during each observation period throughout the day ($P\leqslant0·005$, except $P=0·055$ for numbers at 0900 hours; $df=22$). At 0700 hours, Africanized colonies had three times as many pollen foragers as European colonies. The major pollen resource during this experiment was a 1-ha field of cultivated corn near the experimental apiary. In corn, pollen collection by bees is closely correlated with pollen presentation in the field (Percival 1955). During experiments I and II, anther dehiscence occurred early in the day and the pollen resource was usually exhausted by late morning. The daily flight curves indicate that Africanized colonies exploited this ephemeral pollen source more intensely.

Africanized colonies stored more pollen during the experiment ($P=0·008$, $df=22$). Although European nests had nectar caches that were 15% larger, storage by the two ecotypes was not significantly different ($P=0·240$, $df=22$).

Table II. Division of foraging efforts and changes in food stores ($\bar{X}\pm\text{SE}$) in colonies of tropical and temperate honey bee ecotypes given high or low levels of foraging stimuli* during experiment II

	N	Total foragers (bees/5 min)	Pollen foragers (bees/5 min)	% Foragers with pollen†	Change in nectar stores (g)	Change in pollen stores (sq cm)
High level of stimulus						
Africanized	6	49±4	17±1	27±2^a	37±13	No change‡
European	6	57±5	8±1	12±1^b	68±12	No change
Low level of stimulus						
Africanized	6	35±4	7±1	14±1^b	63±12	123±45
European	6	48±3	2±1	5±1^c	103±22	−206±37

Colonies were those used in experiment I, but with new foraging stimuli levels during the 3 test days.
* High stimulus=930 sq cm brood and no pollen; low stimulus=690 sq cm pollen and no brood.
† Means not followed by the same letter are significantly different ($P=0.010$, least significant difference=5).
‡ Colonies started without pollen stores and consumed all pollen that they collected.
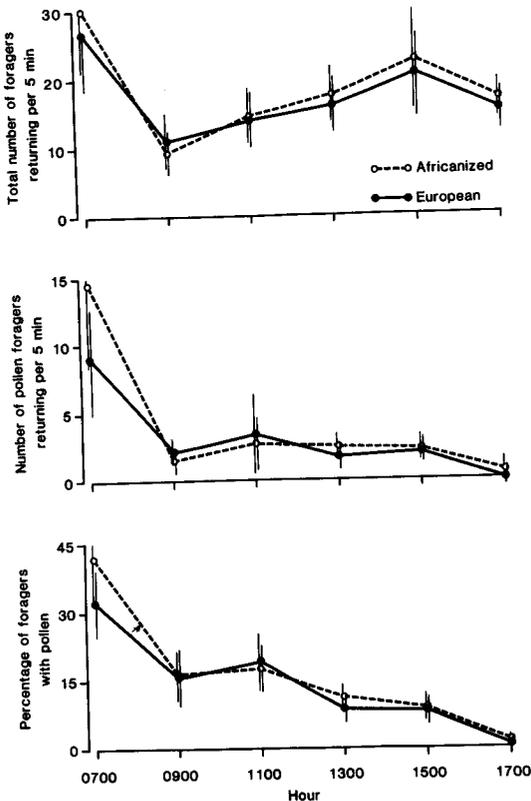
Figure 2. Daily foraging patterns of Africanized and European honey bees when in colonies of mixed ecotypes (experiment III). Means and 95% confidence intervals are derived from 12 colonies of each ecotype.

Experiment II

Foraging trends by the ecotypes followed those found in experiment I ($P\leqslant0.029$, $df=1$, 20; Table II). Also, the high stimulus resulted in increased foraging for each parameter measured ($P\leqslant0.016$, $df=1$, 20). An interaction between ecotype and stimulus was detected for the percentage of pollen collectors ($P=0.025$, $df=1$, 20). The interaction resulted in the percentage of pollen-collecting bees being greatest in high-stimulus Africanized colonies and lowest in low-stimulus European colonies (each $P\leqslant0.010$). There was a suggestion of a similar interaction for the number of pollen foragers ($P=0.078$, $df=1$, 20), but not for the total number of foragers ($P=0.569$, $df=1$, 20).

European colonies stored more nectar ($P=0.018$, $df=1$, 20). A low stimulus caused more nectar to be hoarded ($P=0.023$, $df=1$, 20); high-stimulus colonies probably engaged in pollen collection at the expense of nectar foraging. There was no ecotype by stimulus interaction for nectar collection. Within the low-stimulus class, Africanized colonies stored greater quantities of pollen ($P=0.008$, $df=12$). The pollen collected by high-stimulus colonies was apparently used immediately for brood rearing, as no stores were detected.

Experiment III

When hived together, the ecotypes fielded similar total numbers of foragers ($\bar{X}_{\text{Africanized}}\pm\text{SE}=18\pm2$, $\bar{X}_{\text{European}}=17\pm2$; $P=0.698$, $df=22$), numbers of pollen foragers ($\bar{X}_{\text{Africanized}}=4\pm2$, $\bar{X}_{\text{European}}=3\pm2$;

$P=0.329$, $df=22$), and percentages of foragers gathering pollen ($\bar{X}_{\text{Africanized}}=16\pm4$, $\bar{X}_{\text{European}}=14\pm5$; $P=0.243$, $df=22$). Daily foraging patterns were also similar ($P\geqslant0.120$, $df=22$; Fig. 2). Exceptions were a higher number of Africanized pollen foragers at 0700 hours ($P=0.032$, $df=22$) and a higher percentage of Africanized bees gathering pollen at 0700 and 1700 hours ($P\leqslant0.051$, $df=22$). Late-afternoon differences arose because Africanized bees represented most of the very few bees which collected any pollen at that time. There were no interactions of any foraging parameter with the brood and queen ecotype in a colony ($P\geqslant0.344$, $df=6$).

DISCUSSION

The two honey bee ecotypes showed a fundamental divergence in diet selection when colonies were established under identical foraging conditions. Relative to European bees, Africanized bees showed a preference for pollen. Inferences can be made from these comparative data about how diet selection of each ecotype is related to specific ecological constraints found in their contrasting evolutionary environments. In temperate bee colonies, reproductive swarming generally occurs after a new colony has overwintered (Seeley 1978). Colonies must store large quantities of honey to survive winter successfully; this is the primary consideration regulating overall resource collection and use. The reproductive success of temperate bees may be limited in large part by nectar availability (Seeley & Visscher 1985) and nectar-foraging success. The necessity of accumulating large winter stores may also explain the relatively greater foraging activity in European colonies (this study; Danka et al., in press). Other research has shown the superiority of European bees in nectar foraging and honey production under higher nectar availability conditions (Pesante 1985; Rinderer et al. 1985).

Tropical colonies, in contrast, are not required to amass large honey stores. Relative to their temperate counterparts, tropical bees exhibit *r*-selected life histories. Reproductive effort can continue throughout much or all of the tropical year, which allows seasonal swarming rates three to six times those of temperate honey bees (Winston 1980; Winston et al. 1981). Swarming is limited by brood and bee production. By apportioning foraging effort to include a relatively high level of pollen collection, tropical bees may maximize brood production. Also, greater pollen storage by Africanized bees may provide a means for brood production during times of pollen dearth. Pesante (1985) found pollen-foraging trends were consistent throughout the year; also, Africanized nests contained more brood. The reproductive success of tropical colonies may in large part be limited by pollen availability and pollen-foraging success.

The behavioural mechanisms underlying differential diet selection, although not entirely resolved, seem to lie in the interactions of adult nestmates. Foraging trends of the two ecotypes were similar when assembled in mixed colonies, regardless of the ecotype of the brood in the nest. Hence, by Free's (1967) hypothesis, interactions among nurse bees and foragers must have governed pollen foraging; this could have occurred directly or through storage-cell preparation. Mixing adult bees might be expected to produce intermediate foraging-stimuli levels, which in turn could have resulted in intermediate foraging efforts. This possibility needs to be examined directly. In the only other study of foraging in mixed-ecotype colonies, Winston & Katz (1982) found that Africanized and European workers initiated foraging at different ages when in their own colonies, but that cross-fostered individuals tended to begin foraging at the same ages as bees in host colonies. Our experiments likewise show that mixing these bee ecotypes, which normally show distinct differences in total foraging and pollen-foraging activities, yields foraging patterns that are similar for bees within a colony. This situation holds potential as a tool for further dissecting the mechanisms which govern diet selection by honey bees.

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