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# NECTAR-FORAGING CHARACTERISTICS OF AFRICANIZED AND EUROPEAN HONEYBEES IN THE NEOTROPICS

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## Summary
Africanized and European honeybees (*Apis mellifera*) responded differently to daily fluctuations in nectar resources. In side-by-side comparisons, the relative energy content of the nectar loads collected by the two geographical types varied with day. Daily variation was found in the volume of nectar collected but not in its concentration. Africanized bees collected more highly concentrated nectar. The success rates of foragers of the two types differed considerably. European bees generally were more successful in securing a load of nectar but their percentage of successful foragers tended to be either high or low. Africanized bees returned more often to their nest without a nectar load but had intermediate as well as high and low percentages of successful foragers. Finally, European colonies had greater numbers of foragers under the nectar-resource conditions of the study.

## Introduction
Collectively, floral resources used by honeybees follow annual patterns of nectar secretion and availability (Crane, 1975; Oertel et al., 1980). In temperate regions, availability of nectar typically is low in early spring, then increases sharply to the annual maximum in late spring or early summer. Nectar-secreting plants tend to be of many different species and to produce abundant nectar. A decline in both number of species and abundance of nectar follows, and by late summer usually only a few low-quality sources exist. Different ecosystems in the natural temperate-zone distribution of honeybees all show this general pattern since they are all constrained in some degree by winter. However, the pattern varies between temperate ecosystems in certain details which are consistent with climatic differences (Ruttner, 1975). Tropical ecosystems in the natural distribution of honeybees also have characteristic patterns of plant flowering and nectar secretion (Frankie et al., 1974). In Africa, *Apis mellifera scutellata* occupies many regions having more than one period of nectar flow per annum (Fletcher, 1978).

In temperate areas the availability of empty honey-storage comb in a feral honeybee nest coincides temporally, and varies directly with, changes in the availability of nectar in the field. Honeybees that evolved in temperate areas respond to experimentally increased amounts of empty comb by engaging in stronger dance-recruitment activities, by being more selective in their acceptance of nectar sources, and by producing more honey during periods of good nectar availability but less during periods of poor nectar availability. Thus, the seasonal occurrence of empty comb in the nests of temperate-climate honeybees regulates the intensity of their nectar foraging and their selection of nectar sources in ways that result in the storage throughout the year of the maximum amount of honey possible under the existing conditions of colony population and nectar flow (Rinderer, 1981, 1982*a*, 1982*b*; Rinderer & Baxter, 1978, 1979, 1980).

Presumably, honeybees in tropical ecosystems also have evolved mechanisms that regulate intensity of foraging and selection of nectar sources which are attuned to the ecosystem's pattern of nectar secretion and availability. A few details suggesting such mechanisms are known. Rinderer et al. (1982) reported that in laboratory hoarding tests (Free & Williams, 1972; Kulinčević & Rothenbuhler, 1973) Africanized honeybees descended from *A. m. scutellata* imports (Michener, 1975) removed sucrose solution from feeders and hoarded it in combs more slowly than temperate zone honeybees. Núñez (1973, 1979) comparing Africanized and European honeybees at an artificial feeding station, observed that the Africanized bees spent less time on various components of foraging, made briefer foraging trips, and carried less nectar to the hive on each trip. Fletcher (1978) reviewed several reports of African honeybees foraging in adverse conditions of light and temperature; collectively, the reports suggest that the nectar-foraging characteristics of Africanized bees are different from

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those of temperately adapted bees. However, the reports are not adequate for the development of models of tropical honeybee foraging.

This research addressed the following questions about the comparative foraging of Africanized and European* honeybees. (1) Do bees of both geographical types respond in similar ways to day-to-day fluctuations in nectar availability? (2) Do foragers of both geographical types collect similar amounts of similar nectars? (3) Is the success rate of foragers of the two types similar? (4) Does empty comb affect the foraging of both types equally? (5) Do similar colonies of the two types have equal numbers of foragers? Finally, (6) Do similar colonies of the two types harvest and store similar amounts of honey?

## Methods

The experiment was conducted 5 km N. of Caripe, Monagas, Venezuela, (latitude 10° 17′ N., longitude 63° 2′ W., elevation 1500 m) at Conuco 'el Mirador'. The foraging area accessible to experimental bees contained tracts of tropical dry forest, tracts of secondary successional grassland, and areas of coffee and citrus plantings.

Two weeks before observations of foragers began, 20 colonies of honeybees were made up with newly instrumentally inseminated queens and worker bees shaken from brood-nests of appropriate colonies. The experimental colonies were then transported to the site. Each colony contained 0·9 kg adult worker bees and a mated queen of the same geographical type. Half the colonies contained European bees and half contained Africanized bees. Half of each group were in hives *c.* 20 litres in volume and half in hives *c.* 40 litres. All hives were filled with comb in frames, contained between 1 and 1·5 kg honey, and had 2·5-cm diameter entrance holes.

The colonies were inspected on both the day before and the day after foragers were observed. The combs of each colony, shaken free of bees, were weighed to determine the weight changes of nests. During both examinations, each colony contained the original queen, all stages of brood, sufficient food resources for survival and *c.* 0·8–0·9 kg adult bees. Visual estimates of adult bees were made during the evening after flight had stopped.

Observations of foraging bees from these colonies were made near the end of the wet season from 30 November to 5 December, 1979. Each day, bees foraged from 3 to 6 h in the morning. Light rains fell during the remaining time on all days. During the foraging periods, 10 returning foragers not bearing pollen were collected at each hive entrance and killed with cyanide (Sylvester et al., 1983). Careful blocking of entrance holes and observations of returning bees assured that only returning foragers were collected. Within a half-hour the nectar loads were expelled from the bees (Gary & Lorenzen, 1976) and both their volumes and concentrations were measured and recorded. Volumes were determined to the nearest 5 μl using a graduated micropipette, and concentrations were read on a refractometer.

These measurements permitted estimation of the percentage of successful nectar foraging bees, the average energy content of the loads collected by successful nectar foragers, and the average energy content of the loads collected by all nectar-foraging bees. The curvilinear relationship of mg of sugar/μl nectar to the concentration of dissolved sugar (Bolten et al., 1979) was included in the calculations. The calculations were based on the assumption that the dissolved solids in the nectars were exclusively sucrose.

Other sugars occur in nectar (Wykes, 1953; Percival, 1961) as well as amino acids, lipids and ions (Inouye et al., 1980) and, to a small degree alter the relationship of refractive index to energy content (Junk & Pancoast, 1973; Inouye et al., 1980). However, the method of measurement used was sufficiently accurate to compare the nectar loads of groups of bees collecting nectar in the same foraging area.

On the second, third, and sixth days of the experiment weather conditions remained favourable after foragers were collected and their nectar loads were measured. On these days, 2 h after foragers were collected, the number of bees leaving the nests of each colony in a 1-min period was counted.

*The European honeybees in this study were from North America. Such bees have in their ancestry representatives of mixed subspecies. Africanized bees are descendants of *A. m. scutellata* bees imported from Africa and their hybrids with various subspecies previously imported into Brazil. Neither the European nor the Africanized bees can correctly be called race, subspecies, stock, or line representatives. We use the term 'geographical type' to indicate that the bees we studied showed major characteristics typical of descriptions for temperately or tropically (*A. m. scutellata*) adapted bees.

## Results

### Nectar loads

Analyses of variance of the data from the entire experiment (Table 2) showed that Africanized bees collected significantly more concentrated nectar (P<0·01) but had a lower proportion of successful foragers (P<0·01). Average daily volumes of concentrations of nectar loads and the success rate of foragers all varied significantly throughout the 6-day experiment (P<0·03–<0·0001). Most importantly, there was a significant interaction between the independent variables geographical type and date with respect to nectar volume, energy (calories) collected by successful nectar foragers, energy collected by all nectar foragers, and the success rate of foragers (P<0·01–<0·0001). The interaction of these variables in the analysis of nectar-load concentrations was weak (P<0·08). The independent variables hive-size and date interacted significantly in the analysis of amounts of energy collected by successful nectar foragers (P<0·05). Collectively, these interactions suggested that bees of the two geographical types responded differently to the different daily conditions for nectar foraging. This indicated the desirability of a closer inspection of results by analysing each day's data separately.

The subsequent analyses of variance revealed the nature of the interactions between daily foraging conditions and the nectar loads of Africanized and European bees. On days 1 and 5 of the experiment, responses were sufficiently similar that no measurement was significantly different for the independent variables geographical type or nest size, nor were the interactions

TABLE 1. Foraging success of Africanized and of European honeybees from colonies whose comb filled 20-litre or 40-litre hives.

Five colonies of each geographical type were studied by hive-size combination, 10 bees being sampled from each colony on each of 6 days.
Means ± SE and F and P values are given for nectar loads analysed by analysis of variance. Each set of statistical values in lower part of Table is for column above.
Energy content of nectar loads is expressed in calories (1 cal = 4·19 J) for all nectar foragers (ANF) and successful nectar foragers (SNF). Numbers of successful foragers were analysed by $\chi^2$.

| *Geographical type and hive size* | *Nectar loads* | | | | *SNF* | |
|---|---|---|---|---|---|---|
| | | | *Energy content* | | | |
| | *Vol (μl)* | *Concn (%)* | *SNF* | *ANF* | *No.* | *%* |
| Africanized bees | 19·1 ± 0·9 | 24·4 ± 0·6 | 20·3 ± 1·0 | 13·7 ± 0·9 | 416 | 69 |
| 20-litre | 17·9 ± 1·3 | 23·5 ± 0·8 | 18·5 ± 1·5 | 12·3 ± 1·2 | 199 | 66 |
| 40-litre | 20·3 ± 1·2 | 25·4 ± 0·8 | 22·1 ± 1·3 | 15·3 ± 1·1 | 217 | 72 |
| European bees | 18·8 ± 0·9 | 22·3 ± 0·5 | 18·5 ± 1·0 | 13·8 ± 0·8 | 456 | 76 |
| 20-litre | 18·4 ± 1·2 | 22·0 ± 0·7 | 18·7 ± 1·3 | 13·5 ± 1·2 | 233 | 78 |
| 40-litre | 19·4 ± 1·3 | 22·6 ± 0·8 | 18·4 ± 1·4 | 14·2 ± 1·2 | 223 | 74 |
| 20-litre | 18·1 ± 0·9 | 22·8 ± 0·5 | 18·6 ± 1·0 | 15·3 ± 1·1 | 432 | 72 |
| 40-litre | 19·8 ± 0·9 | 24·0 ± 0·6 | 20·2 ± 1·0 | 14·7 ± 0·8 | 440 | 73 |

| *Source of variation* | *df* | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* | $\chi^2$ | *df* | *P* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Geographical type (T) | 1 | 0·02 | 0·88 | 5·43 | 0·03 | 1·33 | 0·26 | 0·00 | 0·96 | 6·71 | 1 | 0·01 |
| Hive size (S) | 1 | 1·49 | 0·24 | 1·95 | 0·18 | 1·18 | 0·29 | 1·99 | 0·17 | 0·27 | 1 | 0·60 |
| T × S | 1 | 0·21 | 0·65 | 0·50 | 0·49 | 1·60 | 0·22 | 0·73 | 0·41 | | | |
| Date (D) | 5 | 2·73 | 0·03 | 27·23 | 0·0001 | 5·63 | 0·0002 | 5·37 | 0·0003 | 203·33 | 5 | 0·0001 |
| T × D | 5 | 2·65 | 0·03 | 2·03 | 0·08 | 2·72 | 0·03 | 7·0 | 0·0001 | 74·51* | 5 | 0·0001 |
| S × D | 5 | 1·90 | 0·10 | 0·76 | 0·58 | 2·38 | 0·05 | 1·87 | 0·11 | 5·88* | 5 | 0·32 |
| T × S × D | 5 | 1·54 | 0·19 | 1·27 | 0·28 | 1·51 | 0·19 | 1·61 | 0·16 | | | |
| Error | 95 | | | | | | | | | | | |

*Heterogeneity $\chi^2$s obtained by subtracting the $\chi^2$s of pooled data from the sum of $\chi^2$s for the type or size comparison for each day (Snedecor & Cochran, 1967).

of these variables significant (Table 2 and Table 6, respectively). However, significant differences occurred on days 2, 3 and 4 (Table 3–Table 5) and day 6 (Table 7). On day 2 significantly fewer European bees were successful in securing a nectar load ($P<0{\cdot}0004$), and European foragers collected nectar loads of lower concentration ($P<0{\cdot}03$). These two factors

TABLE 2. Foraging success on day 1 of Africanized and European honeybees from colonies whose comb filled 20-litre or 40-litre hives.

Explanation as for Table 1.

| *Geographical type and hive size* | Nectar loads: *Vol.* (μl) | *Concn* (%) | Energy content: *SNF* | *ANF* | *SNF No.* | *%* |
|---|---|---|---|---|---|---|
| Africanized bees | 14·3 ± 1·7 | 29·9 ± 1·6 | 19·3 ± 2·1 | 11·2 ± 1·7 | 58 | 58 |
| 20-litre | 13·8 ± 2·5 | 30·8 ± 2·4 | 19·0 ± 3·2 | 9·9 ± 2·4 | 26 | 52 |
| 40-litre | 14·8 ± 2·3 | 29·0 ± 2·1 | 19·7 ± 2·9 | 12·6 ± 2·4 | 32 | 64 |
| European bees | 17·7 ± 1·9 | 30·3 ± 1·8 | 22·5 ± 2·4 | 10·2 ± 1·7 | 45 | 45 |
| 20-litre | 20·1 ± 2·6 | 28·3 ± 2·5 | 25·2 ± 3·3 | 12·1 ± 2·4 | 24 | 48 |
| 40-litre | 15·4 ± 2·7 | 32·2 ± 2·6 | 19·8 ± 3·5 | 8·3 ± 2·4 | 21 | 42 |
| 20-litre | 17·0 ± 1·8 | 29·6 ± 1·7 | 22·1 ± 2·3 | 10·9 ± 1·7 | 50 | 50 |
| 40-litre | 15·1 ± 1·8 | 30·6 ± 1·7 | 19·7 ± 2·3 | 10·4 ± 1·7 | 53 | 53 |

| *Source of variation* | *df* | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* | $\chi^2$ | *df* | *P* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Geographical type (T) | 1 | 1·82 | 0·19 | 0·03 | 0·86 | 0·95 | 0·34 | 0·18 | 0·67 | 3·38 | 1 | 0·07 |
| Hive size (S) | 1 | 0·56 | 0·46 | 0·18 | 0·67 | 0·53 | 0·48 | 0·05 | 0·83 | 0·18 | 1 | 0·67 |
| T × S | 1 | 1·31 | 0·27 | 1·41 | 0·25 | 0·91 | 0·35 | 1·78 | 0·20 | | | |
| Error | 16 | | | | | | | | | | | |

TABLE 3. Foraging success on day 2 of Africanized and European honeybees from colonies whose comb filled 20-litre or 40-litre hives.

Explanation as for Table 1.

| *Geographical type and hive size* | Nectar loads: *Vol* (μl) | *Concn* (%) | Energy content: *SNF* | *ANF* | *SNF No.* | *%* |
|---|---|---|---|---|---|---|
| Africanized bees | 21·1 ± 2·3 | 31·6 ± 1·3 | 30·1 ± 3·4 | 19·6 ± 2·8 | 65 | 65 |
| 20-litre | 19·5 ± 3·3 | 30·8 ± 2·4 | 28·0 ± 4·9 | 18·0 ± 3·9 | 32 | 64 |
| 40-litre | 22·7 ± 3·4 | 32·1 ± 2·4 | 32·0 ± 4·9 | 21·2 ± 3·9 | 33 | 66 |
| European bees | 19·6 ± 3·1 | 24·7 ± 2·3 | 19·4 ± 4·5 | 8·6 ± 2·8 | 40 | 40 |
| 20-litre | 24·2 ± 3·6 | 25·7 ± 2·6 | 26·8 ± 5·4 | 13·9 ± 3·9 | 26 | 52 |
| 40-litre | 15·0 ± 5·0 | 23·6 ± 3·6 | 11·9 ± 7·4 | 3·3 ± 3·9 | 14 | 28 |
| 20-litre | 21·8 ± 2·5 | 28·3 ± 1·8 | 24·4 ± 3·6 | 16·0 ± 2·8 | 58 | 58 |
| 40-litre | 18·9 ± 3·0 | 28·0 ± 2·2 | 22·0 ± 4·4 | 12·3 ± 2·8 | 47 | 47 |

| *Source of variation* | *df* | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* | $\chi^2$ | *df* | *P* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Geographical type (T) | 1 | 0·15 | 0·70 | 5·87 | 0·03 | 3·54 | 0·08 | 7·51 | 0·02 | 12·53 | 1 | 0·0004 |
| Hive size (S) | 1 | 0·60 | 0·44 | 0·01 | 0·90 | 0·91 | 0·35 | 0·86 | 0·37 | 2·43 | 1 | 0·12 |
| T × S | 1 | 2·56 | 0·12 | 0·38 | 0·54 | 2·70 | 0·12 | 2·96 | 0·10 | | | |
| Error | 16 | | | | | | | | | | | |

Table 4. Foraging success on day 3 on Africanized and European honeybees from colonies whose comb filled 20-litre or 40-litre hives.

Explanation as for Table 1.

| Geographical type and hive size | Nectar loads: Vol (μl) | Concn (%) | Energy content: SNF | Energy content: ANF | SNF No. | SNF % |
|---|---|---|---|---|---|---|
| Africanized bees | 21·8 ± 1·8 | 25·3 ± 1·6 | 21·9 ± 1·5 | 7·8 ± 1·3 | 35 | 35 |
| 20-litre | 20·6 ± 2·6 | 21·4 ± 2·4 | 18·8 ± 2·2 | 6·0 ± 1·8 | 16 | 32 |
| 40-litre | 22·9 ± 2·4 | 29·2 ± 2·2 | 25·0 ± 2·0 | 9·5 ± 1·8 | 19 | 38 |
| European bees | 20·0 ± 1·1 | 21·5 ± 1·1 | 19·5 ± 1·0 | 16·6 ± 1·3 | 85 | 85 |
| 20-litre | 16·2 ± 1·6 | 21·7 ± 1·5 | 16·4 ± 1·4 | 13·8 ± 1·8 | 42 | 84 |
| 40-litre | 23·7 ± 1·6 | 21·3 ± 1·5 | 22·5 ± 1·4 | 19·3 ± 1·8 | 43 | 86 |
| 20-litre | 18·4 ± 1·6 | 21·6 ± 1·4 | 17·6 ± 1·3 | 9·9 ± 1·3 | 58 | 58 |
| 40 litre | 23·3 ± 1·5 | 25·3 ± 1·4 | 23·7 ± 1·2 | 14·4 ± 1·3 | 62 | 62 |

| Source of variation | df | F | P | F | P | F | P | F | P | $\chi^2$ | df | P |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Geographical type (T) | 1 | 0·72 | 0·41 | 3·63 | 0·08 | 1·83 | 0·20 | 21·76 | 0·0003 | 52·00 | 1 | 0·0001 |
| Hive size (S) | 1 | 5·29 | 0·04 | 3·41 | 0·08 | 11·48 | 0·0004 | 5·67 | 0·03 | 0·33 | 1 | 0·57 |
| T × S | 1 | 1·53 | 0·24 | 4·28 | 0·06 | 0·00 | 0·98 | 0·30 | 0·59 | | | |
| Error | 16 | | | | | | | | | | | |

Table 5. Foraging success on day 4 of Africanized and European honeybees from colonies whose comb filled 20-litre or 40-litre hives.

Explanation as for Table 1.

| Geographical type and hive size | Nectar loads: Vol (μl) | Concn (%) | Energy content: SNF | Energy content: ANF | SNF No. | SNF % |
|---|---|---|---|---|---|---|
| Africanized bees | 24·9 ± 2·5 | 22·1 ± 0·7 | 23·3 ± 2·4 | 20·5 ± 2·7 | 87 | 87 |
| 20-litre | 22·5 ± 3·8 | 20·1 ± 1·1 | 19·4 ± 3·7 | 18·4 ± 4·1 | 43 | 86 |
| 40-litre | 27·3 ± 3·3 | 24·2 ± 1·0 | 27·2 ± 3·2 | 22·6 ± 3·4 | 44 | 88 |
| European bees | 18·3 ± 2·4 | 20·1 ± 0·7 | 17·8 ± 2·3 | 16·9 ± 2·6 | 95 | 95 |
| 20-litre | 16·5 ± 3·5 | 19·3 ± 1·0 | 15·2 ± 3·3 | 14·3 ± 3·7 | 47 | 94 |
| 40-litre | 20·2 ± 3·4 | 21·0 ± 1·0 | 20·4 ± 3·7 | 19·5 ± 3·7 | 48 | 96 |
| 20-litre | 19·5 ± 2·6 | 19·7 ± 0·7 | 17·3 ± 2·4 | 16·3 ± 2·8 | 90 | 90 |
| 40-litre | 23·8 ± 2·4 | 22·6 ± 0·7 | 23·7 ± 2·3 | 21·1 ± 2·7 | 92 | 92 |

| Source of variation | df | F | P | F | P | F | P | F | P | $\chi^2$ | df | P |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Geographical type (T) | 1 | 3·47 | 0·08 | 3·83 | 0·07 | 2·65 | 0·12 | 0·90 | 0·36 | 3·91 | 1 | 0·05 |
| Hive size (S) | 1 | 1·47 | 0·24 | 8·10 | 0·01 | 3·69 | 0·07 | 1·50 | 0·23 | 0·24 | 1 | 0·62 |
| T × S | 1 | 0·02 | 0·87 | 1·50 | 0·24 | 0·16 | 0·69 | 0·02 | 0·89 | | | |
| Error | 16 | | | | | | | | | | | |

TABLE 6. Foraging success on day 5 of Africanized and European honeybees from colonies whose comb filled 20-litre or 40-litre hives.

Explanation as for Table 1.

| *Geographical type and hive size* | *Nectar loads* Vol (μl) | Concn (%) | *Energy content* SNF | ANF | *SNP* No. | % |
|---|---|---|---|---|---|---|
| Africanized bees | 18·3 ± 1·7 | 21·2 ± 1·2 | 16·0 ± 1·5 | 14·9 ± 1·4 | 93 | 93 |
| 20-litre | 17·0 ± 2·3 | 21·3 ± 1·6 | 14·4 ± 2·1 | 13·2 ± 2·2 | 46 | 92 |
| 40-litre | 20·0 ± 2·3 | 21·2 ± 1·6 | 17·7 ± 2·1 | 16·6 ± 2·2 | 47 | 94 |
| European bees | 19·1 ± 1·6 | 18·9 ± 1·1 | 16·8 ± 1·4 | 16·1 ± 1·4 | 96 | 96 |
| 20-litre | 17·8 ± 2·3 | 18·4 ± 1·6 | 15·8 ± 2·1 | 14·8 ± 2·2 | 47 | 94 |
| 40-litre | 20·4 ± 2·3 | 19·4 ± 1·5 | 17·8 ± 2·0 | 17·5 ± 2·2 | 49 | 98 |
| 20-litre | 17·3 ± 1·7 | 19·9 ± 1·1 | 15·1 ± 1·5 | 14·0 ± 1·4 | 93 | 93 |
| 40-litre | 20·0 ± 1·6 | 20·3 ± 1·1 | 17·7 ± 1·4 | 17·0 ± 1·4 | 96 | 96 |

| *Source of variation* | *df* | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* | $\chi^2$ | *df* | *P* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Geographical type (T) | 1 | 0·11 | 0·74 | 2·14 | 0·16 | 0·14 | 0·71 | 0·39 | 0·54 | 0·87 | 1 | 0·35 |
| Hive size (S) | 1 | 1·33 | 0·27 | 0·08 | 0·78 | 1·68 | 0·21 | 2·29 | 0·15 | 0·87 | 1 | 0·35 |
| T × S | 1 | 0·00 | 0·99 | 0·09 | 0·77 | 0·10 | 0·76 | 0·04 | 0·84 | | | |
| Error | 16 | | | | | | | | | | | |

TABLE 7. Foraging success on day 6 of Africanized and European honeybees from colonies whose comb filled 20-litre or 40-litre hives.

Explanation as for Table 1.

| *Geographical type and hive size* | *Nectar loads* Vol. (μl) | Concn (%) | *Energy content* SNF | ANF | *SNP* No. | % |
|---|---|---|---|---|---|---|
| Africanized bees | 14·2 ± 1·9 | 16·4 ± 1·0 | 11·1 ± 1·9 | 8·6 ± 1·5 | 78 | 78 |
| 20-litre | 14·0 ± 2·8 | 16·5 ± 1·5 | 11·3 ± 2·8 | 8·1 ± 2·1 | 36 | 72 |
| 40-litre | 14·4 ± 2·6 | 16·3 ± 1·4 | 10·9 ± 2·6 | 9·1 ± 2·1 | 42 | 84 |
| European bees | 18·6 ± 1·7 | 18·4 ± 0·9 | 15·3 ± 1·7 | 14·5 ± 1·5 | 95 | 95 |
| 20-litre | 15·3 ± 2·5 | 18·6 ± 1·3 | 12·6 ± 2·4 | 11·8 ± 2·1 | 47 | 94 |
| 40-litre | 22·0 ± 2·4 | 18·3 ± 1·3 | 18·0 ± 2·4 | 17·2 ± 2·1 | 48 | 96 |
| 20-litre | 14·7 ± 1·9 | 17·5 ± 1·0 | 11·9 ± 1·8 | 12·2 ± 1·6 | 83 | 83 |
| 40-litre | 18·2 ± 1·8 | 17·3 ± 1·0 | 14·4 ± 1·7 | 16·6 ± 1·6 | 90 | 90 |

| *Source of variation* | *df* | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* | $\chi^2$ | *df* | *P* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Geographical type (T) | 1 | 2·93 | 0·11 | 2·11 | 0·17 | 2·74 | 0·12 | 7·72 | 0·02 | 12·37 | 1 | 0·0004 |
| Hive size (S) | 1 | 1·58 | 0·19 | 0·02 | 0·89 | 0·96 | 0·34 | 2·27 | 0·15 | 0·29 | 1 | 0·59 |
| T × S | 1 | 1·47 | 0·24 | 0·00 | 0·98 | 1·34 | 0·26 | 1·10 | 0·31 | | | |
| Error | 16 | | | | | | | | | | | |

resulted in significantly less energy (P<0·02) being harvested by equivalent numbers of groups of European foragers. Days 3 and 6 contrasted with day 2; on both days the percentage of successful nectar foragers was higher in European bees (P<0·0004) and, primarily because of this, European groups collected significantly more energy (P<0·003 and P<0·02 respectively) than groups of Africanized bees. On day 4 more European bees secured nectar loads (P<0·05); yet, because they tended to collect smaller loads (P<0·08) of less concentrated nectar (P<0·07), energy collection was similar for the two geographical types.

The nature of the interaction of date with hive size for energy collected by successful foragers each day is also revealed in the separate analyses of variance. For most days, effects of hive size were insignificant. However, on day 3 (Table 4) successful foragers from 40-litre hives collected significantly more energy (P<0·0004) than successful foragers from 20-litre hives. Significantly greater volumes (P<0·04) and greater concentrations (P<0·08) both contributed to this difference in energy content. On day 3, bees of both geographical types showed a difference for hive size, though that of Africanized bees was weaker.

## Foraging flights

European bees collected proportionately fewer loads on day 2 and proportionately more loads on day 3 and day 6. Yet, on each of these days more European bees left their nests on apparent foraging flights. In a combined analysis (Table 8) the difference was significant (P<0·04). Similar numbers of bees left hives of the two sizes. Bees of both geographical types left nests in greater numbers on day 6 (P<0·01).

TABLE 8. Analysis of variance for numbers of honeybees leaving nests of African and European colonies whose comb filled 20-litre or 40-litre hives during 1-min period on each of 3 days.

| | | | | | *Analysis of variance* | | | |
|---|---|---|---|---|---|---|---|---|
| *Geographical type of bee* | *Hive size (litres)* | *Day* | *No. colonies used* | *Mean (±SE) no. bees leaving in 1 min* | *Source of variation* | *df* | *F* | *P* |
| Africanized | 20 | | 15 | 18·2 ± 3·1 | Geo. type (T) | 1 | 4·50 | 0·04 |
| | 40 | | 15 | 18·4 ± 3·0 | Hive size (S) | 1 | 0·00 | 0·98 |
| | | 2 | 10 | 15·4 ± 2·3 | Day (D) | 2 | 5·52 | 0·01 |
| | | 3 | 10 | 14·1 ± 2·0 | T × S | 1 | 0·01 | 0·97 |
| | | 6 | 10 | 25·5 ± 4·9 | T × D | 2 | 0·03 | 0·92 |
| European | 20 | | 15 | 25·6 ± 3·9 | S × D | 2 | 1·37 | 0·26 |
| | 40 | | 15 | 25·1 ± 4·2 | T × S × D | 2 | 1·59 | 0·21 |
| | | 2 | 10 | 21·9 ± 3·4 | Error | 48 | | |
| | | 3 | 10 | 20·5 ± 4·8 | | | | |
| | | 6 | 10 | 37·7 ± 5·5 | | | | |

| | *Geographical type* | | *Hive size* | | *Day* | | |
|---|---|---|---|---|---|---|---|
| | *Africanized* | *European* | *20-litre* | *40-litre* | *2* | *3* | *6* |
| Mean | 18·3 ± 2·1* | 25·4 ± 2·8* | 21·9 ± 2·5 | 21·8 ± 2·6 | 18·7 ± 2·2 | 17·3 ± 2·6 | 29·6 ± 3·7** |

*Means are significantly different at P<0·04
**Significantly different from other daily means as judged by orthogonal comparisons (P<0·01)

## Nest weights

All nests lost weight during the experiment (Table 9). Nests of European bees lost less but the difference was not significant (P<0·21). Weight losses were similar for hives of the two sizes.

TABLE 9. Analysis of variance for changes in weight over 6 days of nests of Africanized or European honeybee colonies whose combs filled 20-litre or 40-litre hives.

| *Honeybee geographical type* | *Hive size (litres)* | *No. hives used* | *Mean (±SE) wt change (kg)* | *Analysis of variance: Source of variation* | *df* | *F* | *P* |
|---|---|---|---|---|---|---|---|
| Africanized | 20 | 5 | −0·40 ± 0·13 | Geo. type (T) | 1 | 1·73 | 0·21 |
| | 40 | 5 | −0·40 ± 0·09 | Hive size (S) | 1 | 0·01 | 0·94 |
| European | 20 | 5 | −0·24 ± 0·09 | T × S | 1 | 0·01 | 0·94 |
| | 40 | 5 | −0·22 ± 0·18 | Error | 16 | | |

| | *Geographical type: Africanized* | *Geographical type: European* | *Hive size: 20-litre* | *Hive size: 40-litre* |
|---|---|---|---|---|
| Mean | −0·40 ± 0·08 | −0·23 ± 0·09 | −0·32 ± 0·08 | −0·31 ± 0·10 |

## Discussion

Differences found in this study suggest the hypothesis that geographical types of honeybees are genetically adapted to foraging under resource conditions typical of their respective ecological areas. Moreover, adaptations seem to differ substantially between geographical types. Thus, it is likely that responses of foragers of different geographical types to a particular resource situation will rarely be similar.

Reports of comparatively greater honey yields in the tropics by African and Africanized bees than by European bees (see reviews by Gonçalves, 1975; Michener, 1975; Fletcher, 1978) probably stem from dissimilar foraging strategies differently adaptive to specific conditions rather than from absolute differences in nectar-gathering ability. Both the strong interactions between nectar loads and days and the numerically unequal weight losses by nests that we found suggest that in interpreting differential honey storage it is necessary to consider interactions between environment and geographical type.

The tendency of Africanized bees to collect somewhat more concentrated nectar may be rooted in foraging adaptations attuned to tropical nectar resources. Low humidity and high temperatures common during dry seasons can concentrate nectars after they are secreted. A higher threshold of nectar concentration required to stimulate foraging may be energetically efficient for both foraging and nectar-processing activities. However, the expression of this characteristic would be constrained by competition for nectar resources, rainy-season conditions, and availability of floral sources Núñez (1973, 1979), using artificial feeding stations, observed Africanized foragers collecting less food and spending less time foraging. He inferred that these foraging characteristics lead to more communication between bees and result in more rapid exploitation of newly occurring nectar sources. Our results do not support this interpretation. Better communication should lead to higher proportions of successful foragers. Yet, in our study Africanized bees had a lower proportion of successful foragers. Also, Africanized bees had daily rates of foraging success that varied considerably and included mid-range values. In contrast, European bees either had very low or very high rates of foraging success.

Presumably, bees that use increased levels of communication and recruitment and thereby improve their foraging success would be similar to the European bees in our study. Bees with strong tendencies toward group foraging (Johnson & Hubbell, 1975) and that are highly dependent upon communication and recruitment should have either very high or low success rates for foragers. High rates would occur when there is recruitment and low rates would occur when scouts find only a few nectar sources not of sufficient value to stimulate recruitment. Bees showing more reliance on individual foraging would likely have a lower rate of success (mid-range) in conditions where group foragers found favourable sources, especially when these sources are scattered and difficult to find without guidance.

Overall, our results suggest that Africanized bees are adapted to nectar resource conditions that are, in many cases, best exploited by individual foragers (Johnson & Hubbell, 1975). Honeybees encounter such conditions in North America in late summer and fall (Rinderer, 1982*b*). Typically, nectar sources are scattered and supply only limited amounts of nectar. Bees that forage on such sources individually without recruitment, and only use recruitment for those sources that are richer than the minimum requirements for foraging, are more successful under such conditions (Rinderer, 1982*b*).

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## References

BOLTEN, A. B.; FEINSINGER, P.; BAKER, H. G.; BAKER, I. (1979) On the calculation of sugar concentration in flower nectar. *Oecologia* 41 : 301-304

CRANE, E. (1975) The flowers honey comes from. *pp.* 3-76 *from* Honey: a comprehensive survey. *Ed.* E. Crane. *London: Heinemann in co-operation with International Bee Research Association*

FLETCHER, D. J. C. (1978) The African bee, *Apis mellifera adansonii*, in Africa. *A. Rev. Ent.* 23 : 151-171

FRANKIE, G. W.; BAKER, H. G.; OPLER, P. A. (1974) Comparative phenological studies of trees in tropical wet and dry forest in the lowlands of Costa Rica. *J. Ecol.* 62 : 881-913

FREE, J. B.; WILLIAMS, H. I. (1972) Hoarding by honeybees (*Apis mellifera* L.). *Anim. Behav.* 20 : 327-334

GARY, N. E.; LORENZEN, K. (1976) A method for collecting the honey-sac contents from honeybees. *J. apic. Res.* 15 : 73-79

GONÇALVES, L. S. (1975) Do the Africanized bees of Brazil only sting? *Am. Bee J.* 115 : 8-10, 24

INOUYE, D. W.; FAVRE, N. D.; LANUM, J. A.; LEVINE, M. D.; MEYERS, J. B.; ROBERTS, M. S.; TSAO, F. C.; WONG, Y. (1980) The effects of nonsugar nectar constituents on estimates of nectar energy content. *Ecology* 61 : 992-996

JOHNSON, L. K.; HUBBELL, S. P. (1975) Contrasting foraging strategies and co-existence of two bee species on a single resource. *Ecology* 56 : 1398-1406

JUNK, W. R.; PANCOAST, H. M. (1973) Handbook of sugars for processors, chemists and technologists. *Westport, CT, USA: Avi*

KULINČEVIĆ, J. M.; ROTHENBUHLER, W. C. (1973) Laboratory and field measurements of hoarding behaviour in the honeybee (*Apis mellifera*). *J. apic. Res.* 12 : 179-182

MICHENER, C. D. (1975) The Brazilian bee problem. *A. Rev. Ent.* 20 : 399-416

NÚÑEZ, J. A,. (1973) Quantitative investigation of the behaviour of *Apis mellifera ligustica* Spinola and *Apis mellifera adansonii* Latreille: energy factors, forager recruitment and foraging activity. *Apiacta* 8 : 151-154

——(1979) Times spent on various components of foraging activity: comparisons between European and Africanized honeybees in Brazil. *J. apic. Res.* 18 : 100-115

OERTEL, E.; RINDERER, T. E.; HARVILLE, B. G. (1980) Changing trends in Southeastern Louisiana honey production through 25 years. *Am. Bee J.* 102 : 763-765

PERCIVAL, M. S. (1961) Types of nectar in angiosperms. *New Phytol.* 60 : 235-281

RINDERER, T. E. (1981) Volatiles from empty comb increase hoarding by the honeybee. *Anim. Behav.* 29 : 1275-1276

——(1982*a*) Maximal stimulation by comb of honey bee hoarding behaviour. *Ann. ent. Soc. Am.* 75 : 311-312

——(1982*b*) Regulated nectar-harvesting of the honeybee. *J. apic. Res.* 21 : 74-87

RINDERER, T. E.; BAXTER, J. R. (1978) Effect of empty comb on hoarding behaviour and honey production of the honey bee. *J. econ. Ent.* 71 : 757-759

——(1979) Honey bee hoarding behaviour: effects of previous stimulation by empty comb. *Anim. Behav.* 27 : 426-428

——(1980) Hoarding behavior of the honey bee: effects of empty comb, comb color and genotype. *Envir. Ent.* 9 : 104-105

RINDERER, T. E.; BOLTEN, A. B.; HARBO, J. R.; COLLINS, A. M. (1982) Hoarding behavior of European and Africanized honey bees. *J. econ. Ent.* 75 : 714-715

RUTTNER, F. (1975) Races of bees. *pp.* 19-38 *from* The hive and the honeybee. *eds. Dadant and Sons. Hamilton, Il., USA : Dadant & Sons*

SNEDECOR, G. W.; COCHRAN, W. G. (1967) Statistical methods. *Ames, IA, USA : Iowa State Univ. Press*
SYLVESTER, H. A.; RINDERER, T. E.; BOLTEN, A. B. (1983) Honey-sac contents: a technique for collection and measurement in foraging honey bees. *J. econ. Ent.* 76 : 204-206
WYKES, G. W. (1953) The sugar content of nectars. *Biochem. J.* 53 : 294-296

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