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DIFFERENTIAL NECTAR FORAGING BY AFRICANIZED AND EUROPEAN HONEYBEES IN THE NEOTROPICS

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Summary

A one-year study was conducted on nectar foraging and honey storage by Africanized (tropical) and European (temperate) honeybee (*Apis mellifera* L.) colonies. Patterns of nectar foraging were distinctly different in the two geographical types. Among Africanized honeybees, lower proportions of the foraging force were engaged in foraging for nectar only, but a higher proportion foraged for both nectar and pollen. In addition, Africanized bees collected lower volumes per foraging trip than European honeybees, but returned to the colony with nectars having a higher sugar content. The two geographical types contributed similar amounts of joules (energy) per average forager and, therefore, made similar net contributions of carbohydrate energy to the colony. However, European colonies always had more stored honey than Africanized colonies. The observed differences in foraging patterns could not account for all of the measured difference in stored honey; several testable hypotheses are presented to explain this.

Introduction

If two geographical types* of bees evolve under the selective pressures of different ecological conditions, measureable differences should be detectable in their patterns of nectar collection and honey storage. Floral resources used by honeybees follow annual patterns of nectar secretion and availability in both temperate (Crane, 1975; Oertel et al., 1980) and tropical ecosystems (Roubik, 1979; Augspurger, 1983). Such differences in flowering patterns should result in detectable differences in foraging behaviour by bees adapted to each environment. Rinderer et al. (1984, 1985) suggest that Africanized and European honeybees are adapted to foraging under resource conditions typical of their respective ecological areas.

The success of Africanized honeybees in colonizing South America is indirect evidence of differences in their foraging patterns and honey storage from those of European honeybees. Their success contrasts with the failure of European honeybees to establish a large feral population in the same ecosystem after two centuries of repeated introduction (Winston & Katz, 1982).

One geographical type would contribute to the colony higher quantities than the other of energy for carbohydrate metabolism and storage if it (a) had more foragers, (b) had a higher proportion of the total foraging force collecting nectar, (c) collected larger volumes of nectar, (d) collected nectar of higher sugar concentration, (e) made more foraging trips, or (f) had a combination of the above.

This study compares nectar foragers of European and Africanized honeybees throughout a year in the neotropics. It assesses how each geographical type regulates foraging intensity, nectar-resource selection and honey storage in the same environment.

* The European honeybees used in this study were from North America, and their ancestry includes representatives of mixed subspecies. The Africanized bees are descendants of *A. m. scutellata* imported from Africa and their hybrids with various subspecies imported earlier into Brazil. Neither group can be regarded as belonging to a subspecies or race and so each is designated as a geographical type to indicate that its members show major characteristics of bees adapted to temperature or tropical regions as the case may be.

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Materials and Methods

The experiments were conducted 6 km southwest of Sarare, Estado Lara, Venezuela. The floral resources accessible to the experimental honeybees were mainly those of a deciduous, lowland, wet forest surrounded by patches of secondary successional grassland. Inspections of the surroundings of the experimental apiary revealed few feral colonies. Two apiaries, one Africanized (AF) and one European (EU), each with 20 colonies were located 50 m from each other. Experiments were performed from March 1983 to January 1984.

Two different management strategies were employed. Ten of the 20 colonies per geographical type were randomly chosen and equalized throughout the experiment. This involved estimating the comb area covered by sealed brood and adult honeybees of each geographical type, calculating the mean population size and adjusting the population of each colony to the appropriate mean value by adding or removing combs of brood and bees. This resulted in an Africanized apiary with 10 equalized and 10 non-equalized colonies and a European apiary with 10 equalized and 10 non-equalized colonies. The non-equalized colonies of each geographical type were left to expand their nest at their natural rate. This procedure allowed the comparison and characterization of nectar foraging in both uniform and dissimilar colony populations.

Honey production was assessed by weighing the colonies. All colonies had the same initial weight. Each colony was placed, by means of straps, on a hanging scale. The scale was suspended from a swinging boom located at the rear of a four-wheel drive truck. Colony weights were recorded every two weeks. For this study, only colony weights at harvest time were considered.

In order to study the nectar loads of foragers of each geographical type, 30 foragers were collected from each of five Africanized and five European colonies per apiary on the same day. These colonies were chosen randomly, remaining colonies were sampled on successive days. At 06.45 h. min the hive entrances were closed using entrance blocks, and foragers that were back to the hives by 07.00 h. min were collected using hollow cylinders provided with a top and a plastic bag attached to the bottom. Once in the cylinder, honeybees would fly towards the sun and into the collecting bags. When approximately 30 bees per colony had been collected, the bags were removed from the cylinder and placed in a cooler with ice to reduce their metabolic activity.

Within 5 min, the honeybees were placed in a freezer for 30 min to kill them and to avoid the regurgitation problems encountered with other killing methods (Gary & Lorenzen, 1976; Sylvester et al., 1983). This procedure minimized accidental stinging while handling the bees and avoided the use of cyanide.

Thirty foragers were chosen at random, sorted, examined and indexed according presence of a nectar load and volume and sugar concentration of the nectar. This was done by decapitating the honeybee and squeezing the abdomen between the thumb and forefinger so that the contents of the honey sac would flow through the oesophagus and into a 50-µl micropipette calibrated to 5 µl. Sugar concentration was considered equivalent to total amount of dissolved solids and was determined using a hand-held refractometer. The amount of energy (joules) contributed to the colony by each geographical type was calculated as a curvilinear relation between volume and per cent sugar (Bolten et al., 1979).

The same collecting procedure was repeated each day for four days until all 40 colonies were tested. Each four-day test was repeated once each week for the last three weeks of each month. Data were averaged over months to compare rainy- and dry-season influences. A total of 618 samples per geographical type were included in the statistical analysis.

The variables used to test the null hypothesis in each case were: (1) numbers of nectar-only foragers, (2) numbers of nectar foragers that also collected pollen, (3) total nectar foragers (nectar + nectar and pollen), (4) volume of nectar load per successful nectar forager, (5) sugar concentration of the nectar load per successful nectar forager, (6) joules of energy per successful nectar forager, (7) joules per average forager (the total amount of energy contributed by successful foragers divided by the total number of foragers in the sample), and (8) honey production. ANOVA procedures were performed on the data for a completely randomized design with a $2 \times 2 \times 2$ factorial treatment of geographical type, management and season.

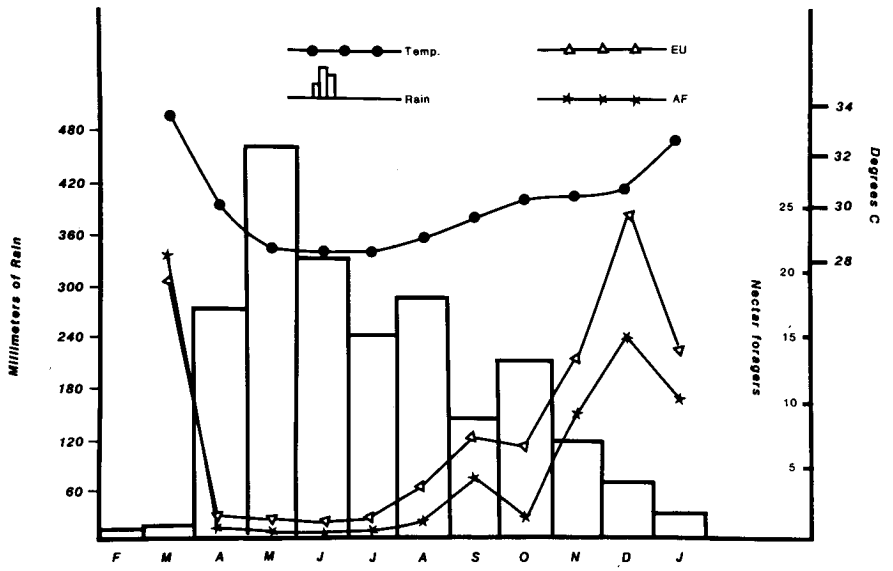

FIG. 1. Monthly mean temperature (°C), total monthly rainfall (mm) and monthly mean numbers of Africanized (AF) and European (EU) nectar-only foragers for the study site from February 1983 to January 1984.

Results

Nectar foraging by Africanized and European honeybees was inversely related to monthly rainfall for the study area (Fig. 1). In the neotropics the nectar flow occurs during the dry season, when the least rainfall and the highest temperatures occur. Fewer workers foraged for nectar during the rainy season (April–September). During this time not only are there reduced numbers of flowers, but nectar can be washed from flowers by the slightest rainfall.

Nectar-only foragers

A significant season–geographical type interaction was detected ($P<0{\cdot}0001$) as a result of European colonies having 2·5 times as many nectar-only foragers during the dry season as Africanized colonies (Table 1). Both honeybee types had reduced numbers of nectar foragers returning with nectar during the rainy season.

A significant management–geographical type interaction was detected ($P<0{\cdot}0223$; Table 1). Equalized Africanized colonies had fewer nectar foragers in the field than non-equalized colonies. European colonies did not exhibit any differences between equalized and non-equalized management, and in both cases had more nectar-only foragers than Africanized colonies.

Nectar and pollen foragers

Among Africanized foragers, twice as many returned to the colony with loads of both nectar and pollen as among European foragers ($P<0{\cdot}0001$; Table 1). A significant season–geographical type interaction ($P<0{\cdot}0001$) was detected. Differences between the two geographical types were non-significant during the rainy season whereas during the dry season Africanized honeybees had more nectar and pollen foragers.

Total nectar foragers

Total numbers of nectar foragers returning to the colony were higher for European than for Africanized honeybees ($P<0{\cdot}0001$; Table 1). A significant management–geographical type interaction occurred ($P<0{\cdot}0218$) as a result of Africanized bees having lower numbers of total

TABLE 1. Foraging success of Africanized (AF) and European (EU) honeybees from equalized (EQ) and non-equalized (NON-EQ) colonies in the neotropics during the dry and rainy seasons.

Least-square means and standard errors are listed for: number of foragers (n = 30) that collected nectar only (NO) and both nectar and pollen (NP) and totals for nectar collectors (TN); average volume in microlitres (VS) and average per cent sugar consent (SCS) of nectar loads of successful foragers; and average energy content (joules) per load for successful foragers (JS) and for all foragers (JA). Members of a group means in a column followed by different letters are significantly different.

Source of variation	*NO*	*NP*	*TN*	*VS*	*SCS*	*JS*	*JA*
Geographical type							
AF bees	3·39±0·33*b*	5·01±0·25*a*	8·40±0·41*b*	11·92±0·33*b*	33·45±0·68*a*	21·83±2·38*a*	2·05±0·29*a*
EU bees	8·54±0·33*a*	2·74±0·25*b*	11·28±0·41*a*	13·99±0·29*a*	29·43±0·60*b*	17·22±2·11*a*	2·77±0·29*a*
Season × type							
AF bees							
Dry season	5·85±0·54*a*	9·41±0·42*a*	15·26±0·67*a*	13·46±0·41*a*	31·82±0·84*b*	8·66±2·96*b*	3·03±0·46*a*
Rainy season	0·92±0·38*b*	0·61±0·29*b*	1·53±0·47*b*	10·39±0·51*b*	35·09±1·06*a*	35·00±3·72*a*	1·07±0·33*b*
EU bees							
Dry season	14·54±0·54*a*	4·75±0·42*a*	19·30±0·67*a*	15·42±0·40*a*	28·31±0·82*b*	6·37±2·90*b*	3·72±0·46*a*
Rainy season	2·54±0·38*b*	0·73±0·29*b*	3·27±0·47*b*	12·55±0·42*b*	30·54±0·87*a*	28·06±3·07*a*	1·82±0·33*b*
Management × type							
EQ colonies							
AF bees	2·58±0·47*b*	4·95±0·36*a*	7·53±0·58*b*	11·18±0·49*b*	34·17±1·00*a*	26·81±3·52*a*	1·98±0·41*a*
EU bees	8·23±0·47*a*	2·93±0·36*b*	11·76±0·58*a*	13·54±0·41*a*	28·52±0·84*b*	13·74±2·96*b*	2·27±0·40*a*
NON-EQ colonies							
AF bees	4·20±0·47*b*	5·07±0·36*a*	9·27±0·58*a*	12·67±0·44*b*	32·73±0·91*a*	16·85±3·19*a*	2·12±0·40*b*
EU bees	8·26±0·47*a*	2·54±0·36*b*	10·80±0·58*a*	14·43±0·41*a*	30·33±0·86*a*	20·71±3·02*a*	3·27±0·41*a*

	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Season (S)	1	323·61	0·0001	316·82	0·0001	661·81	0·0001	45·96	0·0001	9·32	0·0030	57·05	0·0001	22·83	0·0001
Management (M)	1	1·25	0·2662	0·14	0·7086	0·46	0·5003	7·38	0·0079	0·04	0·8395	0·22	0·6401	2·00	0·1610
S × M	1	1·58	0·2113	0·24	0·6274	0·52	0·4729	0·97	0·3281	24·68	0·0001	1·12	0·2923	5·29	0·0236
Geotype (G)	1	119·93	0·0001	39·71	0·0001	24·86	0·0001	22·14	0·0001	19·88	0·0001	2·10	0·1506	3·17	0·0780
S × G	1	56·47	0·0001	43·91	0·0001	3·95	0·0498	0·06	0·8076	0·33	0·5659	0·53	0·4664	0·00	0·9484
M × G	1	5·39	0·0223	0·50	0·4812	5·43	0·0218	0·47	0·4948	3·26	0·0744	7·08	0·0092	1·14	0·2893
S × M × G	1	0·34	0·5636	0·04	0·8451	0·12	0·7275	0·22	0·6395	4·02	0·0480	3·35	0·0706	1·83	0·1793
Error	98														

nectar foragers in equalized colonies compared with European ones. There were no detectable differences between Africanized and European total nectar foragers in non-equalized colonies.

Volume and sugar concentration of nectar loads

European nectar foragers returned to the colony with significantly larger volumes of nectar than Africanized foragers ($P<0{\cdot}0001$; Table 1). Larger volumes were recorded during the dry season for both honeybee types.

Africanized foragers returned to the colonies with nectar of higher sugar concentration than European foragers ($P<0{\cdot}0001$; Table 1).

Joules of energy per successful nectar forager and per average forager

A significant management–geographical type interaction was detected ($P<0{\cdot}0092$); however, non-significant differences for geographical type were observed within management strategy (Table 1).

Non-significant differences were observed in joules per average forager for each geographical type ($P<0{\cdot}7800$; Table 1).

Honey production

Africanized honeybee colonies were observed consistently to have less stored honey, regardless of management. Overall, European colonies averaged 52·5 kg while Africanized colonies averaged 32·0 kg ($P<0{\cdot}0001$; Table 2).

TABLE 2. ANOVA test and mean weights of colony and honey for Africanized (AF) and European (EU) honeybees for equalized (EQ) and non-equalized (NON-EQ) management strategies.

Source	*df*	*SS*	*F*	*P*
Management (M)	1	15·50	0·08	0·7855
Genotype (G)	1	4212·75	20·44	0·0001
M × G	1	1255·74	6·09	0·0185
Error	36			

Mean wt (kg) of colony and honey (n = 10)			
AF		*EU*	
EQ	*NON-EQ*	*EQ*	*NON-EQ*
27±4·5	37±4·5	59±4·5	46±4·5

Discussion

Regardless of management, European colonies consistently devoted a significantly larger proportion of their foraging force to foraging for nectar only, than did Africanized bees. The increase in nectar-foraging intensity of European honeybees should result in larger amounts of nectar being available for storage as honey.

Overall, Africanized honeybees had lower proportions of nectar foragers, with the lowest proportions occurring in colonies subjected to the equalization treatment. This is most likely due to the disturbing nature of the colony manipulation involved in equalizing the colony population (brood and bees) and to a mean density-value. No management effect was observed for the European honeybees.

Africanized honeybees had a larger proportion of their foraging force engaged in foraging for both nectar and pollen than European honeybees. This group makes a contribution of nectar to the colony in addition to that contributed by foragers that collect nectar only. However, European honeybees still had a larger proportion (1·32 times more) of their foraging force engaged in total nectar foraging. Successful European nectar foragers consistently returned to the colony with higher volumes of nectar, suggesting that Africanized bees have honey sacs corresponding to their smaller size, or the possible existence of differences in foraging behaviour, or both. Larger volumes of nectar should result in larger contributions of carbohydrate to the colony by European honeybees.

The higher the absolute concentration of sugars present in the harvested nectar, the greater will be the energetic contribution to the colony and the less the expenditure of energy in processing the nectar into honey. Successful Africanized nectar foragers returned to the colony with nectar of higher concentration than that collected by European honeybees. Moreover, when volume and per cent sugar were considered together, and joules per successful and per average forager were calculated, no significant geographical-type differences were observed. Therefore, although members of the two geographical types exhibited distinct differences in their nectar loads and foraging behaviour, on average both contributed the same amount of carbohydrate to the colony.

Honey storage by the two geographical types is important not only as a measure of reserves for periods of nectar unavailability but for practical considerations in apiculture. European honeybees had more stored honey regardless of management. Africanized honeybees produced more honey under non-equalized management conditions than under equalized conditions. This is in agreement with the reduction in numbers of nectar foragers observed in equalized Africanized colonies, possibly the result of their being more susceptible to disruption by hive manipulation or more sensitive to changes in colony demography. Certainly they fly and run more and become more intensely involved in colony defence than European colonies. Perhaps it takes them longer to re-organize after hive manipulation.

The consistent and significantly lower amounts of stored honey observed for Africanized honeybees is explained in part by the noted differences in foraging behaviour. However, these differences cannot account for all observed differences in stored honey. The higher number of foragers of European honeybees observed by Rinderer et al. (1985) leaving the colony may contribute to, but again cannot account for all, the difference in stored honey.

Lower amounts of stored honey by Africanized honeybees could also be the result of their having a higher consumption of carbohydrates per colony as a result of greater brood production. Africanized honeybees devote a larger proportion of their foraging force to the collecting of pollen, and of pollen and nectar (Pesante et al., 1987). These differences in pollen foraging correlate with an apparently higher demand by Africanized honeybees for pollen resources. Africanized honeybees in French Guiana were observed to cast a high number of swarms and afterswarms (Winston, 1978; Otis, 1980). Higher swarm production should require a higher production of honeybees to accompany such swarms.

Another factor which could possibly contribute to this difference in stored honey is that Africanized honeybees, as a result of their smaller weight (Otis, 1982), may well have a higher metabolic rate per individual. This would increase the carbohydrate maintenance needs and lead to less stored honey.

In conclusion, European honeybees secured larger stores of honey than Africanized honeybees. Therefore, European honeybees, considering their honey production and less aggressive defensive behaviour, remain the commercial bee of choice even in some areas of Latin America known currently to have Africanized honeybees.

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