

HONEY PRODUCTION AND UNDERLYING NECTAR HARVESTING ACTIVITIES OF AFRICANIZED AND EUROPEAN HONEYBEES

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Summary

Comparisons of Africanized and European honeybees (*Apis mellifera*) were made during two periods of different nectar availability in tropical dry forest in Venezuela. Field colonies were used to study honey yields, nectar-load characteristics, and flight activity including flight initiation and cessation. Observation-hive colonies were used to study dance communication and recruitment. Throughout these various measurements significant interactions occurred between geographic type of bee and period of nectar availability. Generally, in conditions of good nectar availability, European bees collected more and larger nectar loads, and produced more honey/colony/day than Africanized bees, possibly because of their more intensive recruitment of foragers. Africanized bees were marginally superior for some variables in conditions of low nectar availability. The results support the conclusion that, based on honey production alone, the European honeybee is the more desirable bee for use in commercial beekeeping.

Introduction

An importation of the African honeybee (*Apis mellifera scutellata*; Ruttner, 1976) to Brazil in 1956 was motivated by a desire to improve honey production (Kerr, 1967). Although the Africanized descendants of these bees continue to have major objectionable characteristics (Michener, 1975; Collins et al., 1982), they are reported to do well as honey producers (Kerr, 1967; Gonçalves, 1975). However, contrary reports of low honey production come from the beekeeping communities of Venezuela, Colombia, Panama and other Latin American countries (personal communication).

Some differences between Africanized (*A*) and European (*E*) honeybee nectar-harvesting activities have been reported. Rinderer et al. (1982a) found that in laboratory experiments *A* honeybees removed sucrose solution from feeders and hoarded it in combs (Free & Williams, 1972; Kulinčević & Rothenbuhler, 1973) more slowly than *E* honeybees. Núñez (1973; 1979), comparing *A* and *E* honeybees at an artificial feeding station, observed that *A* bees spent less time on various components of foraging, made briefer foraging trips and carried less nectar to the hive each trip. Fletcher (1978) reviewed several reports of African bees foraging in adverse light and temperature conditions. Rinderer et al. (1984) studied nectar-load characteristics of *A* and *E* bees and inferred that *A* bees tended to forage as individuals without relying on the communication and recruitment used in group foraging. In contrast, *E* bees tended to be group foragers. These inferences were based on the finding that on some days one geographical type* harvested more carbohydrate energy, while on other days the other type harvested more. Nectar availability during that study was sporadic and impaired by extended periods of rain. Consequently, group differences were only poorly reflected in measurements of stored honey.

Clearly, an in-depth experimental assessment of the value of *A* bees as honey producers was desirable. Accordingly, this research addressed the following questions for two distinct periods of nectar availability. (1) Do bees of the two geographic types have similar rates of nectar-foraging success? (2) Do bees of both types collect similar amounts of similar nectar? (3) Are similar numbers of bees of both types flying throughout the day? (4) Do bees of both types begin and end flight at similar times in the morning and evening? (5) Do foragers of the two types communicate and recruit with similar intensity? (6) Finally, do both types harvest and store similar amounts of honey?

* The *E* bees in this study were from North America. Such bees have mixed subspecies representatives in their ancestries. The *A* bees are descendants of *A. m. scutellata* imports and their hybrids with various subspecies representatives previously imported to Brazil. Neither the *E* nor *A* bees in this study can correctly be referred to as race, subspecies, stock, or line representatives. We use the term 'geographic type' to indicate that the bees we studied showed major characteristics typical of descriptions that have been made of temperately or tropically adapted bees.

Methods

The experiments were conducted 15 km west of Acarigua, Portuguesa, Venezuela (9° 3' N, 69° 12' W, 250 m elevation) during the dry season when the primary nectar sources were trees in the surrounding tropical dry forest.

The study was conducted during two periods of nectar availability (NP). The first NP lasted 10 days (22 January–2 February 1981) and provided relatively high nectar availability. The dominant nectar-secreting plants were widely scattered araguaney trees (*Tabebuia* sp.). Secretion by these trees, primarily at night, provided a rich but uneven source of nectar in the first hours of the morning.

In the second NP, which lasted 15 days (2–17 February), nectar availability was relatively weak. The araguaney trees had nearly finished flowering and they were replaced as a dominant nectar source by fence-row plantings of mataraton trees (*Gliricidia sepium*). These legumes appeared to produce nectar primarily during the day until mid- to late afternoon. Hence, in the second NP there were many more flowers for a longer period each day, with each flower producing much less nectar.

An apiary was established with 20 colonies having approximately equal populations and brood nests. Throughout the experiment, each field colony (FC) had a brood-nest of combs in 10 Hoffman frames measuring 45 × 29 cm and 3 honey-storage chambers each with combs in 10 frames measuring 45 × 13 cm. Honey-storage chambers were managed so that none contained honey at the beginning of a replication of the experiment. Ten colonies were derived from feral *A* queens which remained in the colonies throughout the experiment. The remaining 10 colonies were derived from *E* queens produced commercially in the southern United States.

Several variables were measured in the FC apiary. Honey production was measured as the change in colony weight during a NP. The nectar loads of foraging bees were also analysed. On each of 3 days within each NP, 10 nectar-foraging bees were collected in cyanide vials (Sylvester et al., 1983). Nectar loads were expelled (Gary & Lorenzen, 1976) and their volumes and concentrations recorded. Volumes were determined to the nearest 5 µl using a graduated micropipette. These measurements permitted estimates 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 (see Rinderer et al., 1984). Also, the number of bees leaving or entering each hive was counted during each NP. Additionally, the times at which *A* and *E* bees began foraging flights in the morning and ended flights in the evening was observed for 3 days during each NP.

A second apiary containing 10 observation hive colonies (OC) with approximately equal populations was established in a shaded area 50 m distant from the FC apiary. Each OC contained one brood comb, one empty honey-storage comb and one full honeycomb (each 45 × 13 cm). Five colonies were *A* and five were *E* bees. Mated queens of the appropriate type were introduced to the OC's when they were established.

The OC apiary was inspected on each of 3 mornings during each NP. Both sides of each colony were observed simultaneously for 5 min and the number of newly-initiated recruitment dances by nectar-foraging bees was counted (see Rinderer, 1982). After the counts the maximum number of recruited bees following each of 4 dancing bees was recorded as well as the duration of the dance. Rates of recruitment (number of bees recruited in 5 min) were estimated from numbers of dancing nectar-foragers multiplied by the average number of recruits following a single dancing bee.

Results and Analysis

Nectar loads

Several major differences between geographic types of bees were revealed by the analysis of variance of the data from the entire experiment (Table 1). European bees collected larger nectar loads, both the successful *E* foragers and the groups of *E* foragers harvested more energy, and more *E* foragers were successful in securing nectar loads ($P < 0.001$ for all comparisons).

The nectar periods also differed significantly. Mean values in NP-2 were greater ($P < 0.001$) for all 5 independent variables (volume of nectar loads, concentration of nectar loads, energy collected by successful nectar foragers, energy collected by all nectar foragers and numbers of

TABLE 1. Foraging success of Africanized (*A*) and European (*E*) honeybees from field colonies in 2 nectar-flow periods (NP)

For each NP, 10 bees were sampled from each of 10 colonies of each geographic type on each of 3 days. Each set of statistical values from the analysis of variance in the lower part of the table is for the column above. Energy content is expressed in joules ($0.238 \text{ J} = 1 \text{ cal}$) for all nectar foragers (ANF) and successful nectar foragers (SNF). Numbers of successful foragers were analysed by χ^2 .

Geographic type and NP	Nectar loads				SNF	
	Vol (μl)	Concn (%)	SNF	ANF	No.	%
<i>E</i> bees	30.6±1.1	34.1±0.8	182±7	165±8	1071	89.3
NP-1	26.1±1.5	31.8±1.3	150±8	129±8	510	85.0
NP-2	35.2±1.0	36.3±0.6	215±5	202±8	561	93.5
<i>A</i> bees	21.1±1.3	32.6±1.1	135±9	241±10	964	80.3
NP-1	14.9±1.0	28.6±1.2	90±9	65±8	425	70.8
NP-2	27.4±1.6	36.9±1.4	181±12	166±11	539	89.8
NP-1	20.5±1.1	30.0±0.9	127±7	97±7	935	77.9
NP-2	30.6±1.1	36.6±0.8	198±7	184±8	1100	91.7

Source of variation	df	F	P	F	P	F	P	F	P	χ^2	df	P
Geographic type (T)	1	94.7	0.001	2.5	0.12	35.7	0.001	40.0	0.001	37.0	1	0.001
Period (P)	1	122.3	0.001	48.5	0.001	98.4	0.001	119.2	0.001	88.0	1	0.001
T × P	1	2.9	0.09	4.8	0.03	2.5	0.12	3.2	0.08	3.3	1	0.07*
Day (D)	2	1.8	0.16	2.7	0.07	2.3	0.11	0.7	0.53			
Sampling	108											

*Heterogeneity χ^2 (Snedecor & Cochran, 1967).

successful nectar foragers). Foraging performance for the days within NPs was reasonably constant since no variable differed significantly between days.

The independent variables geographical bee-type and NP interacted significantly ($P < 0.03$) in the analysis of nectar-load concentration data. Bees of both geographic types collected more highly concentrated nectar during period 2 but the difference was greater for *A* bees. The pattern of interaction was also evident for nectar-load volume ($P < 0.09$), for energy collected by successful nectar foragers ($P < 0.12$) and by all nectar foragers ($P < 0.08$), and numbers of successful nectar foragers ($P < 0.07$). Generally, *E* bees were much superior for all nectar-load variables in NP-1. In NP-2, the *A* bees were relatively improved and their performance was closer to that of *E* bees. However, in NP-2, *E* bees remained numerically superior to *A* bees for all nectar-load variables except nectar concentration.

Flight activity

Overall, flight activity of *E* bees, as indicated by numbers entering or leaving the colony, was greater ($P < 0.001$, Table 2). This was true for both NPs since the bee type-NP interaction term in the analysis was not significant. However, the independent variables bee type and hour did interact significantly ($P < 0.014$). Inspection of the data shows that this interaction resulted from a more precipitous reduction in flight activity of *E* bees as the day progressed.

Flight activity between the NPs differed strongly ($P < 0.001$); many more bees flew during NP-2. Flight activity also differed ($P < 0.001$) among the 90-min periods, being greater earlier in the day. Also, the variables NP and time of day interacted strongly ($P < 0.001$), the reduction in flight through the day being sharper during NP-1.

TABLE 2. Least squares analysis of variance, means and standard errors for numbers of bees entering or leaving 10 hives each of Africanized (*A*) and European (*E*) honeybees during six 5-min intervals as observed on 3 days in each of 2 nectar-flow periods (NP). Number of colonies used in each test is denoted by *n*.

Geographic type and NP	<i>n</i>	Mean no. bees at						Analysis of variance				
		7.00	8.30	10.00	11.30	13.00	15.30	Source of variation	<i>df</i>	<i>F</i>	<i>P</i>	
<i>E</i> bees	60	593±50	337±32	239±25	194±23	141±10	158±19	Geographic type (T)	1	17.3	0.001	
NP-1	30	424±55	225±21	147±17	102±11	131±11	159±20	Period (P)	1	196.3	0.001	
NP-2	30	762±36	449±32	335±18	286±17	151±10	157±16	Hour (H)	5	107.5	0.001	
								T × P	1	0.1	0.74	
<i>A</i> bees	60	480±54	236±38	192±24	174±19	145±13	157±21	T × H	5	2.9	0.014	
NP-1	30	306±30	101±10	109±15	128±17	119±9	119±14	P × H	5	18.3	0.001	
NP-2	30	654±69	370±44	274±26	219±29	170±23	194±36	T × P × H	5	1.2	0.27	
								Sampling	216			
NP-1	60	365±33	163±18	126±12	115±10	125±9	139±10					
NP-2	60	708±39	410±28	305±17	253±18	161±12	176±19					

Means for main effects	Geographic type		NP		Hour					
	<i>E</i>	<i>A</i>	1	2	7.00	8.30	10.00	11.30	13.00	15.30
	277±18	231±16	172±11	336±20	534±38	289±26	215±18	184±15	143±8	157±11

Initiation and cessation of flight

On each of the 6 days (3 for each NP) both *A* and *E* bees from every colony in the experiment began flying in large numbers before sunrise when measured illumination at colony entrances was 1 lx. The last bees returned to both *A* and *E* colonies shortly after sunset when measured illumination was *c.* 5 lx.

Dance communication and recruitment

Data in Table 3 indicate that more *E* nectar-foragers performed recruitment dances ($P < 0.01$), more *E* recruit-bees followed dancing nectar-foragers ($P < 0.01$), *E*-bee recruitment dances lasted longer ($P < 0.02$), and the rate of *E*-bee recruitment was higher ($P < 0.003$).

During NP-1, more dances, of longer duration, occurred with *E* nectar-foragers resulting in a greater rate of recruitment ($P < 0.006$).

Most measures of recruitment decreased from the first to the second nectar-flow period for *E* bees but remained about the same for *A* bees. There were significant interactions between the independent variables of bee type and NP for 3 dependent variables related to recruitment: numbers of bees recruited by individual dancing bees ($P < 0.003$), estimated total of recruits ($P < 0.02$) and duration of dances ($P < 0.004$). The same trend occurred in numbers of dancers, though less strongly ($P < 0.23$).

Honey production

Although *E* bees produced slightly more honey than *A* bees over the two NPs (Table 4), the difference was not significant. Honey production for NP-2 was much greater ($P < 0.004$).

Most importantly, there was a strong geographic type-NP interaction ($P < 0.037$). A closer inspection of the data using the *t*-test showed that in the first period the *E* bees produced significantly more honey (*E* production = 0.41 kg/colony/day; *A* production = 0.17 kg/colony/day; $t = 10.73$, $df = 18$, $P < 0.001$), whereas in the second the *A* bees produced more, though the difference here was not significant. The large variance associated with honey production by *A* bees ($SE = 0.18$) was too great to allow a conclusion to be drawn from the difference.

TABLE 3. Numbers of nectar foragers initiating dancing in a 5-min period after foraging, numbers of recruit-bees following individual dancing bees, estimated total recruits and duration of dances in 5 Africanized (A) and 5 European (E) colonies of honeybees on 3 days in each of 2 nectar-flow periods (NP).

Rates of recruitment (no. bees/5 min) are estimated from numbers of dancing nectar-foragers multiplied by average numbers of recruits following single dancers. Each set of statistical values from the analysis of variance in the lower part of the table is for the column above.

Geographic type and NP	No. dancing nectar foragers	No. recruits following a single dancer	Rate of recruitment	Duration of dancing(s)
E bees	8.6±1.0	2.8±0.2	26.2±3.7	47.6±2.7
NP-1	10.9±1.5	3.3±0.2	36.9±5.1	58.3±3.7
NP-2	6.3±1.2	2.3±0.2	15.5±3.8	36.9±4.1
A bees	5.2±0.9	2.3±0.1	13.2±2.6	37.8±3.2
NP-1	5.8±1.3	2.1±0.2	14.2±4.0	35.8±4.3
NP-2	4.6±1.2	2.4±0.2	12.3±3.3	39.8±4.7
NP-1	8.3±1.1	2.7±0.1	25.6±3.8	47.0±2.8
NP-2	5.5±0.9	2.4±0.1	13.9±2.5	38.4±3.1

Source of variation	df	F	P	F	P	F	P	F	P
Geographic type (T)	1	6.0	0.02	6.9	0.01	10.0	0.003	5.4	0.02
Period (P)	1	4.2	0.05	2.7	0.11	8.1	0.006	4.2	0.05
T × P	1	1.5	0.226	9.7	0.003	5.6	0.02	9.1	0.004
Sampling	48								

TABLE 4. Honey production (kg/colony/day) of 10 European (E) and 10 Africanized (A) full-sized colonies of honeybees during 2 different nectar-flow periods (NP) together with analysis of variance.

Geographic type	NP			Analysis of variance			
	1	2	Combined (1+2)	Source	df	F	P
E	0.41±0.02	0.48±0.04	0.45	Type (T)	1	0.78	0.38
				Period (P)	1	9.24	0.0004
				T × P	1	4.64	0.037
A	0.17±0.01	0.64±0.18	0.38				
Combined (E+A)	0.29	0.53					

Discussion

The chief patterns of variation in nectar loads found in this study are consistent with the trends for similar data presented by Rinderer et al. (1984). In both studies, interactions occurred between the independent variables of bee type and conditions of nectar availability. In the present study, E bees were superior during NP-1 in collecting more and larger nectar loads and thus achieving greater energy gains on either an individual or a group basis. In NP-2, the two types were more similar in their performance. In general, then, foraging success and nectar-load characteristics are the result of interactions between bee type and conditions of nectar availability rather than the strict superiority of one type in all conditions.

In both this study and that of Rinderer et al. (1984), more E bees made apparent foraging flights. Colonies in the 1984 study each had identical bee populations by weight. Since A bees weigh less (Otis, 1982; Rinderer et al., 1982b), those E colonies actually had fewer bees. In the present study, colonies of the two geographic types had approximately equal numbers of bees

as judged by field inspections of colonies. A comparison with the number of bees flying in the 1984 study, when colony populations were known precisely, supports the conclusions from the present study that in *E* colonies a greater proportion of the population are foragers.

The larger proportion of foragers in the *E* colonies strongly affects their net honey yield. Extra foragers are highly productive in conditions of high nectar availability when all foragers are collecting resources. However, in conditions of low nectar availability where a large number of the additional foraging bees are unsuccessful the energy costs incurred by a colony remain high. Because of this, European bees, with their larger field force, require better nectar resources than Africanized bees to balance energy gains and energy losses from foraging.

The strict uniformity of flight initiations and cessation of *A* and *E* bees in both NPs strongly suggests that there are no fundamentally important differences in these aspects of behaviour. Reported differences (Fletcher, 1978; Kerr et al., 1970) apparently are not sufficiently ubiquitous to incorporate them into a general model for comparative nectar foraging and honey production.

Measures of dance communication and recruitment also showed strong interactions between the independent variables bee type and NP. The trend of these interactions followed those seen in measures of nectar load. During NP-1, *E* bees used dance communication and recruitment much more intensively than *A* bees. During NP-2, both types of bees reduced their use of dance communication and recruitment and were similar with respect to two measurements.

The significantly greater use of dance communication and recruitment by *E* bees supports the hypothesis of Rinderer et al. (1984) that *E* bees tend to be group foragers whereas *A* bees tend to be individual foragers. Originally, this difference was inferred from dissimilar patterns of foraging success for *E* and *A* bees.

The same general pattern of interaction appears again in the analysis of honey-production data. *E* bees produced significantly more honey during NP-1 but somewhat less during NP-2.

Collectively, our results support the conclusion that *E* bees are superior nectar foragers and honey producers in conditions of rich nectar supply owing to a more intensive use of recruitment. Alternatively, at least some *A* bees are superior honey producers in conditions of poor nectar availability through a more intensive use of individual foraging. Probably these differences exist because natural selection has shaped honeybee foraging patterns differently in different ecological areas (see Rinderer et al., 1984).

Nectar foraging and honey production by *E* bees are highly regulated by the amount of empty comb in their hives (Rinderer, 1982). Honey production by *E* bees can be improved by the provision of either more storage comb during periods of good nectar availability or less storage comb during periods of poor nectar availability. Africanized bees are also subject to regulation by empty comb but respond less to additional comb during periods of strong nectar availability (Rinderer et al., 1984). Thus, *E* bees are more responsive to management procedures useful for maximizing production. Because of their ability to be managed more effectively for different nectar conditions, *E* bees appear to be the more desirable commercial bee type on the basis of honey yield alone. Considering as well the increased management problems attending the more intense colony defence of *A* bees (Collins et al., 1982), *E* bees are clearly the more commercially desirable type.

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