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Research article

Diet selection and foraging distances of African and European-African hybrid honey bee colonies in Costa Rica

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Summary

Diet selection and foraging distances were compared among 3 pairs of matched colonies of African an European-African hybrid honey bees in Northwestern Costa Rica. Mitochondrial DNA (mtDNA) analysis was used to classify each colony as neotropical African (possessing African mtDNA) or hybrid (possessing European mtDNA, and therefore containing workers arising from a European queen mated to African drones). African and hybrid colonies did not differ significantly in population size, the areas of comb devoted to brood rearing and food storage, flight activity, pollen foraging activity, or the distances traveled to pollen and nectar sources. These nonsignificant differences suggest that the foraging behavior of the two colony types may have been more influenced by environmental factors than by genetically determined dietary or movement preferences. Conversely, such genetically determined preferences may have been expressed, but African-like preferences may have been dominant within both colony types. However, while no significant differences were observed, colonies with African mtDNA maintained slightly greater levels of brood rearing, had 1.5 times the level of pollen foraging activity, and traveled on the average 600 m less per round trip of foraging. The potential influence of these slight but consistent differences on the long-term, relative success of African versus hybrid colonies is discussed.

Introduction

Since its introduction into Brazil in 1956–57, the African honey bee race, *Apis mellifera scutellata*, has spread throughout the neotropics and has recently arrived in the southern United States (Hunter et al., 1991; Winston, 1992). During the colonization process, *A.m. scutellata* and European honey bee races have hybridized in some regions, and such hybrids are referred to as the "Africanized honey

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bee" (Winston, 1992; Hall, 1992). However, levels of hybridization are asymmetrical between African and European matrilines. African matrilines exhibit little or no hybridization, while European matrilines are extensively hybridized (Lobo, 1995; Hall, 1992). Substantial hybridization may occur when African swarms first move into an area containing large, pre-existing populations of European colonies, but such populations become increasingly African over time, suggesting a loss of European alleles (Hall, 1990, 1992; Boreham and Roubik, 1987; Sheppard et al., 1991 a; Smith, 1991). As a result, African matrilines now predominate in the feral honey bee population in many neotropical regions, while colonies resulting from European queens mated to African drones (European-African hybrids) are typically confined to managed apiaries maintained at higher elevations or in transitional zones between tropical and temperate habitats (Lobo et al., 1989; Sheppard et al., 1991 a, b; Hall and McMichael, 1992; Spivak, 1992; Rinderer et al., 1991, 1993; Diniz-Filho and Malaspina, 1995; Lobo, 1995). Indeed, while the honey bees of Central and South America are no longer genetically identical to the ancestral population in Africa, recent studies reveal that they are predominantly African in their mitochondrial DNA, nuclear DNA, allozymes and behavioral characteristics over much of their range (Lobo et al., 1989; Hall and Muralidharan, 1989; Hall 1990, 1992; Smith, 1991; Lobo, 1995; McNally and Schneider, 1996). The factors contributing to this asymmetrical hybridization are unclear. African matrilines may simply have a numerical advantage, or European-African hybrids may have a selective disadvantage in tropical habitats (Page, 1989; Hall, 1990, 1992; Smith, 1991; Harrison and Hall, 1993; Diniz-Filho and Malaspina, 1995; Lobo 1995). However, there has been little direct comparison of the behavior and biology of the two colony types in the neotropics.

Two characteristics in which African and European-African hybrid colonies may differ in biologically significant ways are (1) diet selection (an emphasis on pollen versus nectar collection) and (2) foraging distances. Pollen and nectar collection have heritable components. European colonies can be selected for high and low pollen collection behavior (Hellmich et al., 1985; Calderone and Page, 1988, 1992; Page and Fondrk, 1995), and there can be subfamily differences within colonies for pollen versus nectar foraging (Robinson and Page, 1989; Robinson, 1992; Guzman-Nova et al., 1994). Danka et al. (1987) observed greater pollen collection activity for African versus European colonies when foraging in the same environment in Venezuela. Since pollen provides the nutrients necessary for brood rearing, a greater emphasis on pollen collection may contribute to more rapid growth and a higher reproductive rate for tropically adapted bees. Thus, the predominance of African matrilines in the neotropics could be associated with differences in pollen foraging behavior between African and European-African hybrid colonies.

Foraging distances may also differ among bee types. Subfamilies within colonies can exhibit genetically determined differences in foraging distance preferences and in the plant species visited for pollen (Oldroyd et al., 1992, 1993). African and European honey bees exhibit genetically determined differences in waggle dance dialects, which may be causally related to the normal foraging range of each race (Gould and Towne, 1987; Schneider, 1989). The distribution of foragers throughout the environment influences the energy expended on harvesting resources. A difference in foraging distances between African and European matrilines may there-

fore be associated with the relative success of the two colony types in the neotropics. However, pollen collection activity and foraging distances for African versus European-African colonies have not been determined.

The purpose of this study was to compare the foraging behavior of matched colonies of African and European-African hybrid bees occupying the same environment. The specific objectives were to compare the two colony types with respect to: (1) pollen collection activity and recruitment for pollen sites; and (2) foraging distances traveled to pollen and nectar sources.

Materials and methods

Study area

The study was conducted from January to April 1995 on the Stewart Ranch near Bagaces in Guanacaste, Costa Rica. African honey bees have been in Costa Rica for over a decade, and appear to have replaced European bees (Hall, 1990; Spivak, 1991). Colonies in Guanacaste and surrounding regions are predominantly African in their genetic, morphometric and behavioral characteristics (Spivak, 1991; Hall and McMichael, 1992; McNally and Schneider, 1996). Beekeepers in Guanacaste and surrounding areas maintain African colonies, or periodically introduce into their colonies European queens that have been open-mated. Because most colonies in the region possess African mitochondrial DNA (Hall and McMichael, 1992; Lobo, 1995; Schneider, 1995), the majority of drones produced in the area are African. As a result, open mated queens are likely to mate largely or entirely with African drones. Thus, honey bee colonies in Costa Rica are either African or European-African hybrids; "pure" European colonies are rare or absent (Hall and McMichael, 1992; Lobo, 1995).

Determining colony type

The study utilized a total of nine colonies purchased from local beekeepers and transported 10–50 km to the study site. Colonies were originally selected as presumptive African or European-African hybrids based on: (1) capture as feral swarms (likely to be an African matriline); (2) requeening with open-mated European queens (i.e., mated with African drones and thus hybrid); and (3) measurements of cell sizes. African honey bees construct smaller diameter cells compared to European bees when comb is built "naturally" (i.e., not based on a commercially produced wax foundation). We estimated for each colony the mean diameter of naturally constructed worker cells in the brood comb area by measuring the linear distance spanned by 10 cells in each of 3 diagonal rows of cells. In the neotropics European-like colonies have cells sizes that range from 5.0–5.4 cm/10 cells, while African-like colony cell sizes range from 4.6–5.0 cm/10 cells (Spivak, 1991). However, cell sizes for colonies resulting from known levels of hybridization have not been determined, and thus this factor alone is insufficient for conclusively determining colony type.

Final determinations of colony type were based on mitochondrial DNA (mtDNA) analysis. Immediately upon transport to the study site, 25 workers were collected at random from the combs of each colony and preserved in 90% ethyl alcohol. The mtDNA identifications were conducted using a method based on the polymerase chain reaction (Hall and Smith, 1991). Two workers were analyzed from each colony (the remainder of the 25 collected workers were used in a different study). Mitochondrial DNA is maternally inherited and non-recombining (Hall, 1991). Therefore, workers with African mtDNA are the offspring of an African queen. Conversely, workers from an "Africanized" colony that possess European mtDNA are hybrids resulting from a cross between a European queen and African drones. In this study colonies containing workers with African mtDNA were classified as African; those with European mtDNA were classified as hybrids.

Other methods of discriminating between colony types (morphometrics; allozyme analyses; nuclear DNA analyses) were not conducted. We therefore did not directly assess the possibility that our African queens may have mated with European drones, nor did we determine the exact extent to which queens with European mtDNA had outcrossed with African drones. However, recent studies have revealed that feral colonies in northwestern Costa Rica are almost exclusively African in their mitochondrial DNA and predominantly African in their nuclear DNA and allozymes (Hall and McMichael, 1992; Lobo, 1995). These studies suggest that there is little mating between African queens and European drones, and that all colonies arising from open-mated queens contain a substantial African nuclear genetic component. Classifications based on mtDNA, in conjunction with the known histories and cell sizes of the colonies, were therefore considered sufficient to distinguish between African and hybrid colonies in the present study. All mtDNA analyses were conducted after the study ended, and thus the exact nature of each colony was not known during data collection.

Colony set-up and maintenance

Foraging behavior was examined by establishing African and European-African hybrid colonies in four frame, glass walled observation hives maintained in a high-walled nylon tent ($3 \times 5 \times 2$ m) located in the shade and lined internally with heavy brown paper to reduce heat and light levels. Each observation hive abutted a 4×10 cm opening cut into a tent wall to allow free flight to and from the colonies. The entrance for each colony was located on a separate tent wall to minimize the drifting of workers between colonies. Each colony was supplied with water *ad lib* through a gravity feed attached to a screened chamber at the bottom of the observation hive.

Food collection activity can vary markedly within and among colonies as the foraging environment changes (Schneider, 1989; Visscher and Seeley, 1982; Waddington et al.; 1994). A more complete picture of foraging behavior therefore requires that different colonies are examined for extended periods under a variety of foraging conditions. Thus, the present study was subdivided into three, 3-week time periods: Period 1 (Jan. 23–Feb. 10); Period 2 (Feb. 23–Mar. 14); Period 3 (Mar. 23–Apr. 7). Three observation colonies were established in each period, as

follows: Period 1, 2 African and 1 hybrid colony; Period 2, 2 hybrid and 1 African colony; Period 3, 2 African and 1 hybrid colony. Thus, a total of 5 presumptive African and 4 presumptive hybrid colonies were established. Each colony was monitored in only one of the three periods, and thus each period contained a separate set of African and hybrid colonies.

Honey bee foraging behavior is strongly influenced by colony food requirements (Seeley, 1995). To control for the possible effects of nutritional needs on pollen collection and foraging distances, all of our study colonies were established to be as similar as possible with respect to initial population size and amounts of brood and stored food. Colony population size and the areas of comb containing brood, pollen and honey were estimated immediately after each hive was established using a grid of 5 cm × 5 cm squares drawn onto the observation hive walls. Subsequently, population sizes and comb areas were estimated for each colony every 4 days, for a total of six estimates of each variable per colony. Population sizes were estimated by counting the number of bees in 10 randomly selected grid squares, calculating a mean number of bees per square, and then multiplying by the total number of squares of comb. All population counts were conducted in the evening after foraging had ceased so that most bees were present in the hives. Approximately 10% of the initial total comb area in each colony was empty to stimulate foraging activity (Rinderer, 1982).

Monitoring foraging behavior

Foraging activity, diet selection and foraging distances were examined by monitoring flight, pollen collection and recruitment activity. Each colony was monitored on 12 separate days spaced throughout one of the 3-week periods. All colonies established within each 3-week period were monitored on the same days. During each day, each colony was observed for 15 min every hour from 5–17 h. For every hourly period, four 1 min counts were made of the number of bees flying from the hive and the number of workers returning with pollen. Flight counts were not conducted during periods of orientation flight activity, during which younger workers learn the location of the nest and surrounding landmarks (Winston, 1987). Because most other flight activity of honey bee colonies is associated with foraging, the flight counts reflected predominantly food collection activity.

We then determined for each colony for each day: (1) mean number of bees flying from the hive per min over all hourly periods; (2) mean number of pollen foragers returning per min over all hourly periods; and (3) mean number of pollen foragers returning per min between 5–8 h (the period of maximum pollen foraging activity). Twelve daily means were calculated for each colony for each variable, and subsequent analyses were conducted on these daily means.

Foraging distances were inferred by monitoring waggle dances. The waggle-run portion of the dance communicates distance to food sites, with more dance time corresponding to greater distances (von Frisch, 1967; Michelsen et al., 1992). During each 15 min observation period, waggle dancers were selected at random and a digital stopwatch was used to time the duration of 6.5 ± 2.4 different waggle-runs per bee. A mean waggle-run duration was then calculated for each dancer

(obviously inconsistent dance times were ignored). The mean dance times were converted into a distance estimate in meters using calibration curves, established by (1) training marked workers to feeding stations at known distances up to 1200 m from the hives, and then (2) timing their waggle-runs once they returned to the colonies (see Schneider, 1989, 1995; Schneider and McNally, 1992 a for further descriptions of measuring and translating waggle-run durations). Calibration curves were generated for 2 African and 2 hybrid colonies. The curves were very similar within the two colony groups (Fig. 1), and were thus combined to give one curve for each colony type. The resulting curve for both the African and hybrid colonies exhibited a slight change in slope at around 350–400 m, which corresponded to approximately 0.90 s of waggle-run time. Therefore, two regression formulae were generated for each colony type, one for dance times < 0.90 s and one for dance times ≥ 0.90 s. For the African colonies these two formulae were, respectively: Dance time $= -0.0667 + 0.00246 \times$ Distance; and Dance time $= 0.198 + 0.00165 \times$ Distance. For the hybrid colonies the two formulae were, respectively: Dance time $= -0.073 + 0.00246 \times$ Distance; and Dance time $= 0.144 + 0.00157 \times$ Distance. These formulae were subsequently used to translate the distances communicated by all observed dancers.

For each waggle dancer, it was noted if the bee carried pollen loads. Those without pollen were assumed to be nectar or water collectors. However, because colonies were given a constant supply of water directly into the observation hives, there was probably little waggle dancing for other water sites, and any such dancing should have occurred during the hotter times of the day. Typically, little or no waggle dance activity was observed during the hotter hours, suggesting that the majority of dancers without pollen loads were communicating the location of nectar sources.

We then determined for each colony for each day: (1) mean foraging distance communicated by all dancers (mean total foraging distance); (2) mean pollen foraging distance; (3) mean nectar foraging distance; and (4) the proportion of

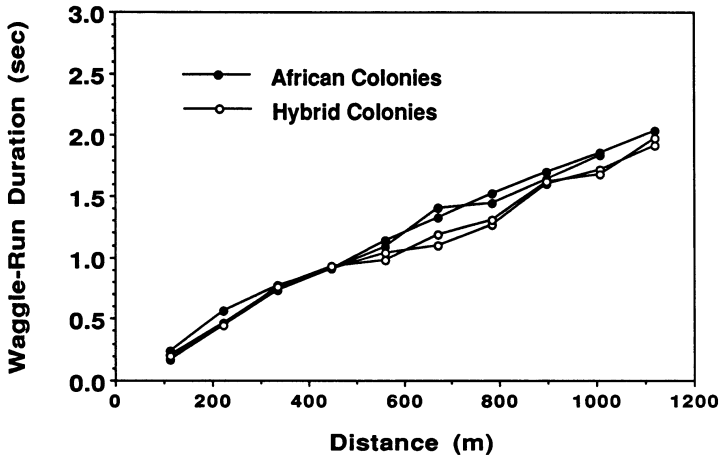

Figure 1. The relationship between flight distance and waggle-run duration for the 2 African and 2 hybrid colonies examined

waggle dancers indicating pollen sites. Twelve daily means were calculated for each foraging distance variable for each colony, and analyses of foraging distances were based on these daily means.

Statistical analyses

Each of the 7 aspects of foraging activity examined was subjected to a two-way repeated measures analysis of variance that had: (1) two between-subjects factors, colony type (African versus hybrid) and period (differences among the 3 periods), with a colony type × period interaction, and (2) one within subject factor (day of observation). All means are reported as ± one SE.

Results

Colony identifications

The cell sizes, results of the mtDNA analyses and the final classification of the colonies during each period of study are presented in Table 1. Colony A1 became permanently queenless shortly after establishment and was excluded from the data analyses, because queenlessness may influence foraging behavior (Winston, 1987). Colony 6 in period 2 and colony 7 in period 3 contained workers with African and European mtDNA (Table 1), suggesting the drifting of workers between colony types prior to transport to the study site. Because mixed colonies exhibit different foraging patterns from either "pure" African or European colonies (Danka et al., 1987), colonies 6 and 7 were also excluded from the data analyses. Thus, the final analyses were restricted to 3 African and 3 hybrid colonies, with one colony of each type occurring in each period (Table 1). The elimination of three of the study colo-

Table 1. The mean cell size, the results of the mtDNA analysis and the final classification of each colony established in the three periods of the study. Two workers were examined in each colony. Colonies with African mtDNA were considered neotropical African (A); those with European mtDNA were classified as hybrids (H)

Period	Colony No.	Cell sice	mtDNA analysis		Final Classification
		(cm/10 cells)	Worker 1	Worker 2	
1	1	4.65	African	African	A1*
	2	5.05	European	European	H1
	3	4.55	African	African	A2
2	4	5.00	European	European	H2
	5	4.75	African	African	A3
	6	5.15	European	African	?**
3	7	4.70	African	European	?**
	8	4.90	European	European	H3
	9	4.75	African	African	A4

* Became permanently queenless and was excluded from the study.
** Excluded from the data analyses because of ambiguous mtDNA results.

nies simplified the statistical analysis to a two-way repeated measures ANOVA without replication, such that there was no colony type × period interaction term.

Colony size and comb areas

The African (A) and hybrid (H) colonies were similar in population size and the proportions of total comb area containing brood and food both when initially established and throughout the different periods of study. When first established, the colonies contained 6465 ± 118 bees, 51.6 ± 3.7% of the comb contained brood, 4.4 ± 0.6% contained pollen, and 34.2 ± 2.0% contained honey (Table 2). The A and H colonies did not differ in any of the initial characteristics (one-way ANOVA; $P > 0.05$ for all comparisons).

Colony population sizes and the different comb areas remained similar between the two colony types as the different periods of observation progressed (Table 2). The mean population size of the A (7029 ± 286 bees) and H (7364 ± 150 bees) colonies did not differ ($F = 0.60$; df = 1,2; $P = 0.52$), and mean population sizes were similar among the 3 periods ($F = 0.10$; df = 2,2; $P = 0.91$). Each of the 6 colonies increased in size during the period in which it was observed, as was reflected by the highly significant effect of day of observation ($F = 8.35$; df = 5,10; $P = 0.002$).

The two colony types did not differ in the mean proportion of comb area devoted to brood rearing ($F = 1.57$; df = 1,2; $P = 0.34$), although in all 3 periods the A colonies consistently contained slightly greater proportions of brood comb (Table 2). There was no effect of period ($F = 5.33$; df = 2,2; $P = 0.16$) or day of observation ($F = 2.70$; df = 5,10; $P = 0.09$) on brood comb areas, suggesting that brood rearing activity remained relatively constant throughout the study.

A and H colonies maintained similar proportions of total comb area devoted to pollen storage ($F = 1.06$; df = 1,2; $P = 0.41$) and honey storage ($F = 8.35$; df = 1,2; $P = 0.10$). There was no effect of period on pollen comb ($F = 1.35$; df = 2,2;

Table 2. The initial and mean (± SE) population sizes and proportions of total comb area devoted to brood production, pollen and honey storage for each of the African (A) and hybrid (H) colonies monitored during the three periods of the study. Initial values reflect colony characteristics at the time of establishment. Mean values were based upon 6 measurements made at 3–4 day intervals for each colon

	Population size		% Brood comb		% Pollen comb		% Honey comb	
	initial	mean	initial	mean	initial	mean	initial	mean
Period 1								
A2	6200	6803 ± 165	50	43 ± 0.4	5	7 ± 1	38	44 ± 7
H1	6500	7449 ± 284	53	36 ± 5	6	6 ± 0	26	45 ± 1
Period 2								
A3	6185	6689 ± 197	37	45 ± 2	4	5 ± 0.4	37	33 ± 3
H2	6506	7571 ± 229	35	29 ± 4	3	4 ± 1	37	36 ± 2
Period 3								
A4	6587	7597 ± 468	60	58 ± 2	4	7 ± 1	30	36 ± 2
H3	6612	7074 ± 200	55	56 ± 0.4	3	3 ± 0.4	37	37 ± 1

P = 0.43). There was, however, a significant period effect on honey comb (F = 116.5; df = 2,2; P = 0.008), because the amount of stored honey in the colonies observed in period 1 was greater than that of the colonies observed in periods 2 and 3 (Table 2). In both colony types, the proportions of pollen and honey comb did not change significantly over the 12 days of observation within each period (for pollen comb: F = 1.79; df = 5,10; P = 0.20, for nectar comb: F = 2.87; df = 5,10; P = 0.07).

Flight activity and diet selection

On the average, the A and H colonies had almost identical numbers of bees flying from the hives/min (13.8 ± 3.8 and 13.6 ± 2.3, respectively; Fig. 2). There was no significant difference in flight activity between the two colony types (F = 0.00; df = 1,2; P = 0.96), nor was there any difference in flight activity among the three periods (F = 0.61; df = 2,2; P = 0.62). However, there was a significant effect of day of observation (F = 2.96; df = 11,22; P = 0.01), suggesting that flight activity varied among the 12 days of observation within each period.

The A and H colonies did not differ in the number of pollen foragers returning/min over the entire day (F = 3.90; df = 1,2; P = 0.19) or during the first 3 hours of observation (F = 5.34; df = 1,2; P = 0.15) (Fig. 3). When viewed over all 3 periods, the 6 colonies had 5.8 ± 1.3 pollen foragers/min over the entire day and 15.5 ± 3.4 returning/min during the first 3 hours. However, on the average, the A colonies had almost double the pollen foraging activity of the H colonies, both for the entire day (A: 7.2 ± 2.4 pollen foragers/min; H: 3.9 ± 0.9 pollen foragers/min), and during the first three hours of observation (A: 19.2 ± 6.1 pollen foragers/min; H: 10.2 ± 2.7 pollen foragers/min) (Fig. 3).

There was no significant effect of period on either measure of pollen collection activity (for both measures: F < 8.30; df = 2,2; P > 0.10), although pollen foraging tended to increase slightly in both colony types in each successive period of study (Fig. 3). There was no effect of day of observation on the number of pollen

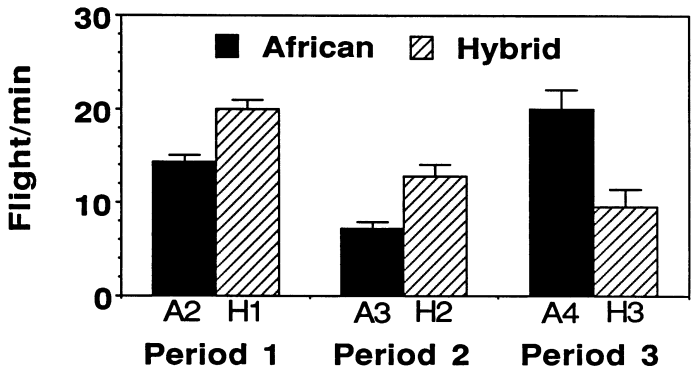

Figure 2. Mean ± SE number of bees flying from the hive per min for the African (A) and hybrid (H) colonies monitored during each period of the study

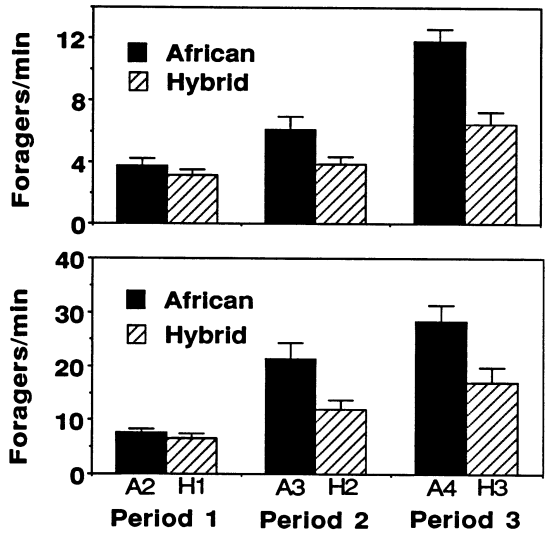

Figure 3. Mean ± SE number of pollen foragers returning per min over the entire day (upper figure) and during the first three hours of observation (lower figure) for the African (A) and hybrid (H) colonies monitored during each period of the study

foragers/min over the entire day ($F = 1.92$; $df = 11,22$; $P = 0.09$), while the number of pollen foragers returning/min during the first 3 hours did vary significantly among the 12 days of observation for the different colonies ($F = 4.59$; $df = 11,22$; $P = 0.001$).

The proportion of recruitment activity focused on pollen sites did not differ between the A and H colonies ($F = 11.06$; $df = 1,2$; $P = 0.08$), although in all three periods the A colonies had a slightly greater emphasis on pollen recruitment (Fig. 4). There was a significant period effect ($F = 74.62$; $df = 2,2$; $P = 0.01$), because for both colony types recruitment for pollen sites increased in each successive period of study (Fig. 4). There was no effect of day of observation on pollen recruitment activity ($F = 1.31$; $df = 11,22$; $P = 0.28$).

In summary, the A and H colonies did not differ significantly in levels of flight activity, pollen collection activity, or recruitment for pollen sites. However, in all 3 periods pollen collection activity and recruitment for pollen sites were slightly greater in the A colonies. Recruitment for pollen sites increased in each successive period of study, suggesting that foraging conditions or colony food needs varied among the different periods.

Foraging distances

The A and H foragers did not differ in the mean distance traveled to all food sites ($F = 4.18$; $df = 1,2$; $P = 0.18$), pollen sites ($F = 2.35$; $df = 1,2$; $P = 0.26$), or nectar sites ($F = 4.12$; $df = 1,2$; $P = 0.18$). When viewed over all 6 colonies, the daily mean total

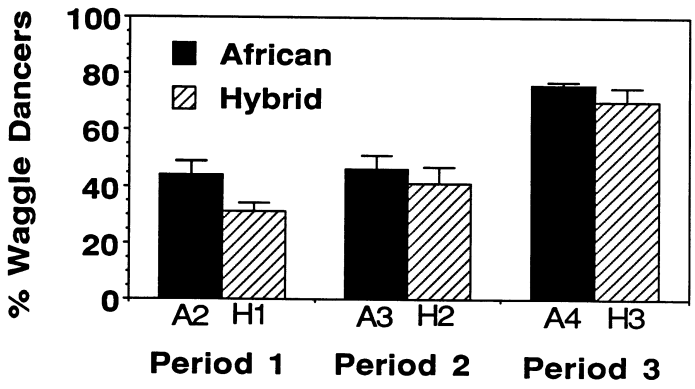

Figure 4. Mean ± SE proportion of waggle dancers each day that indicated pollen sites for the African (A) and hybrid (H) colonies monitored during each period of the study

foraging distance was 1230 ± 144 m, and the daily mean pollen and nectar foraging distances were 1243 ± 178 m and 1122 ± 54 m, respectively. However, the A colonies consistently traveled slightly shorter distances to food sources throughout the study (Fig. 5). The daily mean total foraging distance for the African colonies (1073 ± 52 m) was about 300 m less than the 1387 ± 260 m estimated for the hybrid colonies. Likewise, the mean daily pollen and nectar foraging distances for the African colonies (1085 ± 143 m and 1041 ± 38 m, respectively) were 150–300 m less than those of the hybrid colonies (1402 ± 336 m and 1202 ± 82 m, respectively). Thus, on average hybrid workers traveled about 600 m more per round trip of foraging.

There was no effect of period on foraging distances (for all comparisons: $F < 6.10$; df = 2,2; $P > 0.14$), although the distances traveled tended to increase slightly in both colony types as the study progressed (Fig. 5). There was a significant effect of day of observation only for mean daily pollen foraging distances ($F = 2.65$; df = 11.22; $P = 0.02$).

Discussion

When foraging in the same environment in northwestern Costa Rica, colonies with African and European mtDNA that were initially matched for size and comb areas maintained populations of about 7200 bees, devoted about 44% of comb area to brood rearing, had about 6 pollen foragers returning/min throughout the day, and traveled about 1200 m to food sources. The two colony types did not differ significantly in population size, brood rearing or food storage activity, or in any of the aspects of foraging examined. Thus, we found no differences that suggested any immediate selective advantage of African over hybrid colonies within the time periods examined. However, throughout the study the colonies with African mtDNA consistently had slightly greater brood production, almost twice as much pollen collection activity, and traveled approximately 600 m less per round

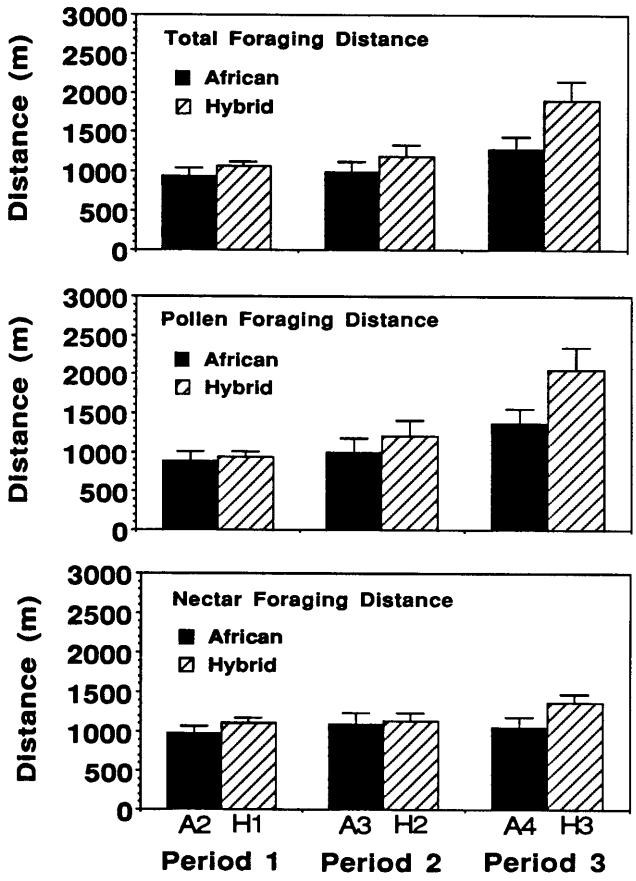

Figure 5. Mean ± SE distances communicated each day by waggle dancers in the African (A) and hybrid (H) colonies monitored during each period of the study

trip of foraging. While these differences were not significant, they persisted in all 3 periods despite possible changes in the foraging environment as the study progressed.

The levels of pollen collection activity and recruitment for pollen sites observed in Costa Rica were similar to those previously reported for honeybees in Africa and other neotropical areas. In the present study, the African and hybrid colonies had 3.9–7.2 pollen foragers/min and 43–55% of their waggle dancers recruited for pollen sites. In comparison, *A. m. scutellata* colonies in Botswana, Africa had 7.5 ± 1.1 pollen foragers/min and 56–80% of their waggle dancers were associated with pollen sources (Schneider and McNally, 1992b). Likewise, African colonies in Venezuela had 1.5 – 3.5 pollen foragers/min and 33% pollen dancers (Danka et al., 1987, 1988). Thus, the pollen collection and recruitment activity observed in the present study fell within the ranges previously reported for African honey bees and their New World descendants.

The distances traveled by the African and hybrid foragers in the current study (1041–1402 m) were similar to 745–1413 m reported for European foragers in California and Florida (Waddington et al., 1994). The foraging distances in Costa Rica, however, where: (1) smaller than the 2260 m reported for a European colony in New York and the 1700 m observed for African colonies in Venezuela (reviewed in Roubik, 1989); but (2) larger than the 400–600 m daily foraging distances observed for *A. m. scutellata* colonies in Botswana (Schneider and McNally, 1993). Thus, travel distances may vary markedly within and between different honey bee races depending upon local foraging conditions. Comparisons among races may therefore be valid only if colonies are examined during the same periods in the same environment (Waddington et al., 1994).

The nonsignificant differences in diet selection and foraging distances between the African and hybrid colonies in the current study have three possible interpretations. First, for both colony types foraging activity and foraging distances may have been more influenced by the availability and distribution of floral resources than by genetically determined dietary or movement preferences. Such preferences may have contributed to the slight differences observed between colony types, but their effect may have been minor relative to those resulting from environmental constraints.

Second, dietary and foraging distance preferences may have had major genetic components. However, African-like preferences may have predominated in both colony types due to dominant African nuclear alleles. All colonies examined in the current study contained African or European queens that had mated to some extent with African drones. While the actual level of such matings was unknown, the abundance of African matrilines in northwestern Costa Rica suggests that most drones in the region are African. Thus, colonies such as ours, which contain open-mated queens, would have a substantial African nuclear DNA component. Diet selection and foraging distance are behavioral tendencies that are likely to be regulated largely by nuclear genes. Indeed, several nuclear genetic loci have recently been demonstrated to have major effects on pollen foraging and storage in European honey bees (Hunt et al., 1995). If African alleles at these loci are dominant, then colonies sired by African drones may exhibit similar levels of pollen foraging activity, regardless of mtDNA type. This hypothesis is consistent with recent evidence that African nuclear alleles for defensive behavior are dominant over European alleles, such that colonies arising from European queens mated to African drones exhibit levels of defensiveness similar to that of African colonies (Guzman-Novoa and Page, 1994).

Third, African and hybrid colonies may have true differences in foraging behavior that result from a combination of African and European nuclear genes that are additive, with intermediate expression occurring in hybrids. However, we may have been unable to detect such differences because of our small sample sizes and statistical methods. Because we examined 1 of each colony type in 3 different periods, the error term for our between-subjects factors had only 2 degrees of freedom. The statistical comparisons between the African and hybrid colonies therefore became very conservative, such that only extremely large differences would have reached significance. Also, we do not know if further outcrossing with African drones occurred in our hybrid colonies. If the hybrid colonies had superceded the originally

introduced European queens, the new queens would have been European-African hybrids that mated primarily with African drones. This in turn would have resulted in hybrid colonies with even greater African nuclear genetic components. It is unknown if such supercedure occurred, but such outcrossing may have increased African behavioral traits, thus further masking any possible differences between African and hybrid colonies. Nevertheless, despite these possible limitations we did observe consistent, slight differences between the African and hybrid colonies in both pollen foraging activity and foraging distances that could *potentially* influence relative colony success in 2 biologically meaningful ways.

First, because pollen provides the nutrients necessary for brood rearing, the greater pollen collection activity of the African colonies could contribute to higher growth and reproductive rates over a colony's life time. Indeed, the African colonies had slightly greater proportions of comb area devoted to brood rearing than did the hybrids throughout the current study. A higher reproductive rate, in turn, could contribute to a numerical advantage of African matrilines in the neotropics.

Second, the hybrid foragers traveled about 600 m more per round trip, yet both colony types had similar levels of flight activity and food storage. If all other aspects of foraging (i.e., load sizes, flight speed, energetic costs) were equal between the two colony types, then hybrid colonies must have expended more energy to maintain similar levels of food collection, and thus may have been slightly less efficient at foraging. Indeed, the metabolic capacities of hybrid workers with European mtDNA are lower than those of workers with African mtDNA (Harrison and Hall, 1993). Metabolic capacities could influence maximal flight performance and exacerbate differences in energy expenditure during food collection (Harrison and Hall, 1993). A slight difference in foraging efficiency could therefore reflect an interaction of nuclear and mitochondrial genes, and potentially influence the long-term success of hybrid colonies. This, in turn, could contribute to the repeated observation that European-African hybrids survive in managed apiaries, but over time become rare or absent in feral populations (Boreham and Roubik, 1987; Hall, 1990).

Any possible differences in the foraging efficiency of African and hybrid honey bees must remain speculative at this time, because of our small sample sizes, relatively brief periods of observation and the unknown African nuclear DNA component in our study colonies. Furthermore, if differences in foraging efficiency do exist, then their importance may vary with environmental conditions. We observed our colonies during the dry season when floral resources are more abundant, and thus when differences in foraging efficiency may have less of an influence on growth and survival. However, during the rainy season when the abundance of blooming plants is reduced, slightly less efficient foraging by hybrid colonies may have a more pronounced impact on colony success. Thus, foraging behavior needs to be re-examined during the rainy season, using colonies of more precisely known genetic composition.

Numerous investigations of honey bee colony foraging behavior in the neotropics have compared matched colonies of African and European bees in the same habitat. These studies have revealed that compared to European colonies, African colonies store less honey but more pollen, rear more brood, and have greater pollen collection activity per unit time (reviewed in Rinderer and Collins, 1991). The

similarities observed between the African and European-African hybrid colonies in the present study suggest a predominance of African behavioral traits. However, the consistent, slight differences in pollen foraging activity and travel distances suggest potential factors that could influence the relative, long-term success of hybrids in the neotropics. A more complete analysis of these possible differences will require that large numbers of African and European colonies and reciprocal crosses be examined over extended periods under feral and managed conditions.

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