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Seasonal patterns of foraging activity in colonies of the African honey bee, *Apis mellifera scutellata*, in Africa

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Key words: Apis mellifera scutellata, African honey bee, foraging, brood rearing.

Summary

Seasonal foraging patterns were investigated using six observation colonies maintained in the Okavango Delta, Botswana. Pollen collection, flight from the hive, and recruitment for pollen and nectar sources occurred throughout the 11 months of the study. However, the distribution of foraging activity throughout the day changed seasonally. Colonies emphasized recruitment for pollen sites throughout most of the year. Brood production occurred in all months except May, and there was a significant, positive correlation between the proportion of recruitment activity devoted to pollen sources and the amount of brood comb in the colonies. The seasonal foraging patterns of *scutellata* in the Okavango were similar to those of Africanized honey bees in the neotropics. The extended foraging season and emphasis on pollen collection may be associated with the high swarming rates and migrational movements of tropical honey bees.

Introduction

Temperate and tropical races of the honey bee, *Apis mellifera*, exhibit numerous behavioral differences (Winston et al., 1983; Winston, 1987; Schneider and Blyther, 1988) that are related in part to differences in the duration and predictability of forage abundance in the contrasting environments. Temperate climate honey bees experience a relatively brief, predictable foraging season, during which sufficient food stores must be amassed for winter survival (Rinderer, 1988; Winston, 1987). The accumulation of large food reserves requires the construction of large amounts of comb, large colony population sizes, the collection of food over a large area of the environment, and an emphasis on nectar collection (Visscher and Seeley, 1982; Seeley, 1985; Danka et al., 1987). In contrast, tropical honey bees do not experience an extended cold season, and may forage throughout much of the year (Rinderer, 1988; Schneider and Blyther, 1988; McNally and Schneider, 1992). The amassing of large food reserves may therefore be less critical to colony survival (Winston et al., 1983; Schneider and Blyther, 1988). Also, the continuing availability of harvestable resources may favor high rates of swarming (Otis, 1982; Rinderer, 1988), resulting in an emphasis on brood production, pollen collection, smaller colony population sizes, and thus the ability to meet colony food needs while foraging over a smaller area of the environment (Danka et al., 1987; Schneider, 1989). Thus, many of the behavioral differences between temperate and tropical honey bees are associated with differences in seasonal patterns of colony foraging activity. Seasonal foraging patterns for temperate climate races have been extensively studied (reviewed in Seeley, 1985; Winston, 1987). In comparison, relatively little is known about the seasonal foraging activity of tropical honey bee races, most of which occur in Africa. Annual cycles of foraging activity have recently been investigated for the "Africanized" bee (hybrids of the African race *A. m. scutellata* and several European races) in Central and South America (Pesante, 1985; Rinderer, 1988). However, the results of these studies may have been influenced by the hybrid nature of the Africanized bee, as well as human agricultural activity. There have been no long-term studies of seasonal colony foraging patterns for naturally occurring African honey bees in their native environment.

The purpose of this study was to investigate the seasonal patterns of colony foraging in the African honey bee, *A. m. scutellata*, in the Okavango River Delta, Botswana, Africa. The Okavango Delta was selected as a study area because it is sparsely inhabited by humans, there are no beekeeping and few agricultural practices, and honey bee colonies are abundant (8/km^2) (Schneider and Blyther, 1988). Also, the Okavango Delta has three fairly distinct seasons defined by rainfall: the hot-dry season (August through October–November), the hot-wet season (November–April), and the cool-dry season (April–May through July–August) (Schneider and Blyther, 1988; McNally and Schneider, 1992). The Okavango therefore provides a unique area in which to study the seasonal foraging activity of a racially pure population of bees in their natural habitat.

Seasonal patterns of forage availability and colony development have recently been determined for the honey bees of the Okavango (Schneider and Blyther, 1988; McNally and Schneider, 1992). Blooming species are available during 10–11 months of the year, although the greatest abundance of forage occurs between July and September. During these months, many new colonies establish in the Delta, rapidly increase in size, and then swarm in October and November. The availability of forage decreases beginning in November at the onset of the rainy season, remains relatively low and somewhat variable until April, and then declines to near zero in May and June. Naturally occurring colonies migrate throughout November–May. During the latter portion of this period, brood rearing virtually ceases, food stores become depleted, and colonies that do not migrate may face starvation (McNally and Schneider, 1992; Schneider and McNally, in prep.). Thus, brood rearing and food storage, and by inference foraging activity and colony diet, fluctuate seasonally.

The study had two main objectives. First, we determined the annual cycle of daily colony foraging patterns and seasonal variations in colony diet (pollen versus nectar collection). Second, we examined the relationship between colony foraging patterns, diet and seasonal changes in brood production and food storage.

Materials and methods

Study sites and observation hive maintenance

The study was conducted from August–December, 1986 and October, 1989–June, 1990. Two different study sites 3–4 km apart were utilized. The 1986 study site was located on the banks of the Santantadibee River (19°34.59′ S; 23°24.74′ E), and that for 1989 was located on the edge of a large lagoon (19°35.42′ S; 23°21.43′ E).

Foraging activity was investigated using a total of six 2-frame observation colonies (colonies 1–6). Each colony was originally excavated in the field. The combs and bees were collected and transferred either directly into an observation hive (colony 1) or into a 45 L hive box with movable frames (colonies 2–6). Once the box colonies began rearing brood, each was transferred into an observation hive. The observation hives were maintained in high-walled canvas tents (3 m × 2 m × 2.5 m high; two colonies per tent) located in the shade and lined internally with heavy brown paper to lower heat and light levels. Previous research revealed that under such conditions *A. m. scutellata* colonies can be maintained for extended periods and exhibit patterns of growth and activity similar to naturally occurring field colonies (Schneider, 1989; 1990a and b). Each colony occupied an observation hive for 7–10 days before we began monitoring daily activity patterns. The glass walls of the observation hives were marked off in a grid of 5 cm × 5 cm squares to facilitate monitoring worker activity. Further descriptions of observation hive maintenance are provided in Schneider (1989; 1990a and b).

Determining colony activity patterns and diet

Daily activity patterns were examined by estimating three different activities each hour between sunrise and sunset: (1) pollen collection, (2) flight from the hive, and (3) recruitment to food and water sources. For each colony observed on a given day, we monitored worker behavior for 30 min each hour. During each observation period, pollen collection and flight activity were estimated by conducting five 1-min counts, each separated by at least 2 min, of (1) the number of bees returning to the hive carrying pollen loads and (2) the number of bees flying from the hive. Estimates of flight activity did not include those observation periods containing orientation flights, because such flights occur in conjunction with young workers learning the location of the hive relative to local landmarks, and are not associated with foraging (Gary, 1975; Winston, 1987). During orientation (but not foraging) flights, *scutellata* workers are strongly photopositive, and will cluster about a light source shone into the observation hive (Schneider, unpublished data). We used such a clustering response to determine the presence of orientation flight activity.

Daily patterns of recruitment activity were determined by conductivity five 2-min counts, each separated by 3–4 min, of the number of workers performing waggle dances. For each dancer observed we recorded if it was a pollen forager (carried pollen loads) or a nectar forager (did not carry pollen loads). Honey bees will also collect and recruit for water (Seeley, 1985). Thus, during the hotter portions of the year (when water collection is most prevalent) some of the waggle dancers we classified as nectar foragers may have been water collectors. However, during the hot seasons most all recruitment behavior occurred during the cooler morning and evening hours (see below), when water collection activity was likely to be low. Also, during the hot afternoon hours when the need for water was greatest, waggle dance activity was very low, suggesting that there was relatively little recruitment for water sites even during the period of greatest water collection. Thus, the majority of the foragers dancing for non-pollen sites in this study probably were associated with nectar collection, and were therefore referred to as nectar foragers. However, since we made not attempt to distinguish between nectar and water collectors, our data on waggle dance activity may slightly overestimate the prevalence of nectar foraging, especially during the afternoon hours of the hot seasons.

Dancers may have made more than one foraging trip during a given observation period, and thus some bees may have been included more than once in the counts of recruitment activity. However, we were interested not in the number of different individual bees performing recruitment dances throughout the day, but in the relative amounts of dance activity occurring during each observation period.

The counts for pollen collectors, flights from the hive, and pollen and nectar dancers were summed to give the total number observed during each 30-min period. Each observation period total was subsequently expressed as a proportion of the grand total of pollen collectors, flights, and waggle dancers observed for the entire day in each colony.

Colony diet was examined using waggle dance activity. We determined for each colony during each month of observation (1) the mean number of pollen and nectar dancers observed per day, and (2) the mean proportion of total waggle dance activity observed per day associated with pollen and nectar sites. Honey bees will collect both pollen and nectar without performing waggle dances (von Frisch, 1967) Hence, the use of waggle dance activity to examine colony diet may have underestimated in some instances the actual number of workers associated with pollen or nectar collection. However, waggle dance activity does provide a reliable estimate of the degree to which recruitment is focused on pollen versus nectar sources (von Frisch, 1967).

Determining colony brood rearing and food storage activities

Once each weeks the grids drawn onto the observation hive walls were used to estimate the amount of comb containing brood (eggs, larvae, and sealed pupae), nectar and pollen. The various comb areas were then expressed as a proportion of total comb area.

All mean values are reported as the mean ± SE. All proportional data were arcsine transformed before analyses.

Table 1. The months, season, total number of days of observation, and fate of each of the observation colonies monitored

Colony	Months/season of observation	Days of observation	Fate
1	Aug–Oct/hot-dry	14	swarmed in Oct
2	Sep–Oct/hot-dry	6	swarmed in Oct
3	Oct–Jan/first part of hot-wet	27	migrated in Jan
4	Nov–Jan/first part of hot-wet	24	migrated in Jan
5	Feb–May/latter part of hot-wet; cool-dry	27	died in May
6	Mar–Jun/latter part of hot-wet; cool-dry	31	ceased brood rearing in May; reinstated brood rearing in June

Results

The total number of days of observation during the months each observation colony was monitored, and the fate of each colony are presented in Table 1. No observation colonies were observed during July.

The behavior of the observation colonies was similar to that of naturally occurring, field colonies. Two of the three colonies monitored in August–October (colonies 1 and 2) swarmed in October. In comparison, swarming in field colonies occurs in October and November (McNally and Schneider, 1992). The two observation colonies monitored in November–January (colonies 3 and 4) migrated from the study area in January. Migration in naturally occurring colonies occurs throughout November–May, although the peak of this activity is in January (McNally and Schneider, 1992). The two colonies monitored from February–June (colonies 5 and 6) did not migrate from the area, but both ceased brood rearing in May, and colony 5 died at this time. February–June represents the latter portion of the migration season for naturally occurring colonies. Brood rearing during these months is erratic and vitually ceases in May (McNally and Schneider, 1992). Hence, maintaining the colonies in observation hives did not appear to alter their normal patterns of growth and development.

Based upon the behavior of the observation colonies and the seasons of the Okavango, we divided the months of study into three periods: August–October (which corresponded with the hot-dry season and the major portion of the establishment and swarming period of naturally occurring colonies; see Introduction); November–January (the first portion of both the hot-wet season and the migration season); and February–June (the latter portion of the migration season, the latter portion of the hot-wet season, and the cool-dry season). Throughout the following discussion of daily activity patterns, reported values at a given hour of the day represent the mean proportion of the activity in question at that time over all days for all hives monitored during a given seasonal period.

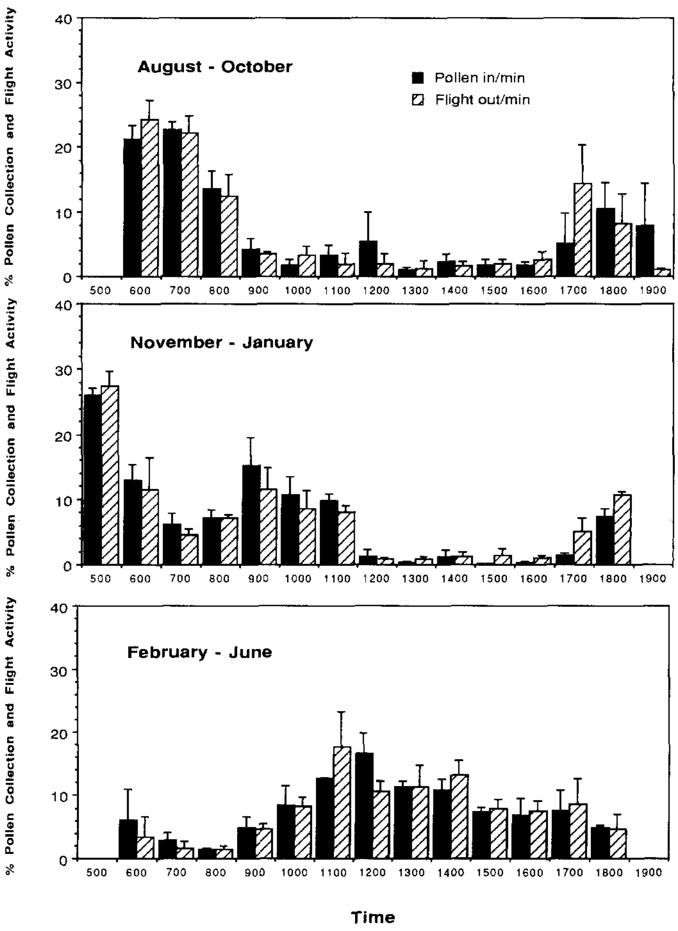

Figure 1. The daily patterns of pollen collection and flight activity for each of the three seasonal periods examined. The vertical bars represents the mean (±SE) proportion of total daily pollen collection or flight activity observed during each hour

Seasonal colony activity patterns

Pollen collection, foraging flights, and recruitment occurred throughout the year (Figs. 1 and 2). However, the distribution of each activity throughout the day varied among the different seasonal periods.

August–October: Pollen collection, flight and waggle dance behavior during the hot-dry season were concentrated in two, brief daily peaks of activity; one between 0600–0800 hours and the second between 1600–1800 hours (Figs. 1 and 2). These two peaks accounted for 75–80% of all daily pollen collection, flight, and waggle dance activity observed. The morning peak alone accounted for 55–58% of the total daily pollen collection, flight, and recruitment activity.

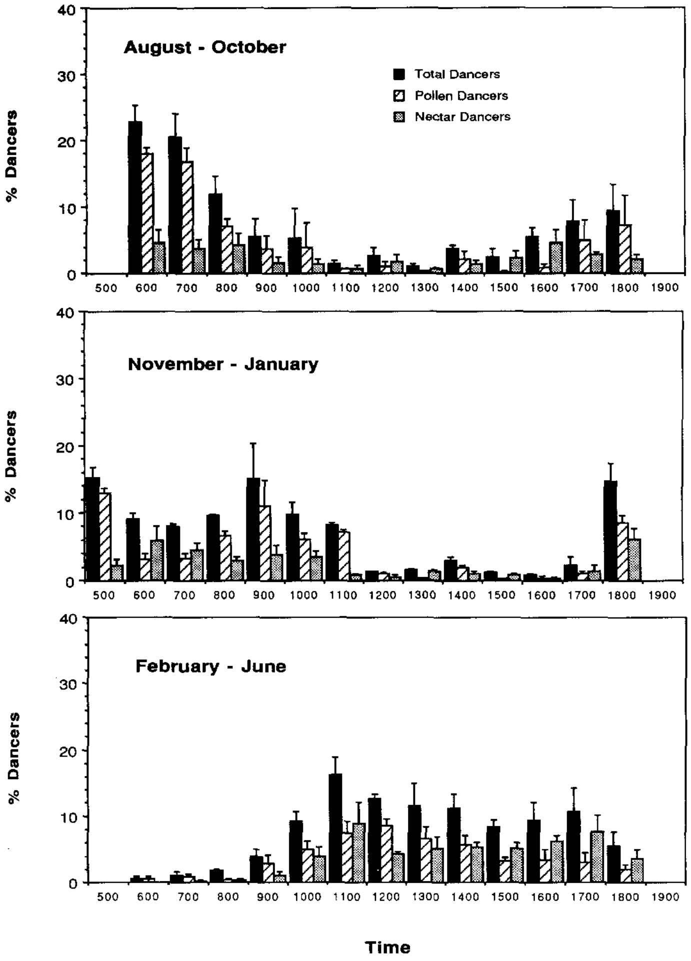

Figure 2. The daily patterns of total recruitment activity and recruitment for pollen and nectar sites. The vertical bars represent the mean (±SE) proportion of total daily recruitment activity observed during each hour

Both the morning and evening recuitment peaks were associated primarily with pollen collection. Dances by pollen carriers between 0600–0800 and 1600–1800 hours accounted for 56% of total daily recruitment activity. Recruitment to nectar sites was also concentrated in the early morning and evening hours (Fig. 2), and the distributions of nectar and pollen dancers throughout the day did not differ ($X^2 = 20.33$; $df = 12$; $P > 0.05$). However, the activity peaks for nectar dancers were not as pronounced as those for pollen dancers (Fig. 2).

All activities examined remained low between 0900–1500 hours. During this time, no single hour of the day contained more than 6% of the total daily pollen collection, flight, or waggle dance activity (Figs. 1 and 2).

November–January: The daily patterns of pollen collection, flight, and waggle dance activity during the first portion of the hot-wet season differed significantly from those observed during the August–October period (Fig. 1 and 2; for all comparisons, $X^2 > 51.0$; $df = 13$; $P < 0.01$). During the November–January period, foraging was extended throughout the morning (0500–1100 hours). These hours accounted for 73–87% of total daily pollen collection, flight, and waggle dance activity. A smaller, brief peak of all three activities occurred between 1700–1800 hours.

Recruitment activity continued to be associated primarily with pollen sites (Fig. 2). Pollen dancers between 0500–1100 and 1700–1800 hours accounted for 56% of total daily recruitment activity. Recruitment for nectar sites was also greatest during the morning and evening hours, and the distribution of nectar and pollen dancers throughout the day did not differ ($X^2 = 14.26$; $P > 0.05$).

As in the August–October period, all activities were reduced during the afternoon hours. No more than 2–3% of the total daily pollen collection, flight, or recruitment activity occurred during any hour between 1200–1600 hours.

February–June: Daily activity patterns changed markedly during the latter portion of the hot-wet season and the cool-dry season (Figs. 1 and 2). The distributions of pollen collection, flight, and waggle dance activity throughout the day during the February–June period differed significantly from those observed during the other two seasonal period (for all comparisons, $X^2 > 53.0$; $df = 26$; $P < 0.01$).

The morning activity peaks observed during August–October and November–January were absent during the February–June period. Pollen collection, flight, and waggle dance activity remained low until 0800–0900 hours, and then occurred at a fairly constant level throughout the remainder of the day (Figs. 1 and 2). No single hourly period accounted for more than 18% of the total daily pollen collection, flight, or waggle dance activity observed during these months. Waggle dances for pollen and nectar sites accounted for similar proportions of the recruitment activity observed during each hour of the day, and had similar temporal distributions ($X^2 = 8.02$; $df = 12$; $P > 0.05$).

Seasonal patterns of colony brood rearing, food storage, and diet

Brood rearing occurred during all months of observation except May (Fig. 3). However, there were significant differences in the proportion of comb areas devoted to brood among the three seasonal periods ($F = 8.94$; $df = 2{,}8$; $P = 0.009$). Brood production in the observation colonies was greatest in the hot-dry season (August–October), at which time 67.3 ± 9.6% of total comb area each month contained brood. Brood production began declining in the first portion of the hot-wet season and accounted for 47.3 ± 6.5% of total comb area in November–January. Brood production was variable during the latter part of the hot-wet and the cool-dry seasons, but on average accounted for only 16.8 ± 7.1% of total comb area between February and June. Brood comb area declined to zero in both observation colonies monitored in May. Colony 5 died at this time (Tab. 1), and brood rearing remained low throughout June in colony 6 (Fig. 3).

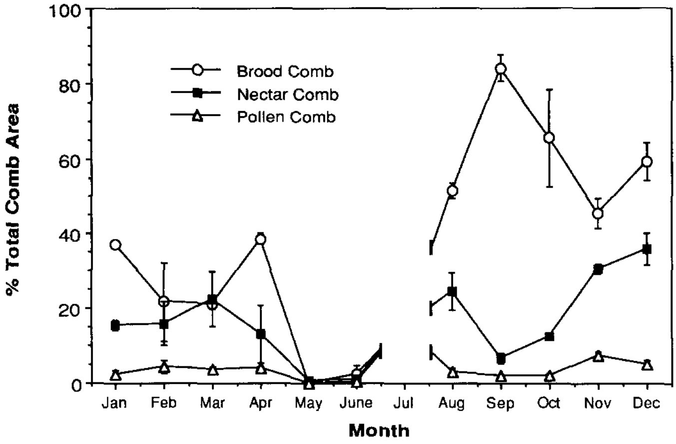

Figure 3. The mean (±SE) proportion of comb area devoted to brood rearing, nectar, and pollen storage during each month of the study. Data were not available for July

Food storage remained low throughout the year and never accounted for more than 40% of total comb area during any month of observation (Fig. 3). Nectar storage accounted for 14.5±5.3% of comb area during each month of the hot-dry season, increased to 27.2±6.2% of comb area during the first portion of the hot-wet season, and then declined fairly steadily throughout the latter portion of the hot-wet season, reaching virtually zero in the cool-dry season. Pollen storage never accounted for more than 7% of total comb area during any month of observation. No pollen stores were observed in May or June (Fig. 3). The seasonal patterns of brood rearing and food storage of the observation colonies were similar to those reported for naturally occurring *scutellata* colonies in the Okavango (Schneider and Blyther, 1988; McNally and Schneider, 1992).

Recruitment activity, and by inference colony diet, was focused on pollen versus nectar collection throughout most of the year. Of the 12289 total waggle dancers observed during the study period, 7396 (59%) were pollen collectors, while 5103 (41%) were nectar foragers (Chi square; $P < 0.001$). During June–April, 64.5±7.2 pollen dancers were observed each day, and pollen dancers accounted for 61.5±4.0% of total waggle dance activity each month (Fig. 4). In comparison, during these months we observed a mean of 40.1±21.9 nectar dancers per day ($t = 2.71$; $P < 0.05$), and nectar dancers accounted for a mean of 38.4±4.0% of total waggle dance activity each month ($t = 4.11$; $P < 0.05$). No waggle dances for pollen sites were observed in May (Fig. 4).

Recruitment for pollen sites varied with brood production. When viewed over all months of observation for each colony, there was a significant, positive correlation between the mean proportion of comb area devoted to brood rearing and the mean proportion of waggle dances associated with pollen sites ($r = 0.599$; $df = 17$; $P < 0.01$). Waggle dances for nectar sites strongly predominated recruitment activity only in May and June, during the period of lowest brood production. The proportion of waggle dancers devoted to nectar sites was negatively correlated with brood

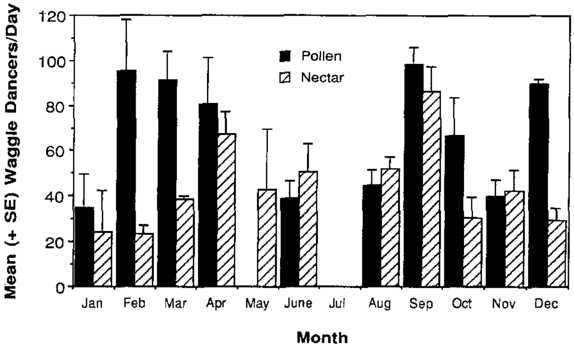

Figure 4. The mean (±SE) number of pollen and nectar dancers observed per day during each month of observation. Data were not available for July

rearing activity ($r = -0.60$; $df = 17$; $P < 0.01$). Recruitment for nectar sites was also negatively correlated with the proportion of comb space devoted to nectar storage (-0.67; $df = 17$; $P < 0.01$).

Discussion

The observation colonies revealed three main characteristics of the seasonal activity patterns of *A. m. scutellata* in the Okavango Delta. First, colonies can forage throughout the year. Pollen collection, flight from the hive, and recruitment to food sources were observed during all 11 months of the study. Extended foraging seasons have also been suggested for the Africanized bees in Central and South America (Otis, 1982; Pesante, 1985; Rinderer, 1988). The prolonged foraging season may contribute to two aspects of tropical honey bee behavior: increased brood-rearing activity and migration. The availability of harvestable resources throughout most of the year may allow for more-or-less continuous brood production. The observation colonies in this study exhibited brood-rearing activity in all months except May. Naturally occurring *scutellata* colonies in the Okavango and other regions of Africa and Africanized colonies in the neotropics also produce brood throughout much of the year (Silberrad, 1976; Winston, 1980; Cobey and Locke, 1986; Schneider and Blyther, 1988; Roubik, 1989; McNally and Schneider, 1992). Extended periods of brood rearing in turn may favor a prolonged period of swarm production. A high swarm rate is characteristic of *scutellata* in Africa and Africanized colonies in the neotropics (Fletcher, 1978; Otis, 1982, 1991), and Africanized colonies may produce swarms during eight months of the year in South America (Winston, 1980; Otis, 1982). However, swarming in the Okavango may occur during only two to three months of the year (McNally and Schneider, 1992), although the dynamics of colony reproduction in the Delta are poorly understood.

The extended foraging season may also be associated with colony migration. While floral resources in tropical habitats are available throughout much of the year, their temporal and spatial occurrence is often unpredictable, due to unpredictable rain patterns (Griffiths, 1976; Sinclair, 1983; Rinderer, 1988; Rinderer and Collins, 1991). Thus, tropical honey bee colonies may be favored to emigrate during locally unfavorable periods. In the Okavango, *scutellata* colonies migrate throughout November–May (the hot-wet season), during which time the availability of blooming plants is reduced (Schneider and Blyther, 1988; Schneider, 1990a; McNally and Schneider, 1992). Migration of *scutellata* in other regions of Africa and Africanized colonies in Central and South America also occurs during seasonal resource dearths (Silberrad, 1976; Nightingale, 1976; Winston et al., 1979). Indeed, deteriorating foraging conditions may be a primary factor stimulating the onset of migration preparations in African honey bees (Schneider and McNally, in prep.; Winston et al., 1979).

The second aspect of *scutellata* foraging behavior revealed in this study was that daily foraging patterns varied throughout the year. In general, foraging shifted from being concentrated in brief, intense periods of activity in the early morning and evening hours (hot-dry season) to occurring throughout first the morning (hot-wet season) and then the afternoon (cool-dry season) hours. During the hot-dry and the hot-wet seasons, daily foraging patterns, and particularly the morning and evening activity peaks, were associated primarily with pollen collection. Morning peaks of pollen collection have also been reported for *scutellata* in other regions of Africa (Clauss, 1983) and for Africanized honey bees and other bee species in the neotropics (Roubik and Buchmann, 1984; Pesante, 1985; Roubik, 1989).

The changing daily activity patterns observed in this study undoubtedly reflected seasonal patterns in the timing of pollen and nectar production by Okavango plants, which are influenced by changes in temperature, relative humidity and rainfall (Palgrave, 1984). However, *scutellata* foraging activity may also have been influenced by temperature in a manner independent of the effect temperature has on the temporal availability of resources. Foragers from the observation colonies could not be trained to visit artificial feeding stations during either the afternoon hours of the hot-dry and hot-wet seasons or the morning hours of the cool-dry season, regardless of the concentration of sugar syrup offered (Schneider, unpublished observations). Thus, the concentration of foraging in the cooler morning hours in the hot-dry and hot-wet seasons and the warmer afternoon hours in the cool-dry season may have resulted in part from temperatures that were more conducive to *scutellata* flight during the various times of the year.

The third aspect of *scutellata* foraging revealed by this study was that colony diet changed during the year, in conjunction with seasonal fluctuations in brood production. Pollen collection dominated foraging activity, and there was a positive correlation between the amount of brood comb in the colonies and the proportion of daily waggle dance activity devoted to pollen sites. Because pollen provides the proteins and fats necessary for the development of brood and young workers (Winston, 1987), the prolonged brood-rearing periods of *scutellata* colonies may require a concomitant emphasis on pollen collection throughout much of the year. An emphasis on pollen versus nectar collection has also been reported for Africanized colonies in South America (Pesante et al., 1987; Danka et al., 1987). In contrast, temperate honey bee races, which must amass large honey reserves for winter survival, emphasize nectar over pollen collection (Seeley, 1985; Danka et al., 1987).

Seasonal patterns of pollen and nectar collection in the Okavango were broadly similar to those observed for Africanized colonies in the neotropics. In the *scutellata* colonies examined in this study, recruitment for pollen sites remained high throughout most of the hot-dry and hot-wet seasons (August–April) and was lowest during the cool-dry season (May–June). In comparison, pollen foraging in Africanized colonies in Venezuela is greatest from October–March and lowest from April–September (Pesante, 1985; Rinderer, 1988). However, the period of lowest pollen foraging in the Africanized colonies coincides with the wet season. Nectar collection and storage in *scutellata* colonies in the Okavango and Africanized colonies in Venezuela are greatest from November–December and lowest from April–July (Pesante, 1985; Rinderer, 1988). In the present study, there was an inverse relationship between the amount of nectar comb present in the observation colonies and the proportion of recruitment activity associated with nectar sites. Thus, recruitment for nectar sites in the Okavango intensified as colony honey stores diminished.

In summary, while *scutellata* colonies in the Okavango Delta can forage throughout the year, foraging activity and diet fluctuate with seasonal changes in the abundance of floral resources and colony growth and development. In both Africa and the neotropics the extended foraging season and emphasis on pollen collection may facilitate increased brood rearing, high rates of swarming, and migration. Seasonal foraging patterns may therefore be associated with the high fecundity and mobility of tropical *Apis mellifera.*

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