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Seasonal cycles of growth, development and movement of the African honey bee, *Apis mellifera scutellata*, in Africa

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Key words: African honey bee, *scutellata*, swarming, absconding, migration.

Summary

The relationship between the annual colony cycle and seasonal patterns of forage availability was investigated for the African honey bee, *Apis mellifera scutellata*, in the Okavango River Delta, Botswana. The annual cycle occurred in three distinct periods. The swarming season occurred from October–November, following two to three months of intense brood production, and coincided with the end of peak forage abundance. The migration season occurred from November–May and coincided with reduced and variable floral resources. During the migration season, brood production and food storage were generally low but quite variable from month to month, and swarms passing over the study area at this time traveled in an easterly direction. The migration season was followed by the establishment period (June–September), in which large numbers of new colonies traveling from the west moved into the study area. The establishment period coincided with, and slightly preceded, the period of peak forage abundance, and colonies devoted resources collected at this time almost entirely to brood rearing, which culminated in swarm production. The data suggest that honey bee colonies in the Okavango are mobile and gear their reproduction and movement to seasonally shifting resource patterns.

Introduction

Colonies of the honey bee, *Apis mellifera*, exhibit seasonal patterns of growth, development and movement that are dependent in part upon the availability of floral resources. Honey bees exist as at least 20 distinct geographic races occupying temperate and tropical environments (Ruttner, 1988). The contrasting climates and seasonal resource patterns of the various habitats suggest corresponding differences in the annual colony cycles of temperate and tropical races. Seasonal colony cycles for temperate climate honey bees have been extensively studied (see Seeley, 1985; Winston, 1987). In contrast, much less is known about the annual cycles of tropical races of *A. mellifera*, most of which occur in Africa (Ruttner, 1988). Furthermore, most investigations of African honey bee biology have concentrated on (1) colonies maintained in areas where human agriculture may influence seasonal resource patterns, or (2) the "Africanized" honey bee of the neotropics, which may have hybridized to varying extends with temperate climate races (Winston, 1980; Rinderer et al., 1991; Sheppard et al., 1991; but see Smith et al., 1989; Hall and Muralidharan, 1989). Indeed, to date there have been no long-term, quantitative studies of the annual colony cycle of a racially pure, naturally occurring population of African honey bees in their native environment.

Available data suggest that the seasonal cycles of African honey bee colonies differ from those of temperate climate races in three major respects. First, African bees tend to raise brood and produce reproductive swarms throughout much of the year, and may swarm 6–12 times per year (Silberrad, 1976; Seeley, 1985; Cobey and Locke, 1986; Winston, 1987; Schneider and Blyther, 1988; Otis, 1991). In contrast, temperate races produce brood and swarms primarily during the spring and summer months, generally swarm only 1–3 times annually, and cease brood rearing during the winter (Seeley, 1985; Winston, 1987).

Second, naturally occurring African colonies store relatively little food throughout the year, although the amount may vary seasonally (Pesante, 1985; Winston, 1980; Rinderer, 1988; Schneider and Blyther, 1988; Rinderer and Collins, 1991; Schneider and McNally, 1992). In comparison, temperate climate races exhibit distinct seasonal patterns of food storage and must amass large food reserves for winter survival (Seeley, 1985).

Third, African honey bees frequently abscond, whereas temperate races rarely exhibit this behavior. Absconding consists of a colony abandoning a nest site and moving into a new area (absconding differs from reproductive swarming in that it does not involve the production of new queens or the fissioning of the colony; Winston, 1987). Absconding is of two types: (1) disturbance-induced, which is an immediate response to a sudden deterioration in nest quality due to predators, pests, fire or overheating; (2) seasonal, which occurs at distinct times of the year, perhaps in response to seasonal changes in forage and water availability, or to some weather factor (Winston, 1987; 1991). Seasonal absconding may represent a type of migration (Fletcher, 1975; 1978; Winston et al., 1979; Schneider, 1990a). The factors regulating seasonal absconding are poorly understood, and colonies occupying the same area and possessing similar amounts of stored food can differ greatly in absconding behavior (Winston et al., 1979; Schneider, 1990a). Furthermore, the interrelationships between the annual cycles of brood rearing, swarming, food storage, and absconding, and how such relationships are associated with seasonal patterns of forage availability, have been largely unexplored for African honey bee races.

The purpose of this study was to investigate the seasonal patterns of growth, development and movement in colonies of the African honey bee, *Apis mellifera scutellata* (hereafter referred to as *scutellata*) in Africa. The objectives of the study were to (1) determine the annual cycle of brood production, food storage, swarming, absconding, and establishment in naturally occurring colonies, (2) examine how these cycles may be associated with seasonal fluctuations in floral abundance, and (3) examine in detail the nests of absconding and non-absconding colonies to determine possible nest characteristics associated with the decision to abandon an area.

Methods and materials

Study area

The study was conducted from August–December 1986, and from October 1989–July 1990, in the Okavango River Delta, Botswana. The Okavango Delta occupies approximately 17 000 km^2, and is composed of narrow stands of trees interspersed in open grasslands. The climate is subtropical, and there are three seasons defined by rainfall: the hot-dry season (August through October–November; maximum daily temperature (mean ± SD): 32.0 ± 2.1 °C; monthly rainfall (mean ± SD): 18.9 ± 16.9 mm); the hot-wet season (November–December through March–April; 32.2 ± 1.3 °C; 61.0 ± 38.9 mm); and the cool-dry season (April–May through July–August; 28.1 ± 2.1 °C; 7.1 ± 13.1 mm) (Schneider and Blyther, 1988). The Okavango is sparsely inhabited by humans, and there are no beekeeping and few agricultural practices. *scutellata* colonies are abundant (8/km^2), and no foreign races of bees have been introduced (Schneider and Blyther, 1988). The Delta therefore provides a unique area in which to study a racially pure population of *scutellata* in a natural habitat.

The study site for 1986 was located on the east bank of the Santantadibee River (Schneider and Blyther, 1988), while that for 1989 was located near a lagoon (19°35.42′ S; 23°21.43′ E) located approximately 3 km southwest of the 1986 site.

Determining seasonal patterns of forage availability

Forage availability was estimated by conducting monthly vegetational surveys of the number of blooming trees (perennials > 3 m in height), shrubs (perennials < 3 m in height), and weed (annuals). Vegetational surveys of trees and shrubs were conducted each month in 20 1000-m^2 sample plots, scattered over an area of approximately 15 km^2 and separated from one another by at least 500 m. Plot locations were selected at random, and plot size was established by pacing (10 m × 100 m). All plots were located within stands of trees. Each month, the total number of blooming individuals of each species of tree and shrub was recorded for each plot. The utilization of a species by honey bees was determined through direct observation or through published reports of plants visited by *scutellata* in other areas of Botswana (Clauss, 1983).

Vegetational surveys of weeds were conducted by establishing 80 50-m line transects, 40 located within the 20 1000-m^2 plots (2/plot) and 40 located in open areas adjacent to the plots. Each month, the total number of blooming weeds was recorded for each transect. All weed transects were conducted from November–June. Transect data were not available for July–October, although casual observations suggested that few weeds were blooming during these months.

During every month of the study, each species of blooming plant was assigned a "bloom value" using the following scale for the estimated number of flowers/plant: 1 (1–100); 2 (101–500); 3 (501–1000); 4 (1001–2000); 5 (> 2000). Each month, the bloom values for all individual plants were totaled for each plot and transect. A mean bloom value was then calculated for trees and shrubs over all plots, and for weeds over all transects, for each month of the year. These mean values provided monthly estimates of the abundance of floral resources.

Determining seasonal patterns of colony development and movement

Colony growth and movement patterns were examined by (1) excavating naturally occurring nests in the field (see Schneider and Blyther for methods of nest excavation), and (2) monitoring the movement of swarms passing over the study area. We determined two major characteristics for the excavated nests. First, for each nest we estimated total comb area (in cm^2) and the areas devoted to brood (eggs, larvae and sealed pupae) and food (honey, nectar and pollen). Comb areas in 1989 were estimated using a grid of $5\,cm \times 5\,cm$ squares. Comb areas in 1986 were estimated by weighing sketches drawn to scale using mean values of comb height and width (see Schneider and Blyther, 1988 for further details of comb measurement procedures).

Second, we noted if each excavated colony exhibited evidence of (1) reproductive swarming, (2) absconding, or (3) being recently established in the nest cavity. A colony was considered to be preparing for reproductive swarming if developing or sealed queen cells were present. A colony was classified as having recently swarmed if it contained a reduced worker population and the remnants of cells from which virgin queens had recently emerged. We further noted the number of queen cells per colony and if recently swarmed colonies had successfully requeened (both a queen and eggs present) or failed to requeen (no queen or eggs present).

For colonies considered to be associated with absconding, it was necessary to distinguish between seasonal versus disturbance-induced absconding. Several weeks before seasonal absconding, the laying activity of the queen is reduced, and workers begin consuming young larvae and food reserves (Woyke, 1976; Winston et al., 1979; Schneider, 1990 a, b). Older larvae and sealed pupae are usually not eaten. As a result, colonies preparing for seasonal absconding contain few eggs, no young larvae, and increasing amounts of empty comb. Departure from the nest is delayed until the sealed brood has emerged, and most remaining food reserves are consumed before the nest is abandoned (Winston et al., 1979). As a result, seasonally absconding colonies leave behind mostly empty comb. In contrast, disturbance-induced absconding does not involve long-term preparations, and often results in colonies abandoning large amounts of brood and food (Fletcher, 1978; Winston et al., 1979). Hence, if a nest was abandoned before excavation the colony was assumed to have undergone seasonal absconding if the combs remained undamaged but contained little or no brood or food. A colony was considered to be preparing for seasonal absconding if the nest was occupied at excavation, but (1) less than 25% of total comb area was devoted to brood, (2) open brood consisted mainly of eggs and older larvae with few or no young larvae, and (3) at least 50% of total comb area was empty. Abandoned nests containing brood and food stores were assumed to have been occupied by colonies that underwent disturbance-induced absconding.

A colony was considered to have recently become established in the nest cavity if at least 75% of the comb consisted of new, white wax.

A total of 109 nests were excavated during the 12 months of the study, with a mean ± SD of 9.1 ± 3.9 nests/month (range = 3–17). The greatest number of nests were examined in October–December, since these months overlapped in the two years of study.

We monitored the movement of naturally occurring swarms over the study area from October 1989–June 1990. For each swarm observed, we recorded the date of observation and determined the direction of travel using a compass. A total of 41 swarms were observed (4.6 ± 3.1/month).

Comparing the nests of absconding and non-absconding colonies

Nests of absconding and non-absconding colonies were compared with respect to (1) total comb area, (2) the proportion of comb devoted to honey and pollen storage, and (3) nest cavity volume. Comparisons of honey and pollen comb were restricted to colonies preparing to abscond because colonies that have absconded leave little or no food behind. Brood comb and empty comb were not compared between the two colony groups, since by definition absconding colonies exhibit reduced brood-rearing, and contain more empty comb (see above). Nest cavity volume was estimated for each excavated colony using the mean values of five to six measurements of cavity height, width, and depth.

Additionally, we compared the two colony groups with respect to recent swarming activity by noting the presence of queen cells from which virgin queens had recently emerged. This comparison was made because Fletcher (1975) and Winston et al. (1979) have suggested that a colony's swarming activity may influence the probability of absconding.

Unless stated otherwise, all mean values are reported as ± one SD. All statistical analyses were conducted using two-tailed levels of significance. Proportional data for comb areas were arcsine transformed prior to analysis.

Results

Forage availability

The vegetational surveys revealed that blooming species were present in the study area during all months of the year except May (Fig. 1a). However, the relative abundance of blooming plants varied markedly throughout the year.

The seasonal patterns in the availability of blooming trees and shrubs could be subdivided into three fairly distinct periods. The period of August–October (the latter part of the cool-dry season and the hot-dry season) exhibited the greatest abundance of blooming plants, with a peak occurring in September (Fig. 1a). During this period, the major blooming species consisted of large, long-blooming trees, such as *Acacia nigrescens*, *Hyphaene ventricosa*, *Lonchocarpus capassa*, and *Croton*

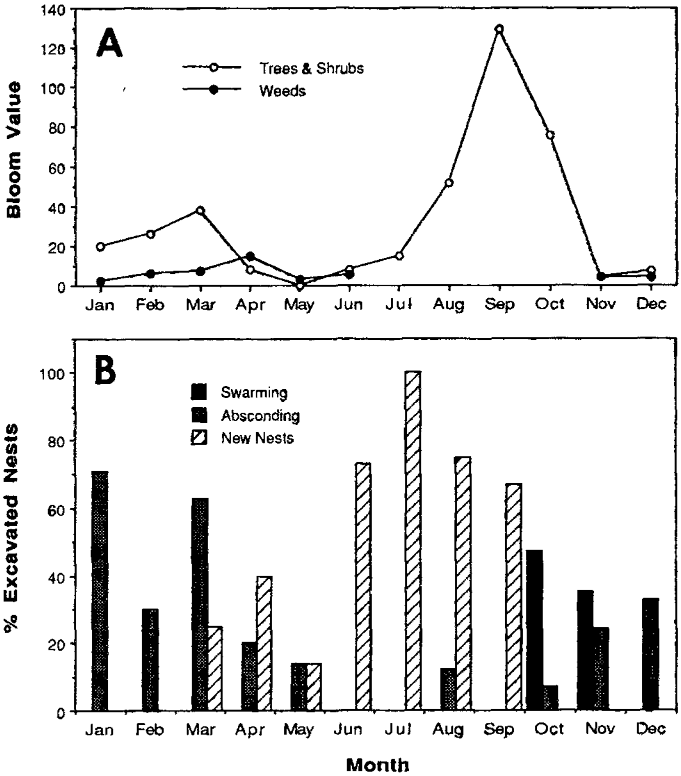

Figure 1. (A) The mean bloom values for trees and shrubs over all plots and for weeds over all transects for each month of the study. Data on the abundance of blooming weeds were not available for July–October. (B) The percentage of excavated nests exhibiting characteristics of swarming, absconding, or recent establishment during each month of the study

megalobotrys, all of which are visited by *scutellata* in the Okavango (Schneider and Blyther, 1988; McNally and Schneider, unpublished data).

During the period of November–March (the hot-wet season), the abundance of blooming trees and shrubs was lower and somewhat variable from month to month (Fig. 1a). Bloom values declined drastically in November and December, began increasing slightly in January, and exhibited a minor peak in March. This peak coincided with the blossoming of the shrub *Combretum apiculatum*, which blooms for only 1–2 days and which was not observed to be visited by *scutellata* in the study area.

During the third period, April–July (the end of the hot-wet season and the cool-dry season), floral abundance was greatly reduced. No blooming trees and shrubs were observed in May (Fig. 1a).

The abundance of blooming weeds remained low throughout the period of observation (Fig. 1a). However, blooming weeds may have provided an important source of food for *scutellata* colonies in April–June, when the availability of blooming trees and shrubs was most reduced. There was a small peak in the

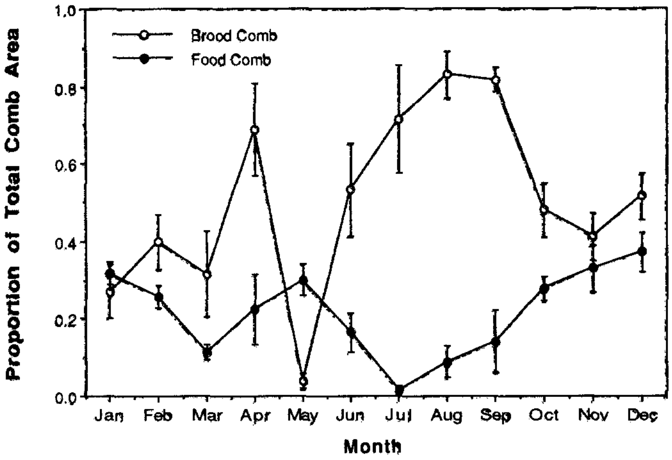

Figure 2. The mean (±SE) proportion of comb area devoted to brood rearing and food storage in the excavated nests during each month of the study

abundance of blooming weeds in April, and our observations revealed that at least 16 % of these species were visited by *scutellata*. However, at present the importance of weeds in the foraging of honey bees in the Okavango is unknown.

Seasonal patterns of colony development and movement

The excavated nests and movement of swarms over the study area suggested that the annual cycle of *scutellata* colonies in the Okavango occurred in three fairly distinct periods: a swarming season, an absconding or migration season, and a period in which new colonies became established in the study area (Fig. 1b).

The swarming season occurred from October–November (Fig. 1b), and coincided with the end of the peak abundance of blooming trees and shrubs (Fig. 1a). Of the 32 nests excavated during October and November, 13 (41 %) were associated with swarming (four were preparing for swarming and nine had recently swarmed). Swarming colonies contained a mean of 4.5 ± 3.6 queen cells (range = 1–13). Of the nine colonies which had recently swarmed, 3 (33 %) had failed to successfully requeen.

Reproductive swarming followed a period of increased brood production and reduced food storage (Fig. 2). During the three months preceding the swarming period (July–September), 72–83 % of total comb area was devoted to brood rearing in the excavated nests. Food storage during these months accounted for only 2–14 % of total comb area. However, during the swarming months (October and November), brood comb declined to 41–48 % of comb area, perhaps because of the reduced laying activity of swarming queens (Allen, 1955; 1960; Schneider, 1990b). Food comb increased to 28–33 % of total comb area during the swarming period (Fig. 2).

The behavior of swarms passing over the study area suggested that there was no distinct directionality in the movement of swarms during October and November. Of

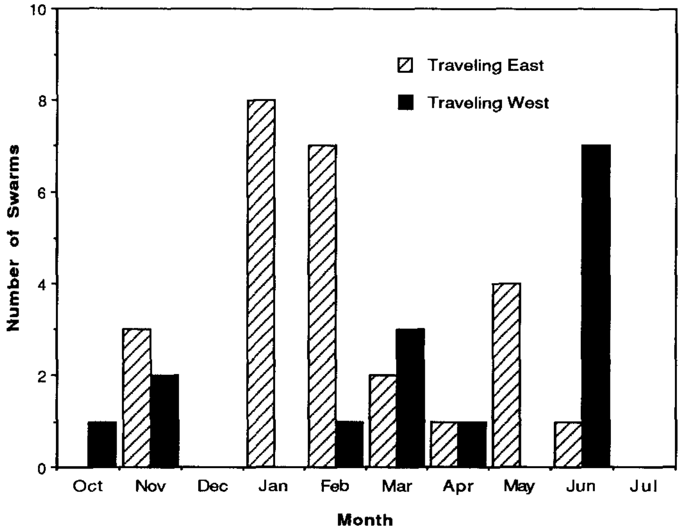

Figure 3. The number of swarms observed over the study area traveling east or west during October–June

the six swarms observed during these months, three were traveling in an easterly direction, while three headed in a westerly direction (Fig. 3).

The absconding season occurred primarily from November–May and followed the swarming season (Fig. 1 b). Of the 63 colonies excavated between November and May, 22 (35%) were associated with seasonal absconding. Fourteen exhibited the reduced brood rearing indicative of migration preparations, while eight had abandoned the nest prior to excavation, leaving behind only empty combs. Peak migration activity occurred in January–March, when 30–71 % of excavated colonies were absconding (Fig. 1 b). Disturbance-induced absconding was observed only once (in August; Fig. 1 b), in a colony that had abandoned the nest cavity because of an invasion of ants.

The absconding season coincided with the period of reduced floral abundance (Fig. 1 a and b). The onset of the absconding season in November and December occurred when the availability of blooming species was drastically reduced. Peak absconding activity in January–March coincided with a period in which forage availability had increased slightly, but was somewhat variable from month to month (Fig. 1). Absconding continued at lower levels throughout April and May, at which time the availability of blooming plants declined to near zero.

During the absconding season, comb areas devoted to both brood rearing and food storage were generally low, but fluctuated greatly on a month-to-month basis (Fig. 2). The mean proportion of total comb space devoted to brood rearing during the seven months of the absconding season, 37.6±20.2%, was less than half that observed during the months of peak brood production (*t*-test; $P < 0.05$). Brood comb accounted for 27–52 % of total comb area between November–March. There was a sudden and rapid increase in brood comb area in April, which corresponded with a slight increase in the availability of blooming weeds (Figs. 1 a and 2). Brood production virtually ceased in May, at which time the availability of blooming plants declined to near zero (Figs. 1a and 2). Food comb increased at the onset of the absconding season (November–December), at which time food storage accounted for a mean of $35.2 \pm 2.9\%$ of total comb area. Food comb declined to 11% of total comb area by March, but then increased to 30% of comb area by May (Fig. 2).

The monitoring of swarms passing over the study area between November and May suggested that the movement of colonies during the absconding season was highly directional. Of the 32 swarms observed from November–May, 25 were traveling in an easterly direction, while seven were headed west (Binomial Test; $P < 0.01$; Fig. 3).

The period of colony establishment occurred primarily from June-September, although some new nests were also observed from March–May (Fig. 1b). The establishment period followed the absconding season, preceded the swarming season, and coincided with (and slightly preceded) the period of maximum forage abundance (Figs. 1a and b). Of the 31 nests excavated between June and September, 23 (75%) contained combs of mostly new, white wax.

During the establishment period, colonies emphasized brood production and stored little food (Fig. 2). Between June and September, the excavated colonies devoted a mean of $72.4 \pm 13.7\%$ of total comb area to brood, but only $10.3 \pm 6.6\%$ to food storage.

The movement of swarms over the study area during the establishment period was monitored only in June. Of the eight swarms observed, seven were traveling in a westerly direction, and one was headed east (Fig. 3). While this difference was not significant (Binomial Test; $P > 0.05$), the available data suggest that there was a directionality in the route of travel during the establishment period that was the reverse of that observed during the absconding season.

Comparisons of absconding and non-absconding colonies

Comparisons of absconding and non-absconding nests were restricted to those nests excavated during the absconding season. Compared to the absconding colonies, the non-absconding colonies had more stored honey ($t_{51} = 2.11$) and pollen ($t_{51} = 2.31$; $P < 0.05$ for both comparisons; Table 1). However, non-absconding and absconding colonies did not differ with respect to total comb area ($t_{58} = 0.67$) or nest cavity volume ($t_{58} = 0.16$, $P > 0.05$ for both comparisons; Table 1). Likewise, the two types of colonies exhibited no significant difference in evidence of swarming activity. Only three of the 21 absconding nests and 12 of the 39 non-absconding nests contained old queen cells ($x^2 = 1.97$, $P > 0.05$).

Discussion

Colonies of *A. m. scutellata* in the Okavango Delta exhibited distinct seasonal patterns of growth, development and movement, which were associated with seasonal fluctuations in forage availability. During and slightly preceding the period

Table 1. Comparison of total comb area, proportions of total comb area devoted to honey and pollen storage, and nest cavity volume for absconding and non-absconding colonies excavated during the absconding season. Food comb data were restricted to colonies preparing to abscond. All proportional data were arcsine transformed prior to analysis

	Non-absconding	Absconding
Total comb area (cm^2)	5637.0 ± 4233.9 ($N = 39$)	4919.1 ± 3318.6 ($N = 21$)
% honey comb	26.7 ± 12.2 ($N = 39$)	18.7 ± 11.8 * ($N = 14$)
% pollen comb	15.0 ± 5.8 ($N = 39$)	10.4 ± 7.6 * ($N = 14$)
Nest cavity volume (L)	26.1 ± 22.3 ($N = 39$)	25.1 ± 28.9 ($N = 21$)

* $P < 0.05$.

of peak floral abundance (June–September), there was a large influx of new colonies into the study area. These colonies devoted almost all comb area to brood production and then swarmed at the end of peak forage availability (October–November). As the abundance of floral resources began to decline, colonies began abandoning the study area, and these movements continued throughout the six to seven months of reduced forage availability (November–May).

Taken together, these observations suggests that *scutellata* populations in the Okavango are highly mobile and follow shifting resource patterns. Colonies may move into the study area to capitalize on the period of maximum forage abundance. Resources collected during this time are converted almost entirely into brood, thereby allowing colonies to increase rapidly in size and swarm. Thus, unlike temperate climate honeybees which develop large food reserves during periods of forage abundance, *scutellata* colonies appear to channel resources gathered at such times into reproductive effort. Many *scutellata* colonies observed in this study emigrated as forage availability declined. It is unknown if the colonies abandoning the study area in the absconding season were the same ones that moved into the area during the establishment period. However, the pronounced movement of swarms in an easterly direction during the absconding season and a westerly direction in the establishment period suggests that these movements represent migrational behavior for Okavango honey bees.

The seasonal colony cycles observed in this study were broadly similar to those reported for *scutellata* in other regions of Africa and Africanized bees in Central and South America. An onset of swarming in October–November after a period of intense brood-rearing activity and low food storage has also been observed for *scutellata* in other regions of Botswana (Clauss, 1983) and in Venezuela (Pesante, 1985; Rinderer, 1988). However, whereas *scutellata* colonies in other regions of Africa and the neotropics may swarm for six to eight months of the year (Silberrad, 1976; Otis et al., 1981; Otis, 1991), those in our study area produced swarms during only a two-month period. The factors associated with the limited swarming season for Okavango bees are unknown. However, the mass movement of colonies out of the study area, beginning in November raises the possibility that Delta colonies have a second swarming season in the new region into which they migrate. The possibility of a second swarming season for migrating colonies has also been suggested for *scutellata* in South Africa (Fletcher and Tribe, 1977; Fletcher, 1991).

A third of the swarming colonies observed in our study failed to requeen successfully. Since queenless colonies are genetically "dead" (except for the possible production of drones; Otis, 1991), these data suggest a fairly high mortality rate associated with reproductive swarming in the Okavango. Relatively high rates of swarm failure have also been suggested for Africanized colonies in South America, and may be related to the loss of virgin queens during mating flights (Otis, 1982; 1991).

In the present study, migration occurred throughout the hot-wet season. Migration also occurs during the wet season in French Guiana (Winston et al., 1979), but primarily during the dry seasons in other regions of Africa (Smith, 1958; Nightingale, 1976; Silberrad, 1976; Fletcher, 1975). The six- to seven-month duration of the migration season observed in the Okavango was similar to the five-month period reported for Africanized bees in South America (Winston et al., 1979; Winston, 1980).

The factors regulating migration in Okavango colonies are unclear at present. Migration does not appear to be strongly associated with nest characteristics. The absconding and non-absconding nests did not differ with respect to total comb area or nest cavity volume. Absconding colonies did have less stored honey and pollen, although these reduced food stores may have been a product of migration preparations, since workers consume food reserves prior to departure (Fletcher, 1978; Winston et al., 1979). Winston et al. (1979) also found no differences in the nest characteristics of migrating and non-migrating Africanized bees in South America.

The absconding and non-absconding colonies examined in this study also did not differ with respect to recent swarming activity. Fletcher (1975) and Winston et al. (1979) have suggested that migration may occur if swarming (1) is repeatedly thwarted by bad weather, or (2) results in colonies that are too small to survive in areas of poor forage. However, in the present study the two types of colonies were equally likely to have swarmed prior to excavation.

Migration may be associated with seasonal changes in forage availability. In the Okavango, other regions of Africa, and the neotropics honey bee migration coincides with a period of reduced or declining floral abundance (Nightingale, 1979; Winston et al., 1979; Schneider, 1990a). A deteriorating foraging environment may therefore contribute to migration decisions. However, it is unlikely that foraging conditions alone trigger migration activity, since colonies occupying the same area (and thus potentially experiencing the same foraging environment) can differ markedly in their absconding behavior (Winston et al., 1979). Thus, internal colony conditions, perhaps such as colony age structure and brood mortality, may interact with changes in floral abundance to influence migration behavior (Winston et al., 1979; Schneider and McNally, in prep.).

The influx of large numbers of colonies into an area, such as was observed in the Okavango in June–September, has been reported for several other areas of Africa (Silberrad, 1976; Nightingale, 1976; Fletcher, 1978). In most cases such immigration events have been associated with the migration of colonies into areas during periods of forage abundance. The distinct directionality observed for swarms during the migration and establishment periods in the present study has also been reported for honey bee swarms in Kenya (reviewed in Otis, 1991).

In summary, the *scutellata* colonies of the Okavango Delta exhibited distinct seasonal patterns in swarming, migration, and establishment, which occurred in conjunction with seasonal changes in brood production and food storage. The different aspects of the annual colony cycle were related to fluctuations in the availability of blooming plants, suggesting that seasonal patterns of growth and movement are associated with seasonal changes in foraging activity. The relationship between seasonal fluctuations in colony foraging, development and movement are examined in a companion paper (Schneider and McNally, 1992).

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