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Factors influencing seasonal absconding in colonies of the African honey bee, *Apis mellifera scutellata*

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Summary

This study investigated the effects of colony growth and development, food storage, foraging activity and weather on the migration behavior of African honey bees in the Okavango River Delta, Botswana. Four observation colonies were studied during the honey bee migration season (November-May), at which time the availability of blooming species was reduced. Two of the colonies (colonies 1 & 2) migrated during the study period, while the remaining two (colonies 3 & 4) did not. During the 4–6 weeks preceding the onset of migration preparations, colonies 1 & 2 exhibited increasing population sizes, high levels of brood production with low brood mortality, relatively large stores of food, and increasing mass. In contrast, the populations of colonies 3 & 4 did not increase, brood-rearing activity was erratic and lower, brood mortality was higher, food stores became depleted and colony mass declined. Both colonies 3 & 4 ceased rearing brood, and colony 3 died of starvation. Colony foraging activity was examined by monitoring waggle-dance activity 2–3 days each week. For 4–6 weeks before the onset of migration in colonies 1 & 2, daily foraging areas and mean daily foraging distances became increasingly large and variable. Colonies 3 & 4 exhibited foraging patterns similar to those observed for colonies 1 & 2 preceding migration. There was no clear association between 7 weather parameters examined and migration behavior. These data suggest that migration is influenced by an interaction of intra-colony demographics, food reserves and foraging patterns. Migration may be feasible only for those colonies that possess (1) a population of appropriate size and age structure to compensate for the natural attrition of older workers during the emigration process, and (2) sufficient food reserves for long-distance travel and the establishment of a new nest. Changing foraging patterns may reflect a deteriorating foraging environment, which may trigger the onset of migration preparations, provided that colony demographics and food reserves are conducive. Colonies that show decreased brood production, higher brood mortality and reduced food stores may be incapable of migrating, even when experiencing deteriorating foraging conditions. Rather, such colonies may have a greater chance of survival if they attempt to persist in a given area.

Introduction

The honey bee *Apis mellifera* exists as distinct races occupying habitats as dissimilar as the temperate climates of North America and Europe and tropical Africa (Ruttner 1988). Temperate and tropical subspecies exhibit numerous behavioral differences,

many of which are associated with the duration and predictability of forage abundance in the contrasting environments (Winston et al., 1981, 1983; Rinderer, 1988; Schneider and Blyther, 1988). Temperate races experience a brief, predictable foraging season, during which large food stores must be amassed for winter survival. In contrast, African subspecies do not experience a winter and may forage virtually all the year round (Schneider and Blyther, 1988; Schneider and McNally, 1992). However, food availability in tropical Africa is often temporally and spatially unpredictable, owing to unpredictable rain patterns (Griffiths, 1976; Sinclair, 1983; Rinderer, 1988). As a result, African races frequently respond to unfavorable periods by undergoing "seasonal absconding" or migration, which consists of a colony abandoning a nest site, presumably to move into an area of greater resource abundance (Fletcher, 1978; 1991; Winston et al., 1979; Schneider, 1990a; McNally and Schneider 1992).

Migration is unique to tropical honey bee races (Winston, 1987; Rinderer, 1988), and may result in the movement of 15–100% of all colonies during certain times of the year (Fletcher, 1978; Winston et al., 1979; Schneider 1990a; McNally and Schneider, 1992). However, colonies occupying the same area, and experiencing the same weather conditions and potentially the same foraging environment, can vary greatly in their migration behavior (Winston et al., 1979; Schneider 1990a). Migration may therefore depend upon some assessment of both environmental and intra-colony conditions. However, little is known about the factors regulating seasonal absconding. Indeed, migration remains one of the least understood aspects of honey bee biology (Seeley, 1985).

The purpose of this study was to investigate the factors influencing migration in the African honey bee *A. m. scutellata* (hereafter referred to as *scutellata*) in Africa. We investigated four interrelated factors that could potentially affect honey bee migration. First, we examined the relationship between colony growth and development patterns and migration behavior. In the Africanized bees (hybrids of *scutellata* and European honey bee races) of Central and South America, migration is associated primarily with colonies that become demographically weakened (through reduced population sizes and increased brood mortality) during periods of reduced forage availability (Winston et al., 1979). Factors such as the number of adult workers and brood mortality may influence the ability of colonies to collect sufficient food or survive long-distance travel, which in turn may affect migration behavior.

Second, we examined the association between changes in colony food reserves and migration behavior. Seasonal absconding often occurs at times of the year when it may be difficult for *scutellata* colonies to build up or maintain stores of food (Winston et al., 1979; Schneider, 1990a; McNally and Schneider, 1992). Also, in colonies maintained by humans, seasonal absconding preparations may be aborted if supplemental feedings are provided (Camazine and Morse, 1988). A colony's migration behavior may therefore depend upon some assessment of its level and rate of energy storage.

Third, we examined the relationship between changes in colony foraging patterns, the sampling of alternate foraging areas, and migration behavior. Migration frequently occurs during periods in which the abundance of blooming plants declines (Winston et al., 1979; Schneider, 1990a; Fletcher, 1991; McNally and Schneider,

1992). Changes in food availability may alter colony foraging patterns and the energy expended in food collection, which in turn may contribute to the decision to abandon an area. Likewise, changing forage abundance may influence the degree to which colonies sample alternate foraging sites (Seeley, 1983), and the ability to locate such sites may affect both the decision to depart and the route of travel (Schneider, 1990 a). Colony foraging patterns were investigated by monitoring waggle dance activity in observations hives. Honey bees use the waggle dance to communicate the location of profitable food sources (Von Frisch, 1967). By translating the distance and direction components of waggle dances it is possible to map colony foraging activity (Schneider, 1989; Visscher and Seeley, 1982), and thus to determine day-to-day variations in foraging area, mean foraging distance, and the sampling of alternate sites. These variations can then be examined with respect to the onset of migration preparations. Waggle dance activity has been used previously to investigate the distance and direction that migrating colonies travel (Schneider, 1990 a). However, to date there has been no attempt to investigate the recruitment behavior of *scutellata* colonies in the period immediately preceding migration.

Fourth, we investigated the relationship between changes in various weather parameters and the onset of migration behavior. Migration frequently occurs during distinct times of the year in the Africanized bee in South America (Winston et al., 1979, 1983) and in *scutellata* in Africa (Nightingale, 1976; Silberrad, 1976; Schneider, 1990 a; McNally and Schneider, 1992). Hence, there may be an influence of weather on colony-movement decisions that occurs independently of the effects of weather on forage availability.

Materials and methods

Study area

The study was conducted from October, 1989 through June, 1990 in Botswana, Africa, in the Okavango River Delta. The Okavango consists of a large inland delta covering approx. 17000 km^2 in which *scutellata* colonies are abundant (8/km^2), the human population is small, and there are few or no agricultural or beekeeping practices (Schneider and Blyther, 1988). There is a distinct honey bee migration season in the Okavango that begins in November–December at the onset of the rainy season, continues for 5–6 months, and coincides with a rapid decline in floral abundance (Schneider, 1990 a; McNally and Schneider, 1992). During each month of this period, 20–70% of all naturally occurring colonies abandon their nests (Schneider, 1990 a; McNally and Schneider, 1992). The Okavango therefore offers a unique location for the study of the migration behavior of a natural population of African honey bees in an environment little influenced by human activity.

The study site was located on the edge of a large lagoon (19°35.42′ S; 23°21.43′ E). Further descriptions of the study area, seasonal abundance of blooming species, and nesting biology of *scutellata* in the Okavango are provided in Schneider and Blyther(1988) and McNally and Schneider (1992).

Observation hive set-up and maintenance

A total of four observation colonies (Colonies 1–4) were examined during the study period. All colonies were excavated in the field, and the bees and combs were collected and transferred into 45-L hive boxes with movable frames. Once a colony had become established and was raising brood it was transferred into a 2-frame observation hive. The walls of each observation hive were marked off in a 5×5 cm grid to facilitate monitoring colony activity.

The observation hives were maintained inside high walled canvas tents (two hives/tent; each tent $2\text{ m} \times 3\text{ m} \times 2\text{ m}$ high), and each abutted a 2×10 cm opening cut into a tent wall which allowed free flight to and from the colonies. Colonies of *scutellata* exposed to strong heat and light may abandon the nest (Fletcher, 1978; Winston, 1987), and strong light can interfere with waggle dance activity within observation hives (Von Frisch, 1967). To reduce heat and light, each tent was located in the shade and lined internally with heavy brown paper. Under such conditions, observation hives can be maintained for extended periods, and the resulting light levels do not influence recruitment behavior (Schneider, 1989, 1990 a, b). Each colony occupied an observation hive for 7–10 days before data collection was begun. Further details of observation-hive maintenance are given in Schneider (1989, 1990 a, b).

The following criteria were used to determine whether a colony was preparing for migration during the study period. Three to four weeks before seasonal absconding, workers begin to eat the young larvae, and laying activity by the queen is reduced (Woyke, 1976; Winston et al., 1979; Schneider, 1990 b). The onset of reduced brood rearing occurs rapidly, and is characterized by the sudden disappearance of young larvae and eggs, and increasing amounts of empty comb within the brood area. In colonies not preparing for migration, young larvae and eggs typically make up 20–40% of the total brood comb area, and only 3–7% of comb within the brood area is empty (Schneider, unpublished data). Hence, in this study an observation colony was considered to be preparing for migration if (1) brood rearing suddenly decreased, such that young larvae and eggs comprised less than 20% of total brood comb area, and (2) the empty comb in the brood area increased to at least 10% of the total brood comb area. Comb areas were measured using the grids drawn onto the observation hive walls. None of the 4 colonies exhibited evidence of migration preparations at the time of excavation or when initially established in the observation hives.

Monitoring colony growth and development patterns

Three aspects of intra-colony demography were examined: population size, amount of brood comb and the mortality of young brood. Colony populations were measured at least once each week by (1) calculating the mean number of bees in 10, randomly selected grid squares, and (2) multiplying the mean by the total number of squares of comb. All population counts were conducted in the early morning or late evening when nearly all workers were in the hive.

The amount of brood comb in each colony was estimated once every six to seven days, by using the grids to determine the areas of open brood (eggs and young larvae) and sealed brood (pupae). The sum of these areas was then expressed as a percentage of the total comb area. The areas of open and sealed brood were also used to estimate brood mortality. In *scutellata* the first eight days of development consist of the egg and larval stages. Brood cells are then sealed when the larvae pupate, and new adults emerge 12 days after sealing (Winston, 1987). Hence, it was assumed that on average 1/8 of the area of open brood measured on a given day would be sealed on each subsequent day, while 1/12 of the measured sealed brood area would emerge on each subsequent day. We then calculated the amount of sealed brood expected each day between two consecutive measurements. The difference between observed and expected values was used to estimate the percentage of brood dying before being sealed. It was assumed that the mortality of sealed brood was zero (see Fukuda and Sakagami, 1968). These methods may underestimate brood mortality to some extent in certain instances (Otis, personal communication). However, the methods allow for a reliable comparison of relative brood-rearing success among colonies, and have been used in previous studies (Winston, 1979; Winston et al., 1981).

Estimating colony energy reserves

Colony energy reserves were estimated in two ways. First, each week we used the grids to determine the total comb area containing food (honey or pollen), and these areas were then expressed as a proportion of total comb area. These data provided a direct estimate of colony food reserves. Second, each observation hive was maintained on a battery powered, Kabuto KA-10 digital platform scale calibrated in 5-g increments, and was weighed at the end of each day after foraging activity had ceased. The mass of the empty hive was then subtracted from each day's weighing, which resulted in a value for the combined mass of all workers, brood, food, and combs in the colony. We then determined the mean mass for each 7-day period, and used this value as an indirect estimate of whether colonies were experiencing a positive energy budget (gain in mass), negative energy budget (loss of mass), or just meeting energy needs (no change in mass).

Monitoring waggle-dance activity and determining colony foraging patterns

The methods for recording waggle dances and mapping foraging activity in this study were essentially the same as those described in Schneider (1989, 1990a), and are only briefly summarized here. Each observation colony was monitored 2–3 days each week, throughout the time it occupied an observation hive. Whenever possible, different colonies were observed on the same days. On each day of observation, a colony was monitored for 30 min each hour from sunrise to sunset. Throughout these periods, individual waggle dancers were selected at random and the direction and distance components of their dances were recorded. Honey bees communicate the direction to a food source through the orientation of the waggle-run portion of the

waggle dance with respect to the vertical (Von Frisch, 1967). Therefore, the directions indicated by the dancers in this study were estimated by measuring the angles of the waggle runs relative to the vertical, using a protractor. The dance angles were later converted to a direction with respect to north by (1) calculating the sun azimuth for the time of observation, using an Astrosoft program for an IBM personal computer, and (2) adding the azimuth value to the recorded dance angle.

The distance to a food source is correlated with the duration of the waggle run (Von Frisch, 1967). The distance communicated by each dancer examined in this study was estimated by (1) recording the time of 5–10 different waggle runs (5.92 ± 4.92) using a digital stopwatch, (2) calculating a mean waggle-run time (obviously inconsistent times were ignored), and (3) converting this time into a distance estimate in meters. The conversion of waggle-run duration into distance was accomplished using a curve expressing the relationship between waggle-run duration and distance. This curve was established by training marked foragers from colony 1 to feeding stations at known distances up to 1 km from the hive, and then timing their waggle runs once they returned to the hive. The distance-dance time relationships for different *scutellata* colonies in the Okavango are similar (see Fig. 1; Schneider, 1989), and hence we used the curve for Colony 1 to estimate the foraging distances for all 4 observation colonies.

The translation of dance times greater than those covered by the waggle-run duration-distance curve for colony 1 was accomplished by extrapolation. We could not use the waggle-run duration-distance curve to translate dance times shorter than 0.4 s, since these times could not be recorded accurately using a digital stopwatch. Dance times less than 0.4 s were assigned a distance value as follows. A waggle-run time of 0.4 s corresponded to a distance of approximately 120 m (Schneider, 1989). All trained foragers began performing consistently oriented waggle runs at 15–20 m from the hives, although these runs could not be timed. Hence, dance times less than 0.4 s were assigned the mean distance between 20 and 120 m, or 70 m. All round dances were assigned a distance of 17 m.

For each day of observation in a given colony, a foraging map was constructed by plotting the location communicated by each dancer (see Schneider (1989, 1990a) for examples of such maps). The maps were used to determine for each day of observation: (1) total number of dancers observed, (2) mean foraging distance indicated by all dancers, and (3) foraging area, defined as the circular area encompassing 95% of all sites indicated by dancers (see Visscher and Seeley (1982) for similar methods of estimating foraging areas). Comparisons of foraging distances and areas within and among colonies were conducted on these daily values, using either t tests or Anova (Sokal and Rohlf, 1981). Where necessary, data for foraging areas and mean daily foraging distances were log-transformed to ensure equality of variances among colonies.

Additionally, we used the daily foraging maps to estimate the extent to which each colony sampled foraging sites outside their daily foraging range (hereafter, such sites are referred to as long-distance sites). A dancer was considered to be sampling outside the daily foraging range if it communicated a distance at least 1.5 times as great as the radius of the circular area encompassing 95% of all sites indicated on a given day. We then determined for each colony the total number of long-distance dancers observed

during all days of observation and the mean distance communicated by these dancers. The foraging area and long-distance dances observed on a given day were not independent measures. For example, if there was a large number of long-distance dancers, some of these would have been included in the 95% of dancers used to estimate the foraging area. However, we used the criterion listed above to identify long-distance foragers because (1) it provided an estimate of the relative degree to which foragers traveled beyond the regular foraging range on any given day, and (2) the number of long-distance dancers observed for each day was too low to affect strongly estimates of foraging area (see below).

Monitoring weather conditions

On a given day, temperature, relative humidity (% RH), and barometric pressure (BP) were recorded each hour using a Schenk CT-2001 battery-powered portable weather station. Wind direction was determined each hour using a compass. These weather parameters were recorded for 4–7 days/week throughout the study period, and were always recorded on the days the observation hives were monitored. For each day, we determined maximum and minimum temperature, % RH and BP, plus the number of times the wind changed direction.

Two different analyses were performed using the weather data. First, we determined whether any of the weather parameters examined was correlated with the date of observation, expressed in Julian days ranging from day 1 (October 15, 1989) to day 243 (June 15, 1990). Any weather parameter which changed significantly during the observation period could have provided colonies with cues for migration.

Second, we used canonical correlation analysis to examine whether there was an association between the weather parameters measured and a colony's daily foraging pattern. This portion of the analysis was conducted to determine to what degree weather was associated with any observed relationship between colony foraging patterns and migration behavior. Canonical correlation analysis quantifies the relationships between two sets of variables (Kachigan, 1982). A linear combination is first constructed for one set of variables, which has a maximum (canonical) correlation with a linear combination constructed from the second set. The analysis generates a set of canonical vectors that indicates the relative importance of each of the variables to a given vector. Other orthogonal pairs of vectors are similarly constructed, and each successive pair is less correlated. The canonical correlations may be tested for significance. The two sets of variables examined in this study were daily foraging area and mean daily foraging distance (set 1), and the 7 weather parameters measured (set 2). We report in this paper the standardized canonical vectors, which have been adjusted for the differences in the variance of the different variables.

Unless otherwise stated, all statistical tests were conducted using two-tailed levels of significance. Proportional data for areas of comb devoted to brood and food were arcsine transformed prior to analysis. All mean values are reported as $\pm$ one standard deviation.

Results

Of the four colonies monitored, colonies 1 & 2 migrated during the study period, while colonies 3 & 4 did not. The migrating colonies were installed in the observation hives in October–November, 1989; the non-migrating colonies were installed in February–March, 1990. As a result, the two colony groups were not observed during the same months. However, all colonies were observed during the honey bee migration season in the Okavango (see **Methods and materials**). Peak migration activity occurred in January, at which time 70% of all naturally occurring colonies abandoned the study area (McNally and Schneider, 1992). However, during February–May, when the two non-migrating observation colonies were monitored, 20–63% of naturally occurring colonies continued to emigrate from the region each month (McNally and Schneider, 1992). Thus, all four observation colonies experienced environmental conditions conducive to migration. Comparisons between the migrating and non-migrating colonies were therefore considered to be justified. However, we recognize that some of the observed differences between the migrating and non-migrating colonies could potentially have resulted from seasonal factors not directly associated with migration behavior (as well as genetic differences among colonies). Therefore, the comparisons of this study must be interpreted cautiously.

Migration preparations in colonies 1 & 2 began in early January, at which time brood rearing began to decrease rapidly (Fig. 1). Each colony abandoned the study area in late January-early February, after 14–16 weeks of observation. Because the migration of colonies 1 & 2 coincided with that of naturally occurring colonies, it was assumed that the departure did not occur in response to any stress induced by the experimental conditions. Since this study was concerned with the factors that regulate migration behavior, the results described below for colonies 1 & 2 deal only with the data collected during the 10–12 weeks preceding the onset of migration preparations. The behavior and recruitment activity of colonies during migration preparations has been described previously (Schneider, 1990a & b).

Growth and development patterns of the migrating and non-migrating colonies

Prior to migration preparations, colonies 1 & 2 exhibited increasing population sizes, high and constant levels of brood-rearing activity and low brood mortality (Fig. 1). Both colonies had a rate of population increase significantly greater than zero (colony 1: $t = 10.92$; $N = 13$ weeks of observation; colony 2: $t = 12.42$; $N = 12$ weeks; $P < 0.01$ for both colonies), and both were similar with respect to the rate of increase ($F = 0.07$; d.f. = 1,22; $P \gg 0.05$) and mean population size (colony 1: 4586 ± 1422 bees; colony 2: 4578 ± 1747 bees; $t = 0.01$; d.f. = 23; $P \gg 0.05$).

During the first three to four weeks of observation, brood accounted for 40–50% and 25–45% of total comb area in colonies 1 & 2, respectively (Fig. 1). Brood mortality fluctuated between 2–30% (colony 1) and 2–20% (colony 2) (Fig. 1). However, during the six to seven weeks of observation preceding migration preparations in each colony, brood comb consistently accounted for 50–65% of total comb area, and brood mortality declined to 2–15% (Fig. 1). The mean

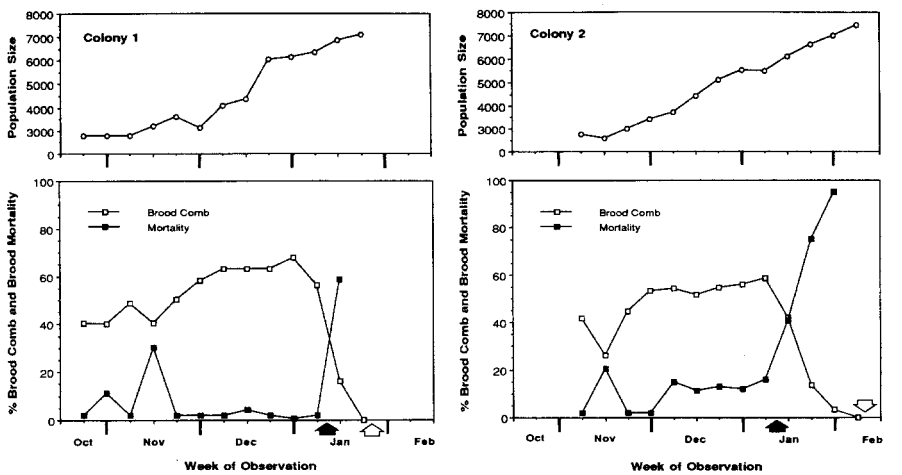

Figure 1. The population size, proportion of total comb area devoted to brood, and brood mortality (%) during each week of observation in colonies 1 & 2. The closed arrows indicate the onset of reduced brood rearing, and thus the beginning of migration preparations. The open arrows indicate when each colony migrated

proportion of brood comb (53.5±10.8% and 49.0±10.1% for colonies 1 & 2, *respectively*) and mean brood mortalities (5.4±9.4% and 10.4±6.8%, respectively) did not differ in the two colonies (for both comparisons, $t < 1.35$; d.f. = 17; $P > 0.05$). Once migration preparations began, brood comb are a declined and brood mortality increased rapidly (Fig. 1), presumably because of worker cannibalism of young larvae.

In contrast to the migrating colonies, the non-migrating colonies exhibited static population sizes and erratic patterns of brood rearing and brood mortality. The mean population sizes of colonies 3 & 4 (4887±641 and 4498±366 bees, respectively) were similar to those of colonies 1 & 2 ($F = 0.20$; d.f. = 3,44; $P > 0.05$). However, the population growth rates in the non-migrating colonies did not differ from zero (colony 3: $t = 1.55$, N = 11 weeks of observation; colony 4: $t = 0.51$; N = 12 weeks; $P > 0.05$ for both colonies) and were significantly lower than those for the migrating colonies ($F = 42.28$; d.f. = 1,42; $P < 0.01$).

During February and March, brood comb in the non-migrating colonies accounted for 5–30% of total comb space, and brood mortality ranged between 3–97%. Brood comb increased to 45–55% of comb area in early April, and brood mortality declined to 2–6%. The proportion of brood comb then decreased rapidly, beginning in late April, and brood mortality approached 100%, culminating in the cessation of brood rearing in both colonies in May (Fig. 2). Colony 3 died at this time, and colony 4 had no brood throughout May. The cessation of brood rearing in colonies 3 & 4 was evidently not associated with migration preparations, but rather appeared to be associated with the depletion of colony food stores (see below). The mean proportions of brood comb in colonies 3 & 4 (26.6±15.6% and 16.4±21.1%, respectively) were significantly lower than those observed for the migrating colonies

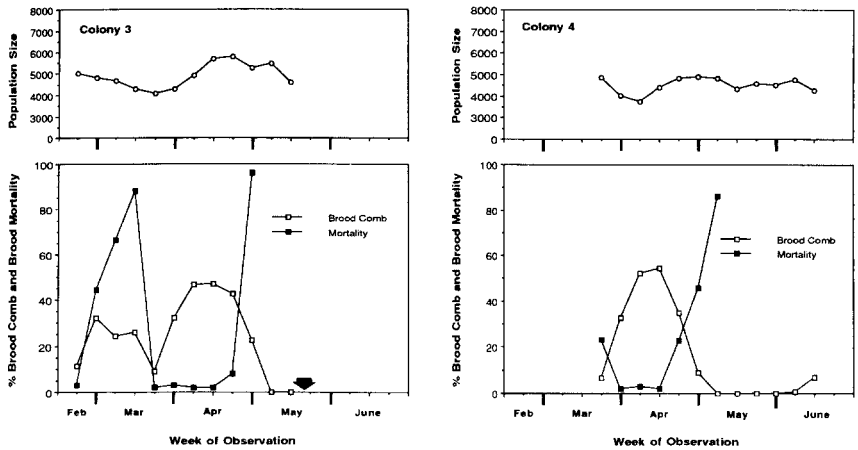

Figure 2. The population size, proportion of total comb area devoted to brood, and brood mortality (%) during each week of observation in colonies 3 & 4. The arrow indicates the death of colony 3

($F = 13.36$; d.f. = 3,38; $P < 0.01$). Likewise, mean brood mortalities in the non-migrating colonies ($31.7 \pm 39.7\%$ and $29.1 \pm 38.9\%$, respectively) were 2.9–5.8 times greater than those of colonies 1 & 2.

Colony energy reserves

For five to six weeks before the onset of migration preparations, the proportions of food comb and colony mass remained constant or increased in colonies 1 & 2 (Fig. 3 & 4). Food comb accounted for 20–30% of comb area during the first month of observation, but then increased and remained constant at 40–50% of comb area until migration preparations began (Fig. 3).

The mass of colonies 1 & 2 remained relatively constant during the first four to five weeks of observation, but then increased steadily throughout the final six weeks preceding the onset of migration preparations (Fig. 4). When viewed over all weeks of observation, there was a positive and significant ($P < 0.01$) correlation between mass and time for both colonies 1 & 2 ($r > 0.93$; $N = 11$ weeks of observation for each colony). The colonies exhibited similar temporal patterns of weight gain ($r = 0.96$; $P < 0.01$) and had similar mean weights during the study period (1993 ± 780 g for colony 1; 2185 ± 473 g for colony 2; $t = 0.61$; d.f. = 16; $P > 0.05$). These data suggest that colonies 1 & 2 did not migrate in response to an immediate threat of starvation.

Compared to the migrating colonies, the non-migrating colonies had less stored food and lower masses. In colonies 3 & 4 the amount of food comb ranged between 10–50% of total comb area during the study period, but was generally low (Fig. 3). The mean proportions of food comb in colonies 3 & 4 ($18 \pm 16\%$ and $11 \pm 11\%$, respectively) were significantly lower than those observed for the migrating colonies ($F = 11.83$; d.f. = 3,37; $P < 0.01$). Food reserves in both non-migrating colonies declined to zero in May (Fig. 3). The mass of the nonmigrating colonies decreased

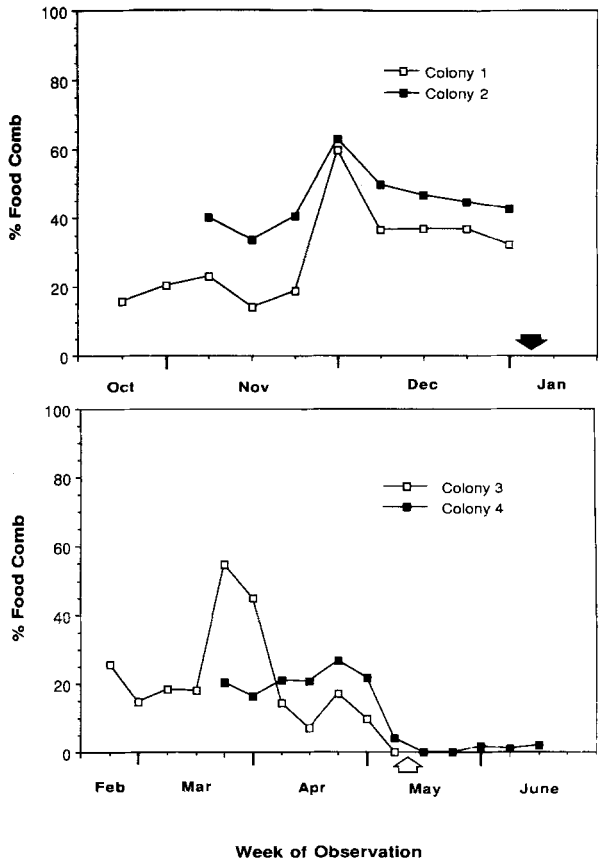

Figure 3. The proportion of total comb area devoted to food storage during each week of observation in the four colonies monitored. Closed arrow indicates the onset of migration preparation in colonies 1 & 2; the open arrow indicates the death of colony 3

throughout much of the study period. There was a significant ($P < 0.01$), negative correlation between mass and time for both colonies 3 & 4 ($r < -0.61$; $N = 11$ and 12 weeks of observation, respectively). The mean masses of colonies 3 & 4 (1224 ± 473 g and 1224 ± 325 g, respectively) were significantly less than those observed for the migrating colonies ($F = 11.64$; d.f. = 3,37; $P < 0.01$). The diminishing food reserves and declining masses coincided with the cessation of brood rearing and the death of colony 3 in May (Fig. 3). Hence, colonies 3 & 4 may have faced starvation three to four months after colonies 1 & 2 migrated.

Foraging patterns of the migrating and non-migrating colonies

The daily foraging patterns of colonies 1 & 2 changed markedly prior to the onset of migration preparations (Fig. 5). The first four to five weeks of observation (the

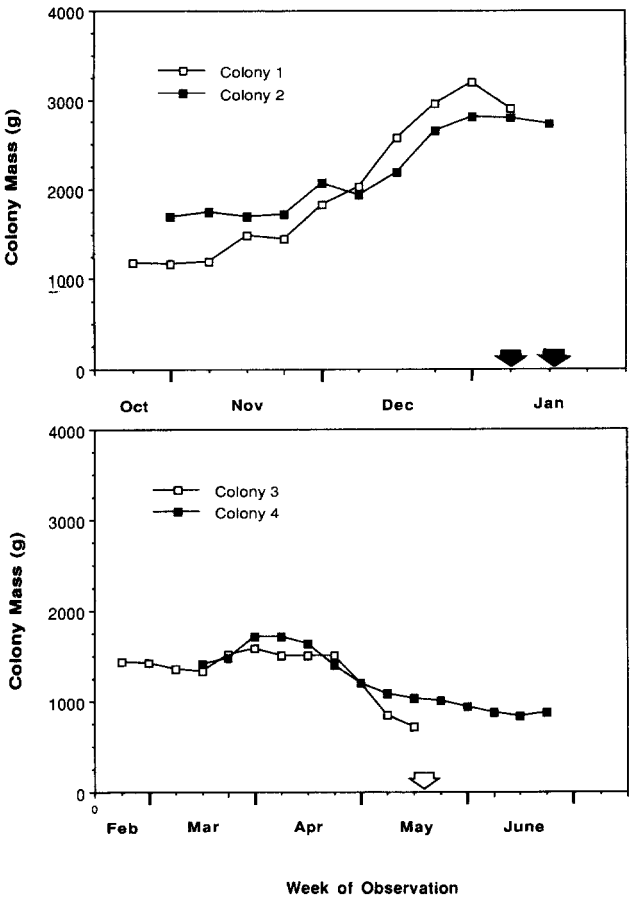

Figure 4. The mean mass of each of the four colonies examined during each week of observation. Colony mass consisted of the combined weight of bees + brood + food stores + combs. Closed arrows indicate the onset of migration preparations in colonies 1 & 2; the open arrow indicates the death of colony 3

"constant" periods) were characterized by mean foraging distances and foraging areas that were small and constant from one day of observation to the next. In contrast, during the final five to six weeks preceding migration preparations (the "variable" periods), foraging distances and areas became increasingly large and variable on a day-to-day basis (Fig. 5; there were no waggle dances observed for one day of observation for Colony 2 in January, and this day was not included in the following analyses). In both colonies, mean foraging distances and areas increased significantly when comparing the constant and variable periods (Table 1; $P < 0.001$ for all comparisons). Also, in both colonies the day-to-day variance in mean foraging distances and areas was significantly greater in the variable versus the constant periods (for both comparisons for colony 1: $F > 6.15$; d.f. = 12,13; $P < 0.01$; for colony 2: $F > 13.5$; d.f. = 10,12; $P < 0.01$; Table 1). However, the mean number of waggle dancers observed per day did not differ between the two periods in either

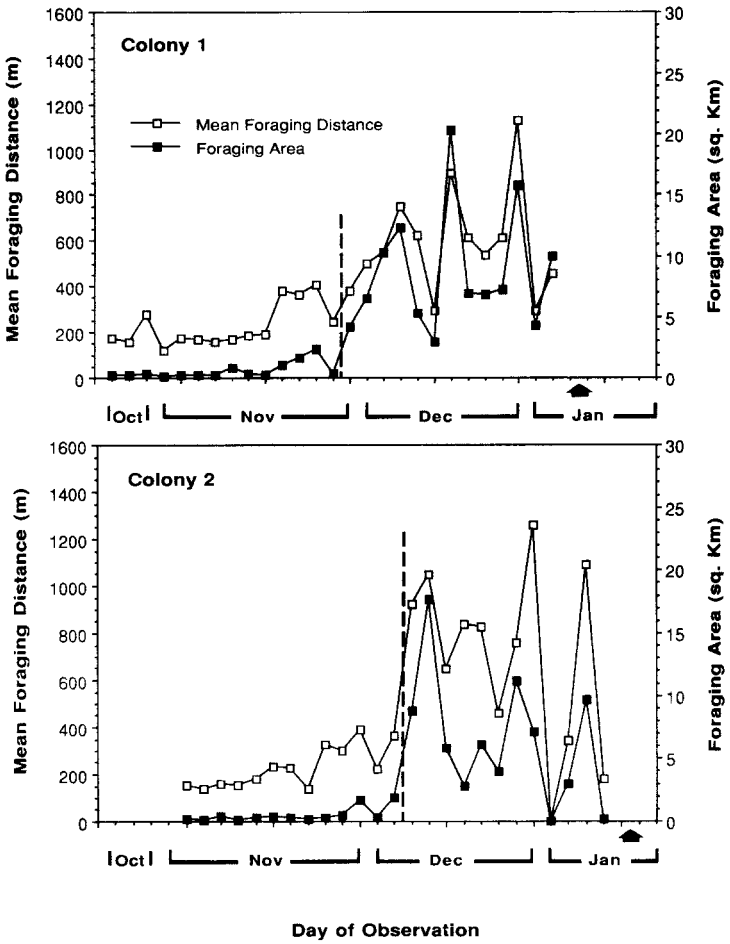

Figure 5. The mean foraging distance and foraging area for each day of observation in colonies 1 & 2 before the onset of migration preparations. The dashed, vertical lines indicate the division between the "constant" and "variable" observation periods. Arrows indicate the onset of migration preparations. No waggle dancers were observed during one day of observation in January in Colony 2

colony (Table 1; $P > 0.05$), suggesting that the changing foraging patterns did not arise from fluctuations in the level of colony foraging effort. Colonies 1 & 2 were similar during both periods with respect to the mean number of waggle dancers observed per day, mean foraging distances and daily foraging areas (Table 1; 2-way ANOVA; $P > 0.21$ for all comparisons), and there were no colony-X-period interactions for any of the variables examined ($P > 0.40$ for all comparisons). In summary, these data suggest that before migration colonies 1 & 2 began exploiting increasingly larger and more variable areas of the environment, and that the colonies exhibited these changing foraging patterns to similar extents.

The changing foraging patterns of colonies 1 & 2 may have resulted in part from changes in population size. The increasing populations of the migrating colonies

(Fig. 1) may have required the exploitation of larger foraging areas. However, there were no significant correlations between population size, mean foraging distances and daily foraging areas during either the constant or variable periods in colony 1 or 2 (for all comparisons, $r < 0.48$; $N = 14$ and 13 days during the constant periods for colonies 1 & 2, respectively, and 13 and 11 days during the variable periods; $P > 0.05$). Therefore, while population size undoubtedly influenced colony foraging activity, this factor alone seemed insufficient to account for the observed changes in spatial foraging patterns.

The sampling of long-distance sites occurred at low and relatively constant levels throughout the period preceding migration preparations in colonies 1 & 2. Only 26 and 36 long-distance dancers were observed out of the 2799 and 2207 total dancers monitored in colonies 1 & 2, respectively. The number of long-distance dancers observed during the constant and variable periods for colony 1 (10 versus 16) and colony 2 (23 versus 13) did not differ (2×2 contingency Chi Sq. = 2.90; $P > 0.05$). The mean distances communicated by such dancers in each colony (colony 1: 2650 ± 931 m; colony 2: 2954 ± 957 m) were similar ($P > 0.05$). Thus, the sampling of alternate food sites outside the regular foraging range did not increase prior to the onset of migration preparations.

Foraging distances and areas in the two non-migrating colonies remained large and variable throughout the study period (Fig. 6). The daily foraging patterns of the non-migrating colonies during February–June were similar to those observed for the migrating colonies during the variable periods. The mean number of dancers observed/day, mean daily foraging distances and daily foraging areas for colonies 1 & 2 during the variable periods did not differ from those for colonies 3 & 4 (Table 1; for all comparisons $F < 0.65$; d.f. = 3,72; $P > 0.05$). The four colonies were also similar with respect to long-distance sampling activity. The number of long-distance dancers observed in colonies 3 (25 out of 3385 total dancers) and 4 (39 out of 2622 total dancers) did not differ from that of the migrating colonies (Chi Sq.; $P > 0.05$). However, the mean distances communicated by such dancers in colonies 3 & 4 (3411 ± 1445 m and 3883 ± 2787 m, respectively) were approximately 1000 m greater than those of colonies 1 & 2 ($F = 2.87$; d.f. = 3,119; $P < 0.05$). The similarities in foraging patterns among the four colonies suggests that the foraging conditions experienced by the migrating colonies during the variable periods persisted throughout the four-to five-month interval following their departure from the study area.

The relationship between weather and colony migration

There was no clear association between the weather parameters measured and the onset of migration preparations in colonies 1 & 2. Of the parameters measured, only the minimum temperature changed significantly during the observation period (Tab. 2).

The canonical vectors and correlation coefficients for the associations between the two variable sets (foraging and weather) are presented for colonies 1 & 2 in Table 3. The correlation coefficients for both colonies were not significant. Furthermore, when the first vector (which had the highest correlation coefficient in each colony)

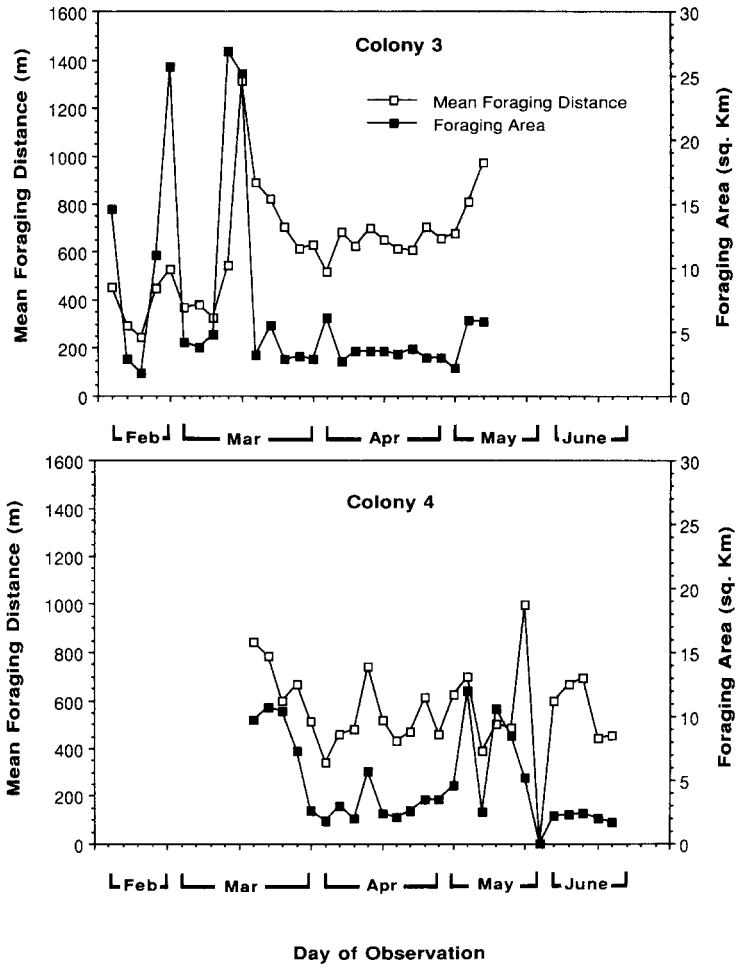

Figure 6. The mean foraging distance and foraging area for each day of observation in colonies 3 & 4. Colony 3 died in May. No waggle dancers were observed during one day of observation in May in Colony 4

was examined, the largest loadings in colony 1 were for the association between maximum and minimum BP and foraging area, while those in colony 2 were for the association between maximum temperature, minimum RH, and mean foraging distance. Hence, there were no consistent relationships between the various foraging and weather parameters measured for the two colonies. Therefore, any influence of foraging activity on migration decisions probably occurred independently of the weather factors examined.

All wheather factors examined except the number of wind shifts/day changed significantly during the periods in which colonies 3 & 4 were monitored (Tab. 2). However, canonical correlation analysis revealed a significant correlation between foraging and weather only for colony 3 (Table 3). The factors loading most heavily in vector one for colony 3 were for the association between maximum temperature,

Table 1. Mean (±SD) values for waggle dance activity, foraging areas and mean daily foraging distances for each of the four colonies examined. Foraging areas were estimated as the circular area encompassing 95% of all sites indicated by dancers on a given day. Sample sizes refer to the number of days of observation

	Waggle dancers observed per day	Foraging area (km^2)	Mean daily foraging distance (m)
Colony 1			
Overall (N = 27)	103.7±55.7	4.47±5.37	399.7±252.5
Constant period (N = 14)	100.1±57.7	0.56±0.57	226.2±94.6
Variable period (N = 13)	107.5±55.6	8.68±4.99	586.5±235.6
Colony 2			
Overall (N = 25)	91.9±50.2	3.45±4.58	472.8±353.4
Constant period (N = 13)	76.2±39.4	0.50±0.58	228.8±88.4
Variable period (N = 12)	101.3±63.0	6.93±4.82	761.1±330.1
Colony 3 (N = 27)	125.4±78.8	7.57±10.02	619.8±226.2
Colony 4 (N = 25)	100.9±75.5	4.86±3.44	578.5±155.5

Table 2. Product-moment correlation coefficients for the relationship between each weather parameter examined and date of observation (expressed in Julian days). Weather was monitored on 47 days during the period in which the migrating colonies were observed, and on 41 days in the period in which the non-migrating colonies were observed. RH = relative humidity (%); BP = barometric pressure; wind shifts = number of times the wind changed direction during a given day of observation (* $P < 0.05$; ** $P < 0.01$)

	Observation period for migrating colonies	Observation period for non-migrating colonies
Max temp	−0.02	−0.54**
Min temp	0.35*	−0.80**
Max RH	0.05	−0.64**
Min RH	0.16	−0.50**
Max BP	−0.24	0.33*
Min BP	0.10	−0.33*
Wind shifts	0.22	−0.02

minimum RH, and foraging area. For the second vector in colony 3, the heaviest loadings occurred for the association between maximum and minimum RH and foraging distance. There was no significant correlation between foraging and weather in colony 4 (Table 3). There was, therefore, no consistent influence of weather on the foraging patterns of the two non-migrating colonies. In summary, colony decisions to migrate or remain in the study area (1) were not correlated with the weather parameters measured, and (2) did not appear to be strongly influenced by interactions between weather and foraging patterns.

Table 3. Standardized canonical vectors (I and II) for all foraging and weather variables for each colony. Canonical correlations (CC) are given at the bottom of each column. Area refers to the daily foraging area in km^2; distance refers to the mean daily foraging distance in m. T = temperature (°C); RH = relative humidity (%); BP = barometric pressure; wind = number of changes in wind direction per day of observation (*$P < 0.05$)

	Colony 1		Colony 2		Colony 3		Colony 4	
	I	II	I	II	I	II	I	II
Area	0.48	−2.41	1.04	−1.55	0.53	−0.86	−0.55	0.99
Distance	0.54	2.40	−0.05	1.87	0.77	0.64	1.14	0.00
Max T	0.93	−0.27	1.28	0.11	1.35	0.06	−0.08	0.66
Min T	−0.08	0.28	0.12	0.90	−0.68	−0.10	−1.41	−0.03
Max RH	0.45	1.42	0.09	0.58	−0.96	1.90	2.87	0.19
Min RH	−0.24	−0.96	1.12	0.49	1.48	−1.38	−1.12	−0.23
Max BP	−1.16	−0.29	−0.36	1.65	−0.35	0.17	−0.69	0.15
Min BP	1.26	0.33	0.75	−1.08	0.87	0.05	0.23	−0.41
Wind	0.59	−0.24	0.93	−0.34	−0.31	0.11	−0.19	−0.79
CC	0.72	0.33	0.77	0.36	0.73*	0.70*	0.47	0.40

Discussion

In the Okavango River Delta, the migration season for *scutellata* colonies (November–May) coincides with reduced forage availability, and the number of blooming species declines to virtually zero in May (McNally and Schneider, 1992). All four observation colonies in this study were monitored during the migration season. Since two colonies abandoned the study area while two remained, *scutellata* colonies may possess two strategies, migrating or persisting, for coping with the period of diminished resource abundance. The factors examined in this study which appeared to be most closely associated with the decision to migrate or persist within an area were (1) colony growth and development patterns, (2) colony energy reserves, and (3) foraging patterns.

During the 5–6 weeks preceding the onset of migration preparations, colonies 1 & 2 steadily increased in size, had large and constant amounts of brood with low mortality, relatively constant amounts of stored food, and increased in mass. In contrast, colonies 3 & 4, which did not migrate, remained relatively constant in size, had lower, more variable amounts of brood with higher mortality, less stored food, and decreasing mass. Hence, migration may be a viable option only for colonies that have (1) a population of the appropriate size and perhaps age structure and (2) sufficient food reserves for long-distance travel and establishment in a new area. A colony of appropriate size and age structure may be necessary to compensate for the natural attrition of adult workers during the migration process. It was not possible in this study to estimate the age distribution of adult workers in the different colonies, because (1) the survivorship of adult bees was not determined and (2) the initial age structures of the colonies were unknown. However, the differences in colony growth, brood-rearing activity and brood mortality suggest that the migrating colonies may have contained a greater proportion of younger workers than did the non-migrating

colonies. The distance that *scutellata* colonies migrate may exceed 100 km (Nightingale, 1976; Silberrad, 1976; Otis et al., 1981; Otis, 1991), and while the time required for such movement is unknown, in other *Apis* species it may involve a week or more (Koeniger and Koeniger, 1980). Once migrating colonies become established in a new area and begin raising brood, new adult workers will not emerge for at least 20 days (Winston, 1987). The life expectancy of adult *scutellata* is about 20–25 days (Winston et al., 1979), although during swarming and migration, worker life expectancy may be somewhat longer (Winston 1979). Hence, only colonies that migrate with a larger proportion of young bees may be able to maintain a sufficient worker force to survive until new adults begin emerging. Sufficient food reserves may be necessary to fuel long-distance movements, since *scutellata* colonies consume all remaining food reserves prior to departure (Winston et al., 1979; Otis et al., 1981). Colonies (such as colonies 3 & 4) which have experienced a period of reduced or erratic brood rearing, increased brood mortality, and declining food stores may be unable to withstand the migration and establishment process. Such colonies may have a better change of surviving if they attempt to persist in a given area, even though they may face the cessation of brood rearing and potential starvation.

While intra-colony demographics and energy reserves may influence the ability to migrate, these factors alone seem unlikely to directly initiate migration procedures. Rather, the onset of migration preparations may be stimulated by changes in the foraging environment. In colonies 1 & 2 migration preparations began following a 4–6-week interval, in which the foraging areas and distances became larger and more variable on a day-to-day basis. Since honey bees base their distance communication upon the energy expended during flight (Von Frisch, 1967), energy expenditures for food collection were also becoming larger and more variable prior to migration. The fluctuating foraging patterns coincided with the declining availability of blooming plants. Thus, the variable foraging patterns of colonies 1 & 2 may have reflected the beginning of a prolonged period of deteriorating foraging conditions in which ever-increasing amounts of effort had to be expended to maintain a positive colony energy budget. The information supplied by waggle dancers in colonies 1 & 2 therefore may have somehow allowed for an assessment of the changes in the foraging environment, which may have triggered migration preparations, provided that demographic and food storage requirements were also met. In contrast, colonies 3 & 4, which exhibited similar foraging patterns, did not attempt to migrate, perhaps became of their differing levels of growth, brood rearing and food storage.

Winston et al. (1979) also suggested that migration in Africanized honey bees in South America depended upon an interaction of intra-colony demographics and deteriorating foraging conditions. However, in contrast to the results of the present study, Winston et al. (1979) found that migrating and non-migrating Africanized colonies had similar levels of brood and food comb, and that the colonies most likely to emigrate were those that had *increased* brood mortality and were demographically too weak to survive in a region of declining resource abundance. However, the majority of the South American colonies that migrated had recently undergone reproductive swarming, in which a colony produces new queens and fissions. While the migration season in the Okavango tends to follow the reproductive swarming season (McNally and Schneider, 1992), none of our observation colonies attempted

to swarm during the study period, and none exhibited any signs of recent swarming (i.e., old queen cells) when originally excavated in the field. While the factors underlying the conflicting results of these two studies are unclear, the available data suggest that swarming history also affects migration decisions in *scutellata*.

It is unclear what role (if any) long-distance sampling activity played in migration or persistence behavior in the present study. Sampling activity in temperature climate honey bees and a variety of other animals often fluctuates with changes in resource availability and energy needs (Seeley, 1983; Tamm, 1987; Shettleworth et al., 1988). Long-distance sampling occurred at a low, constant level in all four colonies examined in this study, but did not increase either when forage availability began to decrease or when food stores began declining. Thus, decisions to initiate migration preparations or remain in an area may not have been contingent upon the ability of colonies to locate potential new foraging areas. Conversely, colonies may monitor such areas at low levels at all times, and such information could potentially influence emigration behavior. Alternatively, the sampling of long-distance sites may occur primarily after migration preparations have begun. During the final 1–2 weeks before departure, long-distance sampling activity in migrating colonies increases, and foragers often recruit for sites 10–20 km from the hive (Schneider, 1990a). These observations point out the need for further investigations in the role of sampling activity in colony movements in the African honey bee.

Honey bee migration is often seasonal, suggesting that seasonal changes in factors such as weather, rainfall, or photoperiod could potentially provide reliable cues for migration. However, none of the seven weather parameters examined in this study were clearly associated with the onset of migration behavior. Also, in both the Okavango Delta and South America, honey bee migration occurs throughout the wet season (Winston et al., 1979; Schneider, 1990a). Different colonies therefore experience widely varying periods of rainy weather before migration preparations are initiated, suggesting that the amount of rainfall *per se* does not trigger colony movement. There is also no strong evidence that migration occurs in response to changes in photoperiod. African colonies within the same area (and thus experiencing the same photoperiod cues) can vary considerably in migration behavior (Winston et al., 1979), and seasonal patterns of brood rearing in Africanized colonies are regulated by resource abundance, not photoperiod (Rinderer, 1988). Cues such as weather, rainfall and photoperiod therefore do not appear to stimulate migratory movements directly. More probably, these factors influence colony movements indirectly, by affecting the availability of blooming plants. Thus, unlike many temperature climate species that migrate in response to seasonally predictable, abiotic cues, *scutellata* colonies may base their migration decisions on a more direct assessment of resource availability, in conjunction with internal colony conditions. Such a difference may be related to the unpredictable seasonal patterns of resource abundance in the tropics (Sinclair, 1983; Rinderer, 1988). However, experimental manipulations are needed to delineate more completely the relationship between migration, weather and photoperiod.

In summary, migration decisions in African honey bees may depend upon an interaction of colony foraging activity, patterns of growth and development, and colony energy reserves. Definite conclusions about the factors regulating migration

cannot be drawn at this time, however, owing to the small number of colonies investigated and the fact that not all colonies were observed during the same months. Likewise, at present nothing is known about possible genetic factors underlying the tendency of different colonies to migrate. Nevertheless, the results of this study suggest that migration is regulated by a suite of interacting factors, all of which are amenable to experimentation. Future studies must determine (1) if manipulations of colony brood rearing, age structure, and food reserves can affect the onset of migration preparations, and (2) the possible mechanism whereby changing colony foraging patterns influence the brood-rearing activity of individual workers.

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