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Nest Characteristics and Recruitment Behavior of Absconding Colonies of the African Honey Bee, *Apis mellifera scutellata*, in Africa

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Absconding behavior was investigated in a naturally occurring population of honey bees in the Okavango River Delta, Botswana. Fifty percent of all colonies excavated in the field between October and December had abandoned the nest or were preparing for absconding, suggesting that an "absconding season" began in the Delta in October or November. However, the factors influencing absconding during this period were unclear, and there were no distinct differences in nest characteristics of the absconding and nonabsconding colonies. Waggle dance activity in observation colonies preparing for absconding was not used to preselect a specific nest site prior to departure. However, in two of the three colonies examined recruitment activity indicated the general direction of colony travel. The distances indicated by these dancers ranged between 6 and 16 km. Since these distances were three to four times greater than those communicated by dancers in nonabsconding colonies, workers from absconding colonies may sample potential forage or nest sites well outside their regular foraging range.

KEY WORDS: *Apis*; African honey bee; absconding; recruitment; waggle dance.

INTRODUCTION

Honey bees, *Apis mellifera*, possess two strategies for surviving seasonally unfavorable conditions: (1) hoarding honey and pollen and (2) absconding, or abandoning a nest site and moving into a new area. [Absconding differs from reproductive swarming in that no new queens are produced and the entire colony

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vacates the nest, rather than fissioning and leaving behind a portion of the workers (Winston *et al.*, 1979).] While all honey bee races hoard food, absconding is primarily a tactic of tropical races (Winston, 1987; Winston *et al.*, 1983). Annual absconding rates in the tropics vary between 15 and 100% (Winston *et al.*, 1979; Fletcher, 1978), yet absconding remains one of the more poorly understood aspects of honey bee biology (Seeley, 1985).

There are two categories of absconding: ''disturbance induced'' and ''seasonal.'' Disturbance-induced absconding can occur at any time of the year and is a more-or-less immediate response to a sudden deterioration in the quality of a nest cavity, brought about by predation, fire, an invasion of pests, or overheating (Winston *et al.*, 1979; Fletcher, 1975).

In contrast, seasonal absconding occurs during distinct times of the year and may be associated with seasonal fluctuations in resource availability, weather, the incidence of pests, or colony size due to reproductive swarming (Winston *et al.*, 1979; Winston, 1987; Fletcher, 1975; 1978; Woyke, 1976). However, the factors influencing seasonal absconding are often unclear. Colonies maintained in the same apiary can vary greatly in their seasonal absconding behavior (Winston *et al.*, 1979; Fletcher, 1978). Likewise, Winston *et al.* (1979) found no consistent differences in the amount of stored food in absconding versus nonabsconding African colonies in South America. However, much of the research on seasonal absconding to date has been conducted on colonies maintained by humans, often in areas where agriculture may influence seasonal patterns of food and water availability (Fletcher, 1975). In contrast, there has been little systematic investigation (especially on the African continent) of the absconding behavior of naturally occurring colonies foraging under unaltered conditions.

It is also unknown at present how far colonies travel during seasonal absconding or if they preselect a destination. It may be possible to explore these aspects of absconding behavior by monitoring waggle dance activity. For example, in colonies preparing for reproductive swarming, waggle dances performed in the nest and on the swarm cluster communicate the location of new nest cavities. Initially, a variety of sites is indicated, but eventually all dancers recruit for the same location, which represents the new nest (Lindauer, 1955; Seeley, 1985). By translating the distance and direction components of these dances (von Frisch, 1967), it is possible to map the area in which a colony searches for new sites, as well as the route the swarm will eventually follow (Lindauer, 1955). Absconding colonies may also recruit for new sites (Fletcher, 1978); however, to date no attempt has been made to map the waggle dance behavior of colonies undergoing seasonal absconding.

The purpose of this study therefore was to examine seasonal absconding in the African honey bee, *Apis mellifera scutellata*. The study was conducted in the Okavango River Delta, Botswana, a vast area (circa 17,000 km^2) containing an abundance of *scutellata* colonies but little human agriculture and no beekeeping practices (Schneider and Blyther, 1988; Schneider, 1989). The Delta therefore offers a unique opportunity to observe a natural honey bee population in an undisturbed environment. The objectives of the research were (1) to describe the seasonal patterns of absconding in naturally occurring colonies, (2) to compare the nests of absconding versus nonabsconding colonies, as a means of exploring possible nest conditions associated with a colony's decision to abscond, and (3) to map the recruitment activity of colonies preparing for seasonal absconding, by monitoring waggle dance behavior.

MATERIALS AND METHODS

The study was conducted from August to December 1986. Descriptions of the study site, seasonal abundance of blooming species, and nesting biology of *A. m. scutellata* in the Okavango Delta have been previously reported (Schneider, 1989; Schneider and Blyther, 1988).

Determining Seasonal Patterns and Nest Characteristics Associated with Absconding

Throughout the study period naturally occurring nests were excavated in the field, and the following were recorded for each: (1) date of excavation, (2) whether the nest was occupied or abandoned, (3) type of nest (earthen cavity, tree cavity, or exposed combs), (4) nest cavity volume (estimated from the mean values of four or five measurements of cavity height, width, and depth), (5) total comb area (cm^2), (6) area of comb containing brood (open and sealed), pollen, and nectar (honey and nectar), and (7) population size. Methods for estimating comb areas and population sizes are described by Schneider and Blyther (1988). Also, it was noted (8) if each nest was infested with ants, wax moth larvae, *Galleria mellonela* (which consume comb), or the hive beetle, *Haplostoma fuligineus* [which consumes honey and capped brood (Claus, 1983)]. These pests may contribute to absconding (Claus, 1983; Fletcher, 1978). Additionally, since absconding may be associated with swarming (Fletcher, 1975; Winston *et al.*, 1979), it was recorded (9) if each colony exhibited signs of recent swarming, such as the remnants of queen cells or reduced worker populations.

The following criteria were used to classify each excavated colony as not absconding (thriving) or associated with seasonal or disturbance-induced absconding. (1) Colonies undergoing seasonal absconding reduce or cease brood rearing 2–3 weeks prior to departure, consume remaining food stores, and delay departure until most all capped brood has emerged (Winston *et al.*, 1979; Woyke, 1976; Fletcher, 1978). As a result, seasonally absconding colonies leave behind mostly empty combs. In contrast, (2) disturbance-induced absconding does not involve long-term preparations and often results in the abandoning of large areas of brood and food (Winston *et al.*, 1979; Fletcher, 1978).

Thus, if a nest in this study had been abandoned prior to excavation, the colony was considered to have undergone seasonal absconding if the combs were undamaged but contained little or no brood or food. Conversely, if the combs of an abandoned nest contained brood and food stores, the colony was assumed to have absconded due to a disturbance. If a colony was occupied at excavation, it was considered to be preparing for seasonal absconding if (1) less than 5% of the total brood comb area contained eggs and larvae, but (2) there was no evidence of a reduced worker population (colonies with few larvae and reduced worker populations were assumed to have recently swarmed). Colonies not exhibiting reduced brood rearing were classified as thriving.

Recording Waggle Dance Activity and Constructing Recruitment Maps for Colonies Preparing to Abscond

Waggle dance activity was monitored in three colonies (Absconding Colonies 1, 2, and 3) excavated in the field and transferred along with the combs into two-frame, glass-walled observation hives. At the time of transfer, each colony contained 6043 ± 2237 bees and 2500–4000 cm^2 of comb. The observation hives were maintained inside a high-wall canvas tent, and each abutted a 2 × 10-cm opening cut into a tent wall, which allowed free flight to and from the colonies. To reduce heat and light levels inside the tent, which can induce absconding and interfere with waggle dance activity, respectively (Fletcher, 1978; von Frisch, 1967), the tent was located in the shade, covered with a fly sheet supporting a thick mat of reeds, and lined internally with heavy brown paper. Previous research had demonstrated that under such conditions (1) observation colonies could be maintained for extended periods without attempting to abscond, and (2) the resulting light level did not influence recruitment behavior (Schneider, 1989).

At the time of excavation, the three colonies exhibited no evidence of reduced worker populations but contained little or no unsealed brood, conditions which are diagnostic of preparations for seasonal absconding. Each colony absconded within 3–10 days of being transferred into the observation hives.

The methods for recording and mapping waggle dance activity in this study were essentially the same as those described in Schneider (1989) and are only briefly summarized here. On each day that a colony remained in an observation hive, it was monitored for 20–30 min each hour from 0600 to 1800, and the direction and distance components of all waggle dances observed were recorded. The directions indicated by the dances were estimated by measuring the angles of the waggle runs relative to vertical, using a protractor. The dance angles were later converted to a direction with respect to the sun 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 communicated by each dancer was estimated by (1) recording the time of 5–10 different waggle runs, 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 dance time into distance was accomplished using a curve expressing the relationship between distance and waggle run time, established by training marked foragers from a separate, nonabsconding observation colony to feeding stations at known distances up to 1 km from the hive (see Schneider, 1989) (Fig. 1). It was necessary to use the distance curve for a nonabsconding colony because none of the absconding observation colonies could be trained to visit a feeding station, despite repeated attempts. However, the distance curve for the nonabsconding colony was assumed to closely approximate those of the absconding colonies, since previous studies had revealed that the distance-dance time relationships for different *A. m. scutellata* colonies in the Okavango were very similar (Schneider, 1989). The translation of distances greater than those used in the training experiment was accomplished by extrapolation.

The color of pollen carried by each dancer (if any) was also recorded. Dancers not carrying pollen loads were assumed to indicate nectar, water, or nest sites (Schneider, 1989).

The locations indicated by the different dancers were plotted (using a sym-

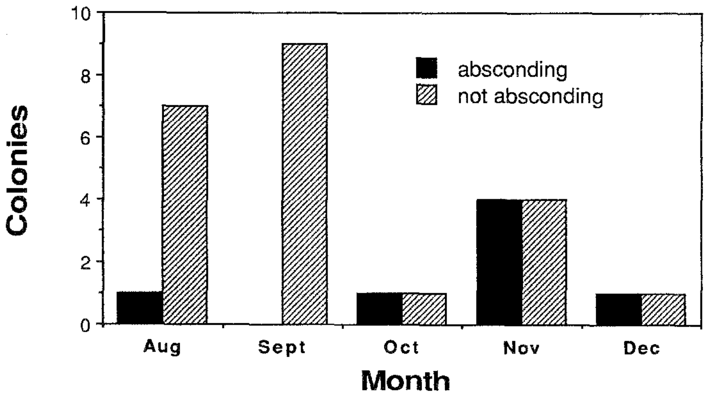

Fig. 1. The seasonal distribution of absconding and nonabsconding nests excavated during the study period ($N = 29$).

bol denoting pollen color or a nonpollen site) and used to construct a recruitment map for each observation colony over all days of study. The maps and distances communicated by the waggle dancers were used to determine the (1) total recruitment activity, (2) recruitment area, defined as the circular area encompassing 95% of all locations indicated by dancers, (3) mean and median recruitment distances, and (4) number of different sites recruited for [see Schneider (1989) for methods of identifying recruitment sites]. The waggle dance activity was also used to assess the day-to-day changes in total dances observed and number of sites indicated to determine if, prior to absconding, recruitment became increasingly concentrated on only one or a few sites.

I also attempted (1) to monitor the waggle dances performed on the surface of the swarm cluster once each colony had absconded and (2) to determine the direction in which the absconding cluster flew upon departure. Upon absconding from the observation hives, all three colonies formed clusters 10–20 m off the ground in dense vegetation. Therefore, it was generally not possible to estimate accurately the distance and direction components of the waggle dances occurring on the clusters. As a result, these dances were not included in the construction of the recruitment maps but were used to provide a relative estimate of changes in the level of dance activity once absconding had occurred. The directions traveled by the absconding colonies were estimated by taking a compass bearing on the flight path of each cluster once it became airborne.

The recruitment maps for the three absconding colonies were compared to those previously reported for two nonabsconding observation colonies also maintained in the Okavango Delta in 1986 (Schneider, 1989). The population size and comb areas of the nonabsconding colonies (6000–8000 bees, 3500–4050 cm^2 comb) were similar to those of the absconding colonies. However, the two types of colonies were observed during different months. The absconding colonies were monitored throughout November–December, while the nonabsconding colonies were observed from August to October, at the end of which time each swarmed. Observations of waggle dance activity in the nonabsconding colonies were terminated 2–3 weeks prior to swarming, since at this time foraging and recruitment declined. Thus, the differences in recruitment activity between the absconding and the nonabsconding colonies reported in this study may reflect changes in resource conditions during the observation months, as well as changes in recruitment associated with absconding.

The recruitment distances of the absconding and nonabsconding colonies were compared using a one-way analysis of variance. The data were log-transformed prior to analysis, since the distance estimates for the different colonies were not normally distributed. All statistical tests were conducted using two-tailed levels of significance. All mean values are reported ±1 SD.

RESULTS

Seasonal Patterns and Nest Characteristics Associated with Absconding

A total of 31 colonies was excavated during the study period. Two were queenless and declining and were not included in the data analyses. Of the remaining 29 nests, 7 were absconding, while 22 were thriving.

Six of the 7 absconding colonies were excavated between late October and December (Fig. 1) and accounted for 50% of the 12 total colonies examined during these months. These six colonies were associated with seasonal absconding. Three had abandoned the nest cavity prior to excavation, leaving behind undamaged, empty combs. The remaining three colonies were present in the nest at the time of excavation but contained little or no developing brood and exhibited no evidence of recent swarming. [The seventh absconding colony, excavated in August (Fig. 1), appeared to have absconded due to an invasion of ants (disturbance-induced absconding).] Thus, an absconding season may have begun in the Okavango Delta in October–November, although the study had to be terminated before the extent of this season could be determined.

There were no consistent differences between the nests of the absconding and those of the thriving colonies. All 29 nests occupied completely enclosed cavities, and absconding and thriving colonies occurred with similar frequencies in tree versus earthen cavities (Fisher exact test; $P > 0.05$; Table I). There were no significant differences between the absconding and the thriving colonies

Table I. Nest Characteristics for Absconding and Nonabsconding Colonies Excavated in the Field.

	Absconding colonies	Nonabsconding colonies
Type cavity		
Tree	4	7
Earthen	3	15
Cavity volume (L)	13.0 ± 6.3 ($N = 7$)	51.4 ± 77.1 ($N = 22$)
Comb area (cm^2)		
Total	3529 ± 1182 ($N = 7$)	3012 ± 4061 ($N = 22$)
Honey	470 ± 541 ($N = 3$)	348 ± 764 ($N = 22$)
Pollen	40 ± 35 ($N = 3$)	355 ± 665 ($N = 22$)
Population	7058 ± 2364 ($N = 7$)	6024 ± 8122 ($N = 22$)

with respect to (1) nest cavity volume, (2) colony population size, (3) total comb area, or (4) areas of honey and pollen comb (for all comparisons, $P > 0.05$; Table I). Winston *et al.* (1979) also found no consistent differences in the nests of absconding versus thriving African colonies in South America.

The two colony types in this study did not differ in their incidence of infestation with hive pests. None of the thriving and only one of the absconded colonies were infested with ants (Fisher exact test; $P > 0.05$). No excavated nest (thriving, abandoned, or preparing to abscond) contained wax moths. Likewise, only two of the absconding and two of the thriving colonies contained hive beetles (Fisher exact test; $P > 0.05$).

The thriving and absconding colonies also did not differ with respect to swarming activity. Only one of the abandoned and two of the thriving nests contained queen cells (Fisher exact test; $P > 0.05$), and no colony exhibited the reduced worker population associated recent swarming. Thus, there were no obvious relationships between nest characteristics and whether a colony absconded or remained in the study area.

Recruitment Activity in Colonies Prior to Absconding

Recruitment maps for absconding colonies 2 and 3 are presented in Fig. 2. A recruitment map for absconding colony 1 was not constructed, since a total of only nine waggle dances was observed during the 3 days this colony was monitored (Table II).

Recruitment activity in the absconding colonies was reduced and concentrated on nonpollen sites. Only 3–10 different waggle dancers were observed per day in each colony (Table II, Fig. 3A), and only 4 of the 121 total waggle dancers observed in the three colonies were pollen foragers ($\chi^2_1 = 103.4$; $P < 0.001$).

The recruitment areas and distances indicated by waggle dancers varied between the three absconding colonies. Recruitment activity in absconding colony 1 was restricted to sites located within 0.5 km of the hive (Table II). In contrast, in absconding colonies 2 and 3 mean and median recruitment distances ranged between 3700 and 5600 m and between 2600 and 4600 m, respectively, and the circular areas encompassing 95% of all observed recruitment activity ranged between 300 and 400 km^2 (Table II, Fig. 2). Also, 17% of the dances in absconding colony 2 and 40% in absconding colony 3 communicated distances 6–16 km from the hives (Fig. 2).

The three absconding colonies recruited for a mean total of 13.0 ± 10.1 different sites during the study period (Table II). However, dance activity did not increase or become focused on only one particular site in any colony prior to absconding. The number of waggle dances observed per day in the observation hives was not correlated with the number of days preceding absconding

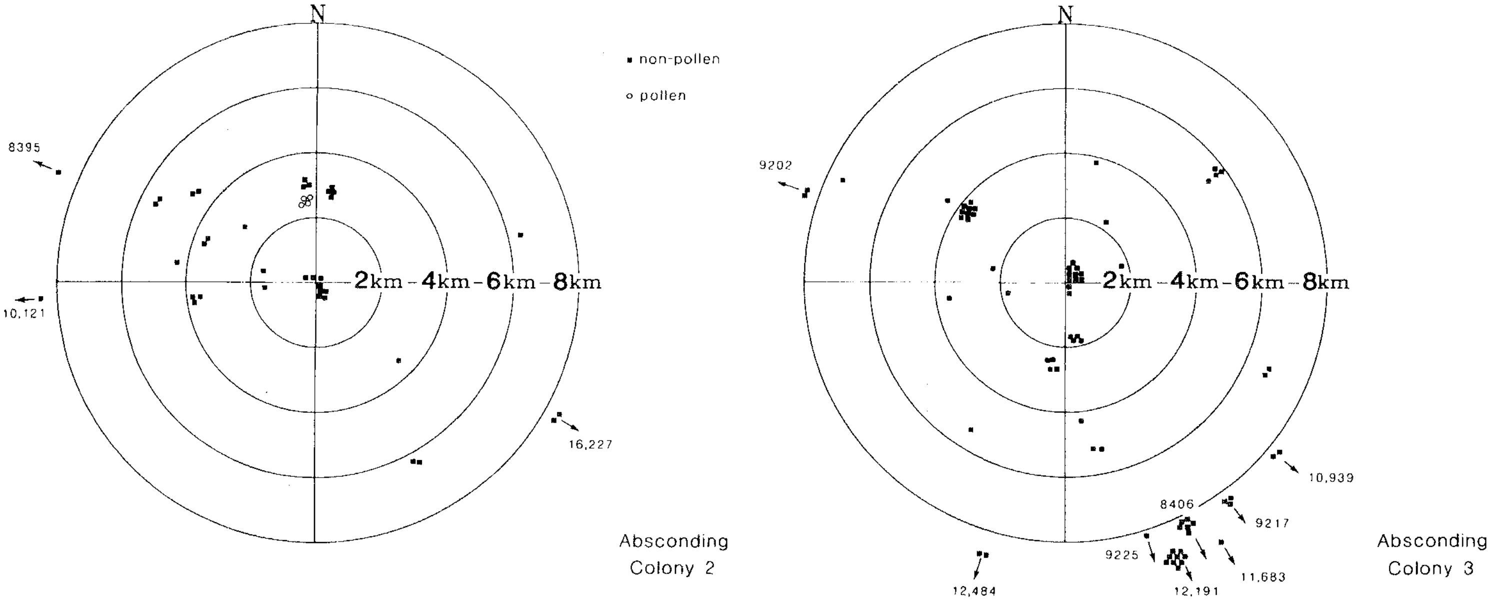

Fig. 2. Locations indicated by waggle dancers over 10 days of observation in absconding colony 2 and over 7 days in absconding colony 3. Sites occurring farther than 6 km from the hives are represented by an arrow, indicating direction, and the distance in meters.

Table II. Recruitment Activity, Distances, and Areas Observed for Three Absconding and Two Nonabsconding Observation Colonies[a]

Colony No.	Days observed	Waggle dancers/day (mean ± SD)	Recruitment distance (m)			Recruitment area (km^2)[c]	Recruitment
			Mean ± SD	Median	N[b]		
Absconding							
1	3	3.0 ± 5.2	356 ± 32	329	9	0.5	4
2	10	4.0 ± 4.1	3764 ± 3663	2657	40	341.4	15
3	7	10.3 ± 9.9	5631 ± 4185	4660	72	413.1	22
Nonabsconding							
1	12	54.7 ± 38.9	1223 ± 1962	295	656	80.3	106
2	4	63.0 ± 12.5	1231 ± 1738	563	252	54.6	43

[a] Data for the nonabsconding colonies are taken from Schneider (1989).
[b] Circular area encompassing 95% of all sites indicated by waggle dancers.
[c] Total dancers observed over all days of observation.

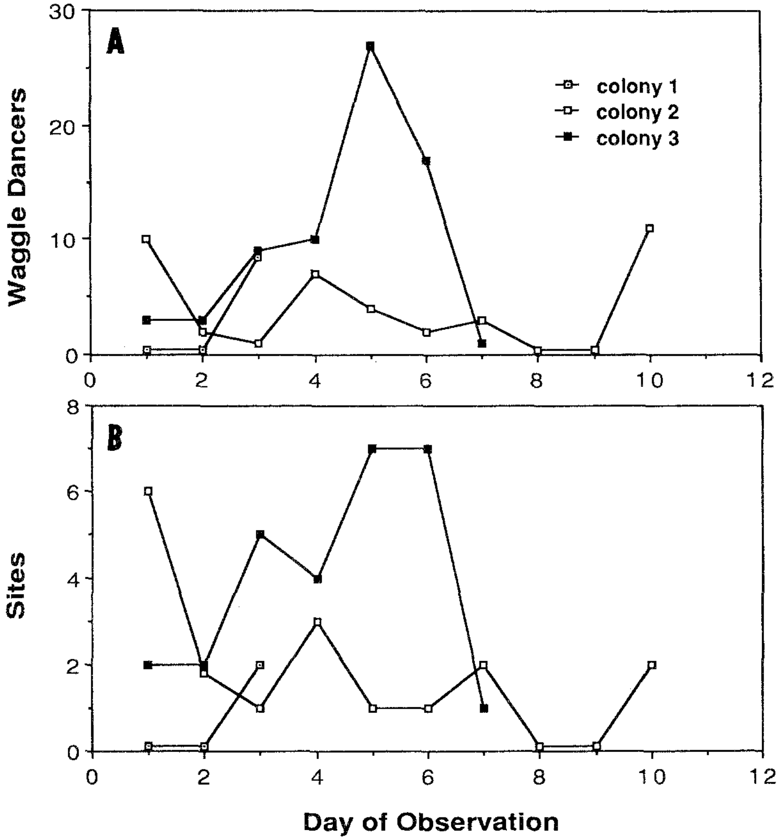

Fig. 3. The number of waggle dancers observed (A) and the number of sites recruited for (B) during each day of observation in the three absconding colonies.

(for absconding colony 1, $r = 0.87$, df = 1; absconding colony 2, $r = 0.11$, df = 8; absconding colony 3, $r = 0.33$, df = 5; $P > 0.05$ for all correlations; Fig. 3A). Likewise, there was no correlation between the number of sites visited per day and the number of days preceding absconding (for absconding colony 1, $r = 0.87$; df = 1; absconding colony 2, $r = -0.61$, df = 8; absconding colony 3, $r = 0.28$, df = 5; $P > 0.05$ for all correlations; Fig. 3B). No site in colony 1 and only 20.0 and 22.7% of those in colonies 2 and 3 were recruited for on more than one day. Furthermore, waggle dance activity did not increase or become focused on a particular site once colonies formed initial absconding clusters away from the hives. Thus, the absconding colonies may not have selected a specific destination prior to departure. Indeed, the behavior of absconding colony 1 suggested that seasonal absconding could occur with virtually no recruitment for new sites.

While the absconding colonies did not preselect a nest site, waggle dance activity may have determined the general direction of travel. In colony 2, 60% of all dances indicated a direction WNW of the hive, while in colony 3 the majority (54%) of dances indicated a SSE direction (Fig. 2). The direction of departure for Colony 2 was approximately 295° WNW, while that of Colony 3 was 150–160° SSE. Colony 1 traveled roughly 250° NNW, although its limited recruitment activity was not concentrated in any particular direction.

The recruitment patterns of the absconding colonies differed from those of the nonabsconding colonies in three major respects. First, compared to the nonabsconding colonies, recruitment activity in the three absconding colonies was greatly reduced. Each nonabsconding colony contained 5–20 times as many waggle dancers per day as did the absconding colonies ($F_{4,31} = 10.05$; $P < 0.001$; Table II). Second, the distribution of recruitment activity among pollen versus nonpollen sites differed between the two colony types. Whereas 545 of the total 908 dancers observed in the nonabsconding colonies indicated pollen sites (Schneider, 1989), only 4 of 121 dancers in the absconding colonies did so ($\chi^2_1 = 138.0$; $P < 0.001$).

Third, the absconding and nonabsconding colonies differed with respect to recruitment distances and areas. The recruitment distances of absconding colony 1 were three to four times less, and the recruitment areas 100–150 times less, than those observed for the nonabsconding colonies (Table II). In contast, the recruitment distances and areas of absconding colonies 2 and 3 were 4–15 times greater than those estimated for the nonabsconding colonies (Table II). An analysis of variance revealed a highly significant difference in the recruitment distances of absconding colonies 2 and 3 versus the nonabsconding colonies ($F_{3,1016} = 50.7$; $P < 0.001$). Pairwise comparisons (GT-2 tests for unequal sample sizes; Sokal and Rohlf, 1981) revealed that the mean recruitment distances for absconding colonies 2 and 3 (1) were significantly greater than those for each of the nonabsconding colonies (for each comparison, $P < 0.05$), but (2) did not differ from one another ($P > 0.05$).

In summary, prior to absconding, the recruitment activity of the observation colonies was reduced. Absconding colony 1 restricted its recruitment to locations within 0.5 km of the hive. In contrast, in absconding colonies 2 and 3 recruitment occurred over large areas at great distances from the hive. Recruitment did not become focused on any single location prior to absconding, although in absconding colonies 2 and 3 waggle dances were concentrated in the general direction the colonies traveled upon departure. When compared to the nonabsconding colonies, the absconding colonies exhibited (1) less waggle dance activity and (2) a concentration of recruitment almost exclusively on nonpollen sites. Also, two of the absconding colonies exhibited an expansion of recruitment areas and distances compared to the nonabsconding colonies.

DISCUSSION

An absconding season for *A. m. scutellata* in the Okavango River Delta appeared to begin in October–November. This time period corresponded roughly with the end of the hot-dry season (August–November) and the beginning of the hot-wet season [December–April (Schneider and Blyther, 1988)]. Seasonal absconding is associated primarily with the cold season in Kenya (Nightingale, 1976) and the hot seasons in Zambia (Silberrad, 1976) and Tanganyika (Smith, 1958). Absconding by the Africanized honey bee in French Guiana increases during the latter half of the wet season [March–June (Winston *et al.*, 1979)]. In contrast, Fletcher (1975, 1978) reported no distinct seasonality for the absconding activity of *A. m. scutellata* in South Africa. However, the agricultural and forestry practices of South Africa may influence colony movements [e.g., thousands of colonies move into blooming *Eucalyptus grandis* plantations (Fletcher, 1978)]. Taken together, these observations suggest that seasonal absconding patterns may be adjusted to regional variations in habitat conditions.

The factors which influenced absconding in the Okavango Delta are unclear at present. Absconding may have occurred in response to deteriorating resource conditions, since the number of blooming species potentially available as forage in the Delta declined by approximately 50% between November and December (see Schneider and Blyther, 1988; Fig. 1). However, at present too little is known of the phenologies and abundance of Delta plants to evaluate fully the relationship between food availability and absconding. Indeed, the lack of consistent differences in the amount of stored food observed for the excavated absconding and thriving nests suggests that the two colony types were experiencing similar levels of foraging success during the absconding period.

Seasonal changes in water availability, temperature, pest infestations, and swarming activity seem unlikely to have influenced the absconding patterns observed in this study. Ninety percent of all observed nests were located within 1 km of fairly permanant bodies of water (Schneider and Blyther, 1988), suggesting that colonies rarely experienced water shortages. While most absconding in this study occurred during the hot seasons, the tree and earthen cavities occupied by the absconding colonies appeared to be well suited for preventing overheating (Schneider and Blyther, 1988). There was no clear evidence, therefore, to suggest that absconding occurred in response to the inability to maintain nest temperatures. The low incidence of ants, wax moths, and hive beetles in the excavated nests suggests that absconding was not greatly influenced by seasonal increases in the abundance of hive pests. Fletcher (1975) and Winston *et* *al.* (1979) have suggested that seasonal absconding is associated with reproductive swarming, in that colonies may abscond (1) if swarming is repeatedly thwarted by bad weather or (2) if swarming results in colonies being too small to survive in areas of poor forage. However, in this study there was no relationship between absconding and recent swarming activity.

Thus, at present no definite conclusions can be drawn about the factors influencing the seasonal absconding patterns observed in the Okavango Delta. A more complete understanding of absconding will require the sampling of a larger number of nests over a greater period of time, plus a more detailed investigation of the interactions of forage availability, food needs, and weather in determining a colony's decision to abandon an area.

An examination of waggle dance behavior suggested two patterns of preabsconding recruitment activity. The first pattern, exemplified by absconding colony 1, consisted of greatly diminished recruitment focused on only a few sites near the hive. In this pattern, recruitment was not used to preselect either a specific new nest site or the general direction of colony travel prior to departure.

The second pattern, illustrated by absconding Colonies 2 and 3, also consisted of recruitment which was not used to preselect a specific nest site. However, in this pattern recruitment activity indicated a larger number of sites and may have helped determine the direction of colony travel, in that colonies 2 and 3 flew in the direction in which the majority of their waggle dances were concentrated.

The mean distances communicated by dancers in absconding colonies 2 and 3 were significantly greater than those observed in the nonabsconding colonies, suggesting that prior to absconding workers may sample sites far removed from the foraging ranges typical of *A. m. scutellata* in the Okavango. Alternatively, the distances indicated by many of the absconding dancers (6–16 km) may have exceeded the energetic limits of honey bee flight [unless workers were periodically consuming nectar during the round trip (Otis *et al.*, 1981)]. Such long-distance dances may not have indicated specific sites but, rather, may have simply communicated the message to fly a long distance in a certain direction. Such "direction dances" also occur during absconding and swarming in African bees in South America (Taylor, personal communication) and are consistent with the observations in this study that recruitment in the absconding colonies was used primarily to establish a route of travel, rather than a specific destination.

The absence of the preselection of nest sites in this study may have been related to the dynamics of seasonal colony movements in *scutellata*. The distance that seasonally absconding colonies travel is unknown but may be as great as 130–160 km (Otis *et al.*, 1981; Nightingale, 1976). If this represents a migratory process (Fletcher, 1978; Winston, 1987), then colonies may periodically stop and forage from swarm clusters to replenish food stores and assess the quality of an area (Otis *et al.*, 1981). If colonies are unlikely to construct combs in the transient stopping points, then the preselection of a nest site prior to absconding may be unnecessary. Thus, it may be more critical for colonies to determine the general direction of movement than to establish the exact site to which they will travel.

In contrast to the results of this study, Fletcher (1978) observed increased waggle dance activity for a particular location in an absconding *scutellata* colony in South Africa, and Koeniger and Koeniger (1980) reported that on migratory swarms of the Asiatic honey bee, *Apis dorsata*, recruitment becomes focused on the specific site to which the colony will move. Thus, in addition to the two patterns of recruitment observed in this study, under some conditions absconding may involve the preselection of a specific destination. The variability among the results of this and other studies prevents definite conclusions from being drawn about the recruitment behavior of absconding honey bee colonies. Nevertheless, these studies suggest that the monitoring of waggle dance activity provides an excellent tool for investigating absconding patterns and, perhaps, for exploring how forage availability and sampling activity interact to determine a colony's decision to abscond.

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