

Spatial Distribution and Nesting Biology of Colonies of the African Honey Bee *Apis mellifera scutellata* (Hymenoptera: Apidae) in Botswana, Africa

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Environ. Entomol. 25(3): 643–652 (1996)

ABSTRACT The spatial distribution and nesting biology were examined for naturally occurring colonies of the African honey bee race *Apis mellifera scutellata* (Lepeletier) in the Okavango River Delta, Botswana. Colonies had a density of 4.2/km² but exhibited considerable spatial clumping. Nest aggregations did not appear to result from short swarm dispersal distances, clumped resources or benefits derived from increased nest defense. Nests occurred predominantly in wooden cavities, particularly in abandoned woodpecker nests in dead palm trees. Nest cavities had a volume of ≈33 liters and south-facing, top-located entrances. Colonies constructed ≈6,000 cm² of comb, devoted the majority of comb area to worker brood production, stored relatively little food, and allocated ≈8% of comb area to drone rearing. A comparison of the *A. m. scutellata* colonies in the Okavango with neotropical African colonies throughout Central and South America revealed that the neotropical colonies were more likely to construct exposed comb nests and less likely to occupy wooden cavities. However, no differences were found between the Okavango and neotropical colonies in nest density, cavity volume, total comb area, or the proportions of comb devoted to worker brood production, food storage or drone rearing. Thus, the aspects of nesting biology examined appear to have remained largely unchanged from the ancestral African condition during the colonization of Central and South America.

KEY WORDS *Apis mellifera scutellata*, nesting biology, combs, nest cavity, nest, brood

INVESTIGATIONS OF THE NESTING BIOLOGY and the spatial distribution of colonies of the honey bee, *Apis mellifera* L., can provide insights into developmental, survival, and dispersal strategies. For example, temperate climate (European) honey bee races occupy large well-insulated cavities, construct large amounts of comb and amass large reserves of honey, all of which promote winter survival (Seeley 1985, Winston 1987). Also, feral European colonies can be aggregated spatially, which may reflect dispersal behavior and colony-level responses to the distribution of resources, predators, or mating constraints (Taber 1979, Oldroyd et al. 1995a). In contrast, tropical races occupy smaller cavities, may exhibit less selectivity in cavity choice, build smaller amounts of comb, and emphasize brood production over food storage (Schneider and Blyther 1988, Winston 1992). Tropical colonies may forage year round but experience high predation rates, which may favor decreased food storage, increased brood rearing and reproductive swarming, and thus smaller colony size (Schneider and Blyther 1988, McNally and Schneider 1992, Schneider and McNally 1992a). The spatial distribution of tropical honey bee col-

onies has not been explored in detail. Indeed, compared with the nesting biology of European races, which has been studied extensively (Seeley and Morse 1976, 1978; Taber 1979; Wenner 1989, 1992; Gambino et al. 1990; Schmidt and Thoenes 1992; Oldroyd et al. 1994, 1995a), that of tropical honey bees has received less attention (Winston et al. 1981, Schneider and Blyther 1988, Ratnieks et al. 1991, McNally and Schneider 1992).

Interest in the nesting biology and spatial distribution of tropical honey bees has increased dramatically in the past 4 decades following the introduction of the African honey bee race *A. m. scutellata* into Brazil in 1956–1957. A knowledge of nesting biology and colony aggregation patterns is central to programs designed to monitor and control the spread of the neotropical African bee by using swarm traps and “bait hives” (Rinderer et al. 1982, Schmidt et al. 1989, Schmidt and Thoenes 1990), and the incorporation of this bee into agricultural and beekeeping practices. Also, comparisons of nest architecture among the different regions of South America, Central America, and Africa may reveal if the nesting behavior of the African bee has changed as it colonized the neotropics. Such changes may, in turn, reflect selection pressures acting on the African bee in the new

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world or hybridization with European honey bee races. Yet, our understanding of neotropical African bee nesting biology is often hindered by a lack of information on the behavior of *A. m. scutellata* in its native African environment (Seeley 1988). Indeed, at present there has been only 1 systematic investigation of the nests of a naturally occurring *A. m. scutellata* population in Africa (Schneider and Blyther 1988). This study, however, examined a limited number of nests during a time of the year when many colonies were recently founded. The size and developmental patterns of these colonies may therefore not have been representative of more established nests.

The current study extended the investigations of Schneider and Blyther (1988) by examining a larger number of *A. m. scutellata* nests throughout a 12-mo period. The specific objectives were to determine the density and spatial distribution of naturally occurring nests and to examine nest cavity types and nest architecture. Additionally, where possible we compared the nests of *A. m. scutellata* in Africa with those of the neotropical African bee along a south-to-north gradient in the New World, to assess possible changes in nesting biology during the colonization process.

Materials and Methods

Study Area. The study was conducted in the Okavango River Delta, Botswana. The Okavango Delta occupies $\approx 17,000 \text{ km}^2$ and is sparsely inhabited by humans. *A. m. scutellata* colonies are abundant, no foreign races of honey bees have been introduced, and as far as can be determined, there are no beekeeping and few agricultural practices in the area (Schneider and Blyther 1988). Further descriptions of the study area are provided in Schneider and Blyther (1988) and McNally and Schneider (1992).

The study was conducted from October 1989 to July 1990. Local guides were used to locate an area that potentially contained a large population of honey bee colonies. The study site was centered around a camp ($19^\circ 35.42' \text{ S}$, $23^\circ 21.43' \text{ E}$) established within a dense cluster of colonies (Fig. 1), and nests were subsequently examined within a roughly circular area with a radius of $\approx 4 \text{ km}$. The study area was subdivided into 4 quadrants: north (the region within the arc of $\approx 315\text{--}44^\circ$), east (the region between 45 and 134°), south ($135\text{--}224^\circ$) and west ($225\text{--}314^\circ$). Each quadrant was searched for nests for 4–5 h on at least 1 d every 2 wk of the study period. Search times were therefore divided fairly equally among the different regions of the study area. To provide a larger sample size collected throughout a full year period, the data from the current study were combined with those of Schneider and Blyther (1988), collected in the Okavango from August–December within a 6-km^2 area.

Determining the Density and Spatial Distribution of Nests. The density and distribution of nests were examined in 2 ways. First, the nearest neighbor distance between nests was estimated by pacing, and a mean distance was calculated over all nests. Second, during the 1989–1990 data collection period, the location of each nest was recorded by determining the distance (estimated by pacing) and direction (estimated using a magnetic compass) from the study camp. A map with the study camp at the center was then constructed, indicating the position of all located nests, and was used to estimate nest density.

The map was also used to investigate the spatial distribution of nests, using 2 techniques. First, chi-square analysis was used to compare the number of nests located in the 4 quadrants of the study area. Second, the map was overlaid with a $2 \times 2 \text{ cm}$ grid, such that the center of the grid corresponded to the center of the map. Fifty-two grid squares fell within the circular area of the map, and the number of squares containing 0, 1, 2, and so on, nests was counted. The resulting frequency distribution was then examined using Poisson analysis to determine if the distribution of nests deviated from random, and the negative binomial to compare the observed distribution of nests with that expected if colonies were spatially aggregated (Ludwig and Reynolds 1988). Additionally, we calculated an index of dispersion (d) as:

$$d = \sqrt{2(ID)(N - 1) - \sqrt{[2(N - 1)] - 1}}$$

where N is the total number of sampling units (i.e., grid squares), and ID is the variance of the frequency distribution divided by the mean (Ludwig and Reynolds 1988). A distribution is likely to be random if $d < 1.96$, and clumped if $d > 1.96$ (Ludwig and Reynolds 1988).

We also examined the distribution of floral resources to explore if the availability of forage potentially influenced the spatial distribution of colonies. Within each quadrant of the study area, we established five $1,000\text{-m}^2$ vegetation plots separated by at least 500 m. Once every month, we recorded the number of each species of blooming tree ($>3 \text{ m}$) and shrub ($<3 \text{ m}$) in each plot. Each species of blooming plant was assigned a bloom value, using the following scale for the estimated number of flowers per plant: 1 (1–100), 2 (101–500), 3 (501–1,000), 4 (1,001–2,000), 5 ($>2,000$). A mean bloom value was calculated for each month over all plots in each quadrant. Analysis of variance (Sokal and Rohlf 1995) was then used to compare the monthly means among the 4 quadrants. Approximately 75% of the plant species surveyed are visited by honey bees in the Okavango (Schneider and Blyther 1988). However, the extent to which bees utilize each species is unknown. Therefore, our vegetational surveys reflected the availability of potential forage for honey bees in the different regions of the study area.

Determining Nest Characteristics. For each located colony, we determined the type of nest cavity (tree cavity, earthen cavity, exposed combs), the number of nest entrances, and the compass orientation of each entrance. Nest entrance orientations were examined in 2 ways. First, statistics for circular distributions (Zar 1984) were used to calculate the mean angle and angular deviation of entrance orientations, and Raleigh's z , which indicated whether the distribution of entrance orientations differed from random. Second, chi-square analysis was used to compare the number of entrances facing toward the north versus the south. In the tropics, south-facing entrances would receive less direct sunlight, which may influence colony thermoregulation (Seeley 1985, Schneider and Blyther 1988). We compared the number of nests with entrances facing in a generally northerly (270–89°) versus southerly (90–269°) direction, and the number facing toward the north versus south quadrant, because such entrances would be oriented most directly toward or away from the sun during the hottest hours of the day.

Whenever possible, nests were dissected in the field and the combs removed. For each dissected nest the following 5 characteristics were recorded, using a 5 × 5 cm grid when necessary: (1) the location of each entrance (top, middle, or bottom 3rd of the cavity); (2) cavity volume, based on 4–5 measurements (in centimeters) of cavity height and width; (3) total comb area (in square centimeters); (4) proportion of total comb area that contained brood (eggs, larvae and pupae) and food (honey and pollen); and (5) the proportion of total comb area that consisted of drone comb.

Comparing *A. m. scutellata* Nests in Africa with Neotropical African Nests. The combined data of the current study and those of Schneider and Blyther (1988) were compared with those reported for the neotropical African bee in French Guiana and Peru (Winston 1979, Winston and Taylor 1980, Winston et al. 1981), Panama (Boreham and Roubik 1987), and Mexico (Ratnieks et al. 1991). Additionally, data are presented for 3 naturally occurring nests dissected by S.S.S. in Costa Rica in 1993. Methods for data collection on the Costa Rican nests were identical to those described above. Although the sample size for Costa Rica is small, there are currently no other data on nesting biology available for this region of Central America. Comparisons among the different areas were conducted using Student t -tests and proportions tests (Sokal and Rohlf 1995).

Unless otherwise stated, all mean values are reported as ± 1 SE.

Results

Spatial Distribution and Density of Nests. In total, 144 nests were observed in the Okavango Delta during the combined studies. Of these, 140 were active during the study periods, whereas the

remaining 4 had been abandoned or destroyed shortly before the studies began. The nearest neighbor distance among the active nests was 225.0 ± 38.3 m.

The spatial distribution of the 93 nests located in 1989–1990 study are depicted in Fig. 1. *A. m. scutellata* colonies in the Okavango tended to be aggregated. Nests were clustered toward the E-SE, and there was a highly significant difference in the number of nests occurring within the 4 quadrants of the study area (number of nests located in the north, east, south, and west quadrant = 6, 41, 31, and 11; $\chi^2 = 36.8$, $df = 3$, $P < 0.01$). The observed distribution of nests differed significantly from that expected based on the Poisson distribution ($\chi^2 = 44.7$, $df = 3$, $P < 0.01$), but not from that expected based on the negative binomial distribution ($\chi^2 = 0.40$, $df = 2$, $P > 0.05$) (Table 1). The index of dispersion ($d = 4.94$, $P < 0.01$) also suggested a clumped distribution. Colonies frequently occurred as clusters separated by only 100–200 m. It was not uncommon to find nests separated by 10–20 m, and nests located in the same tree and separated by only vertical distance were also occasionally observed.

Floral resources did not appear to be strongly aggregated within the study area. The mean monthly bloom value for the north (31.6 ± 12.0), east (34.9 ± 10.9), south (27.5 ± 10.7), and west (35.1 ± 12.5) quadrants of the study region did not differ ($F = 0.09$; $df = 3, 44$; $P = 0.96$). Furthermore, subsequent to the establishment of the vegetation plots, 5 were found to contain 1 or more honey bee nests, or to have a nest located within 50 m. The mean monthly bloom value for these 5 plots (40.4 ± 13.5) did not differ from that for the 15 plots that did not contain nests (29.2 ± 10.3 , $t = 0.65$, $df = 22$, $P > 0.05$). These results suggest that there was not a strong relationship between the spatial distribution of forage species and the aggregation of honey bee colonies in the Okavango.

The overall density of nests was $1.8/\text{km}^2$ (excluding the 4 nests located >4 km from camp; Fig. 1). However, nest density within the area of clumping was $4.2/\text{km}^2$ (Fig. 1), which was approximately half the 7.8 nests per square kilometer reported for Okavango colonies by Schneider and Blyther (1988). The nest densities of the neotropical African bee in Panama and Mexico are similar to that of *A. m. scutellata* in the Okavango Delta (Table 2).

Nest Architecture. Nest Cavity Types. Of the 144 nests observed in the Okavango, 114 occurred in tree cavities, 29 in earthen cavities (28 in abandoned termite mounds), and 1 consisted of exposed combs. The single most commonly occurring type of nest cavity consisted of abandoned woodpecker nests located in the trunks of dead palm trees, *Hyphanea ventricosa*. Such nests accounted for 42 (37%) of the colonies that occupied wooden cavities.

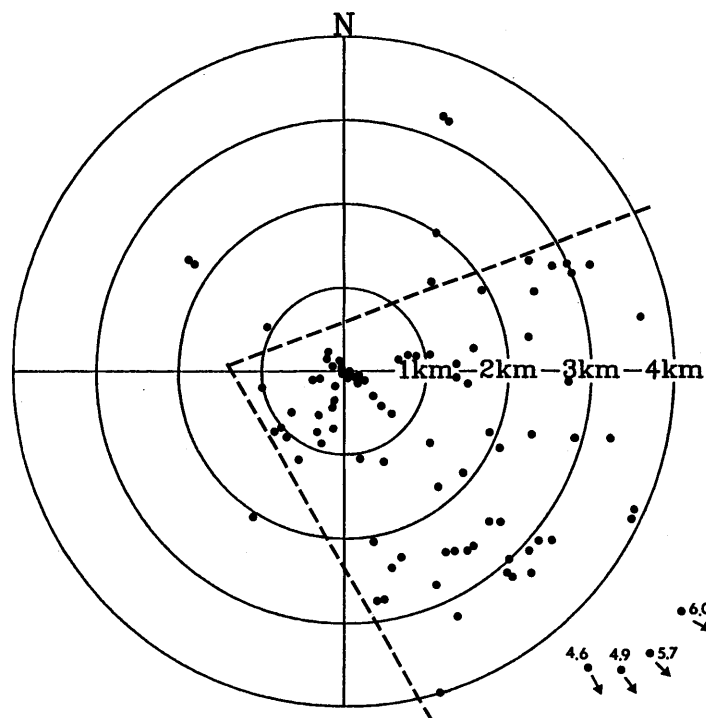


Fig. 1. Spatial distribution of 93 *A. m. scutellata* colonies observed in 1989–1990 study. The study camp was selected as the center of the map and was located within a dense cluster of colonies. Nests >4 km from the study camp are represented by an arrow indicating direction and the distance in kilometers. Dashed lines delineate the region of greatest nest clumping, which was used in the final determination of nest density.

In comparison to the Okavango nests, the distribution of neotropical African nests among wooden cavities, earthen cavities, and exposed combs in Panama was 6, 36, and 31 (Boreham and Roubik 1987); for Mexico these values were 6, 18, and 4 (Ratnieks et al. 1991). There was a highly significant difference in the distribution of colonies among the different nest types in the 3 areas ($\chi^2 = 69.0$, $df = 4$, $P < 0.001$). This difference resulted primarily from the greater number of exposed-comb nests and the lower number of wooden cavity nests in the neotropics versus the Okavango habitat.

Table 1. Observed number of *A. m. scutellata* colonies per square in the grid used to examine spatial distribution of nests, and the number expected under the Poisson and negative binomial distributions

No. colonies per grid square	Observed frequency	Expected frequency	
		Poisson	Negative binomial
0	26	9.4	26.0
1	9	16.1	9.0
2	4	13.8	5.1
3	4	7.8	3.3
4+	9	4.9	8.5

Numbers of grid squares containing 4 or more nests were combined to increase expected values. The mean \pm variance for the observed frequency distribution was 1.7 ± 7.54 nests per square.

Nest Cavity Volume. Cavity volumes were determined for 113 dissected nests (Fig. 2). The mean cavity volume (33.5 ± 5.1 liters) was less than that observed for neotropical African nests in Peru ($t = 2.01$, $df = 121$, $P < 0.05$) but did not differ from that observed in Costa Rica ($t = 0.22$, $df = 114$, $P > 0.05$) or Mexico (Mann-Whitney U test, $P = 0.61$, Ratnieks et al. [1991]) (Table 2).

Nest Entrances. Nest entrances were examined for 129 Okavango nests, 108 of which had 1 entrance and 22 had 2 or more. Examinations of entrance orientation and location with respect to the nest cavity were restricted to the single-entrance nests.

Nest entrance orientations for the Okavango colonies were highly variable (Fig. 3). The mean angle of orientation was 259° , the angular deviation was 109° , and the distribution of entrance orientations did not differ from random (Raleigh's $z = 2.80$, $0.01 > P > 0.05$; Fig. 3). However, of the 108 single-entrance nests examined, 40 had a generally north-facing and 65 a generally south-facing entrance ($\chi^2 = 5.5$, $df = 1$, $P < 0.05$; the remaining 3 nests had entrances that faced upward and had no compass orientation). Furthermore, 38 nest entrances were oriented toward the south quadrant, whereas 20 were oriented toward the north quadrant ($\chi^2 = 4.98$, $df = 1$, $P < 0.05$). Thus, despite the variability in entrance orientations, colonies

Table 2. Nest characteristics for *A. m. scutellata* in the Okavango Delta, Botswana, and African colonies in the neotropics

Characteristic	Okavango	French Guiana and Peru	Panama	Costa Rica	Mexico
Nests/km ²	4.2–7.8	—	4.7–7.1	—	5–9
Cavity vol (liters)	33.5 ± 5.1 (n = 113)	70.8 ± 24.5 (n = 10)	—	26.5 ± 12.4 (n = 3)	24.4 (n = 16)
Combs					
Total area, cm ²	6,061 ± 484 (n = 80) ^a	8,000 ± 1,031 (n = 13)	—	4,242 ± 2,091 (n = 3)	1,897 ± 273 (n = 18)
% utilized	78.0 ± 2.4 (n = 81) ^b	86 (n = 10)	—	78.4 ± 6.5 (n = 3)	—
% brood	54.5 ± 3.1 (n = 81) ^b	54–67 (n = 10)	—	54.4 ± 6.1 (n = 3)	—
% food	23.5 ± 1.9 (n = 81) ^b	19–25 (n = 10)	—	24.4 ± 12.9 (n = 3)	—
% drone comb	8.3 ± 0.7 (n = 59) ^c	—	—	5.3 ± 0.9 (n = 3)	5.9 (n = 18)

Values are presented as the mean ± 1 SE. Data for French Guiana and Peru were taken from Winston (1979), Winston and Taylor (1980), and Winston et al. (1981) for Panama from Boreham and Roubik (1987); and for Mexico from Ratnieks et al. (1991). Data for Costa Rica were collected by S.S. Schneider (in 1993). % brood, comb containing worker and drone brood; % food, comb containing honey and pollen. —, Missing data for each area.

^a Estimates of total comb area excluded newly established nests.

^b Estimates of brood and food comb areas excluded queenless and absconding colonies.

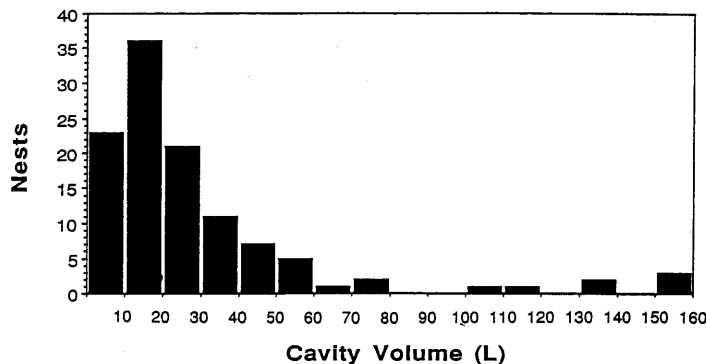
^c Dissected colonies that contained drone comb.

may have had a tendency to occupy cavities with entrances that faced toward the south.

We investigated nest entrance orientation in more detail by examining the subset of colonies that occupied abandoned woodpecker nests. Woodpecker nests in the Okavango had entrances that faced in all compass directions. Thus, a natural experiment for possible entrance-orientation preference was conducted by comparing 32 single-entrance woodpecker nests that were occupied by *A. m. scutellata* with 70 woodpecker nest cavities that were unoccupied. The mean angle and angular deviation for the entrances of the occupied nests were 214 and 83°, respectively, and the distribution of entrance orientations differed significantly from random (Raleigh's $z = 3.98$, $0.01 < P < 0.05$; Fig. 4). In contrast, the mean angle and angular deviation for the unoccupied nests were 345 and 111°, respectively, and these entrance orientations were distributed randomly (Raleigh's $z = 1.60$, $P > 0.05$; Fig. 4). There was a highly significant difference

between the mean angles for the occupied and unoccupied nests (Watson-Williams test; $F = 48.69$; $df = 1, 100$; $P < 0.001$). The number of cavities with a generally southerly versus northerly oriented entrance for the 32 occupied nests (21 versus 11) and 70 unoccupied nests (27 versus 43) was significantly different ($\chi^2 = 5.3$, $df = 1$, $P < 0.05$). Likewise, the number of entrances facing toward the south versus north quadrant for the occupied (14 versus 4) and unoccupied (18 versus 27) nests was significantly different ($\chi^2 = 6.03$, $df = 1$, $P < 0.05$). Numerous other aspects of the woodpecker nests undoubtedly influenced selection by honey bees. Nevertheless, these results suggest that if there are sufficient opportunities for choice *A. m. scutellata* colonies in the Okavango may preferentially occupy those cavities with entrances oriented toward the south.

Colonies tended to occupy nest cavities with entrances located at the top. Of the 91 single-entrance nests for which entrance location could be

**Fig. 2.** Distribution of cavity volumes for 113 dissected nests.

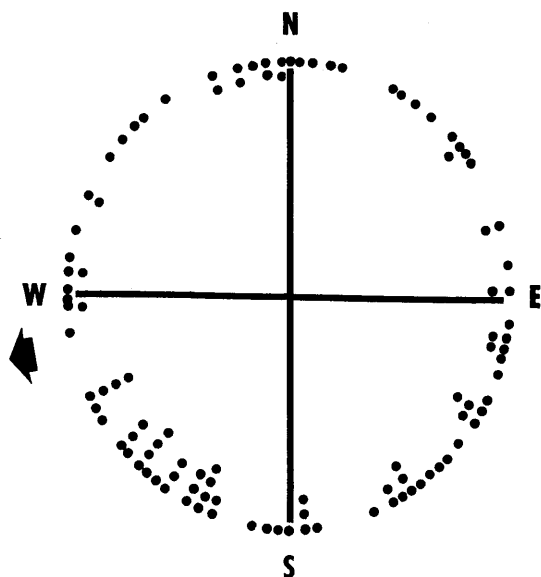


Fig. 3. Compass bearing for the nest entrances of 105 single-entrance nests. Arrow indicates the mean angle of orientation; angular deviation was 109° . Cavities containing >1 entrance were not included in the analysis of nest entrance orientation.

determined, 61 had a top-located, 10 a middle-located, and 20 a bottom-located entrance ($\chi^2 = 48.2$, $df = 2$, $P < 0.001$). Data for nest entrance orientation and location are not available for neotropical African bees.

Combs. Comb areas were measured for 106 Okavango colonies, of which 55 were established and thriving, 26 were newly founded, 4 were queenless and declining, and 21 were associated with seasonal absconding. The total comb area for all dissected nests was $4,909 \pm 415 \text{ cm}^2$ (Fig. 5). However, when excluding the newly established nests, which typically contained small amounts of comb, the total comb area for the remaining 80 colonies was $6,061 \pm 484 \text{ cm}^2$. This value did not differ from that reported for neotropical African bees in French Guiana ($t = 1.5$, $df = 91$, $P > 0.05$) or Costa Rica ($t = 0.7$, $df = 81$, $P > 0.05$; Table 2). Mean comb area for the Okavango colonies was larger than that reported for neotropical African bees in Mexico ($t = 4.1$, $df = 96$, $P < 0.01$; Table 2). However, many of the Mexican colonies may have been newly founded (Ratnieks et al. 1991), which may have contributed to their small comb areas. The mean total comb area for the newly founded Okavango colonies ($1,485 \pm 270 \text{ cm}^2$) did not differ from that of the Mexican colonies ($t = 1.04$, $df = 42$, $P > 0.05$).

The utilization of comb area for brood production and food storage was examined for the 81 established and newly founded colonies; the queenless and absconding colonies were excluded from the analysis because of their reduced brood rearing and food storage activity (McNally and Schneider

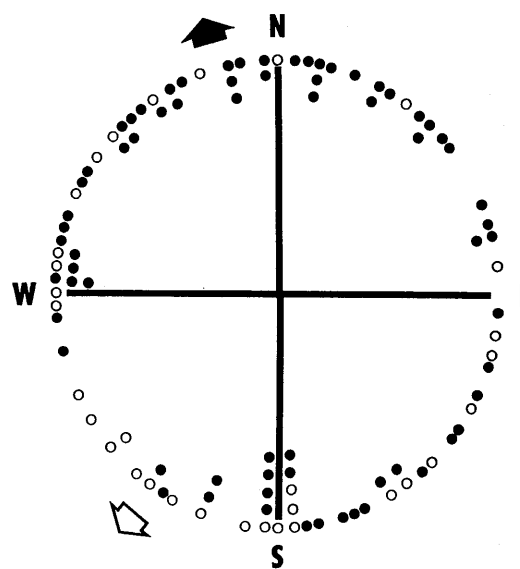


Fig. 4. Compass bearing for the entrances of 32 single-entrance woodpecker nests occupied by *A. m. scutellata* colonies (open circles) and 70 unoccupied woodpecker nests (closed circles). Mean angle of entrance orientation for the occupied nests is indicated by the open arrow; that for the unoccupied nests by the closed arrow. Angular deviation for the occupied and unoccupied nests were 83° and 111° , respectively. Nest cavities containing >1 entrance were not included in the analysis.

1992, Schneider and McNally 1992b). The Okavango colonies utilized $\approx 78\%$ of total comb area at any given time, the majority of which was devoted to brood rearing, with relatively little used for food storage and drone production (Table 2). The proportions of brood, food, and drone comb did not differ from those reported for African colonies in all neotropical areas examined (proportions tests; $P > 0.05$ for all comparisons; Table 2).

Discussion

Apis mellifera scutellata colonies in the Okavango Delta occurred at a density of 4.2 nests per square kilometer, were spatially clumped, occupied wooden and earthen cavities with top-located, south-facing entrances, built relatively small amounts of comb, devoted most comb area to brood production, and stored little food. Because the study site was selected to occur within an area containing a large population of colonies, it is unknown if the observed density of nests is characteristic of other regions of the Okavango Delta. However, the nest density observed in the current study was similar to the 6 nests per square kilometer estimated for neotropical African colonies for all of tropical America (Roubik 1988). The density of European colonies in temperate habitats tends to be lower, at ≈ 0.5 nests per square kilometer (Visscher and Seeley 1982). However, feral

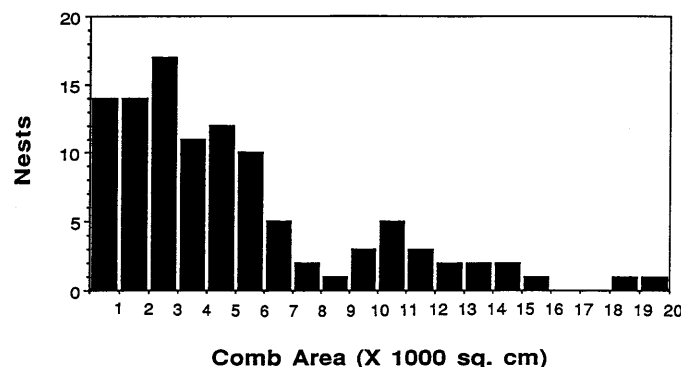


Fig. 5. Distribution of total comb areas for 106 dissected nests.

colony density can vary enormously in all environments, and densities in excess of 70 nests per square kilometer have been reported for both tropical (reviewed in Otis 1991) and European (Oldroyd et al. 1995a) colonies in some regions.

In the current study, nests were aggregated in the E-SE section of the study area and were frequently observed in clusters. The spatial distribution of tropical *A. mellifera* colonies in other regions of Africa and the neotropics has not been examined. Aggregated nests have been observed for European colonies in several regions of Australia (Oldroyd et al. 1995a, b) and along the Verde river in Arizona (Taber 1979). However, no such clumping was observed for European colonies on Santa Cruz Island in California (Wenner 1989).

The spatial distribution of honey bee colonies will be strongly influenced by the availability of nest cavities. However, when sufficient cavities are available 5 possible factors may contribute to nest aggregations (Oldroyd et al. 1995a). First, aggregations may result from a preference for short dispersal distances by swarms when leaving the natal nest. Waggle dances in swarming colonies in the Okavango and Costa Rica suggest that African swarms frequently travel 2–5 km from the natal site (Schneider and McNally 1993, Schneider 1995), which is 9–20 times greater than the 225 m nearest neighbor distance observed in the current study. Also, during certain times of the year many colonies migrate into the Okavango, perhaps from great distances (McNally and Schneider 1992), such that settlement in an existing aggregation may be little influenced by a dispersal distance preference. Furthermore, short dispersal distances should result in clusters of related colonies. Although relatedness was not examined in the current study, Oldroyd et al. (1995a) found that European nest aggregations in Australia could contain unrelated colonies. Thus, it is unlikely that short dispersal distances contributed strongly to the aggregated pattern observed for colonies in the Okavango Delta.

Second, colonies could aggregate in response to a clumped distribution of some resource, such as

nest cavities, forage, or water sources. We did not determine the distribution of potential nest cavities in the study area. However, the weekly searches for honey bee colonies suggested that dead palm trees containing abandoned woodpecker nests (the preferred nest cavity of *A. m. scutellata* in this study) were abundant in all quadrants of the study region. Daily colony foraging areas in the Okavango are generally small (5–8 km²) and mean daily foraging distances often range between 400 and 700 m (Schneider 1989; Schneider and McNally 1992b, 1993). Colonies could therefore have clustered in areas in which the distribution of blooming plants was conducive to small foraging ranges. However, we observed no clumping of forage species, either when comparing the different quadrants of the study area or vegetational plots with and without occupied nests. Okavango colonies typically are located within 1 km of water, and thus could cluster around the more permanent waterways (Schneider and Blyther 1988). However, water sources did not appear to be more abundant in the regions of the study area that contained the highest density of colonies. Thus, there is no strong evidence that the clustering of colonies arose from an aggregated distribution of resources.

A 3rd factor that may contribute to colony aggregation is increased nest defense, in that the disturbance of 1 colony may cause neighboring colonies to attack (Oldroyd et al. 1995a). It is unlikely that this factor influenced the observed clustering of nests in the current study. Okavango colonies typically display little or no defensive behavior (Schneider and Blyther 1988, Schneider and McNally 1992c). We frequently dissected 2 neighboring colonies within a 1- to 2-h period. Yet, we never observed that the 2nd had increased defensiveness.

A 4th factor that may contribute to spatial clumping may be that nest aggregations improve mating efficiency (Oldroyd et al. 1995a). Virgin queens mate on the wing away from the nest and are thus exposed to predation and other risks (Winston 1987). Successful mating depends on the queen locating a drone congregation, mating with

unrelated drones (because inbreeding reduces brood viability, Woyke 1963, Page and Metcalf 1982, Ratnieks 1990), and returning to the colony. Aggregations of unrelated nests could decrease both the chance of inbreeding and the duration of mating flights and exposure to risks (Oldroyd et al. 1995a). About 30% of swarming colonies in the Okavango fail to successfully requeen (McNally and Schneider 1992). High rates of swarm failure have also been suggested for neotropical African colonies in South America and may be related to the loss of virgin queens during mating flights (Otis 1991). Thus, any advantages that clustering may convey to queen survival and mating success could be strongly favored in Okavango colonies.

Finally, nest aggregations may occur if scout bees searching for new nest sites are attracted to the odor of existing colonies and preferentially select nearby cavities, provided any are available (Oldroyd et al. 1995a). Colonies that select cavities near existing nests might benefit by settling in areas that can support bees and possibly increasing mating efficiency in their future queens. Scout bees are attracted to artificial nest cavities baited with Nasonov pheromones (Schmidt and Thoenes 1992, Schmidt et al. 1989, Schmidt 1994). They also prefer previously occupied cavities over those that have never contained a nest (Seeley and Morse 1978), and this preference may be mediated by odor cues. Such odor preferences could have potentially contributed to the frequent clustering of colonies in the Okavango, although it is unknown if African scouts are influenced by the odors of existing colonies when selecting cavities.

In summary, the spatial aggregation of *A. m. scutellata* nests in the Okavango Delta did not appear to result from short dispersal distances, clumped resources, or increased nest defense. Aggregations may have resulted from odor-mediated preferences for cavities near existing colonies, and such clustering may have conveyed mating advantages. However, at present too little is known about swarm dispersal, settlement and odor preferences in African honey bees to allow for definite conclusions.

Several of the nest characteristics observed for *A. m. scutellata* may aid in reducing heat stress, and thus coping with the high temperatures that occur throughout most of the year in Botswana (Schneider and Blyther 1988). Wooden and earthen cavities provide insulation that facilitates maintaining a constant internal nest temperature despite high ambient temperatures (Johannsmeier 1979, Schneider and Blyther 1988). Likewise, nest cavities with top-located, south-facing entrances may help prevent overheating, because a top entrance would facilitate convective heat loss and in the southern hemisphere a south-facing entrance would receive less direct sunlight (Seeley 1985, Schneider and Blyther 1988). In contrast, temperate climate colonies, which are adapted for winter survival, tend to occupy wooden cavities with bot-

tom-located, south-facing entrances (Seeley and Morse 1976, 1978; Avitabile et al. 1978). Such nest cavity characteristics may help conserve heat, because bottom-located entrances may reduce convective heat loss and in the northern hemisphere south-facing entrances would receive more direct sunlight (Seeley and Morse 1976, Seeley 1985). However, the degree to which these different characteristics are observed in natural honey bee nests will vary depending on the availability of cavities and factors such as cavity volume and height above the ground that also influence nest site selection (Schmidt and Thoenes 1987a, b; Seeley and Morse 1978; Rinderer et al. 1982). For example, a preference for a certain nest entrance orientation was observed for African colonies in the Okavango and has been reported for European colonies in several areas in the northeastern United States (Avitabile et al. 1978, Seeley and Morse 1978). No such preference, however, was observed for European colonies in Australia or California (Gambino et al. 1990, Oldroyd et al. 1994).

The small size, emphasis on brood production and low levels of stored food observed for *A. m. scutellata* colonies in the current study may be related to the extended foraging season and high predation rates experienced by honey bees in the Okavango. These factors may favor frequent swarming, which in turn would require high levels of worker production and result in small colony size (Schneider and Blyther 1988, McNally and Schneider 1992, Schneider and McNally 1992a). Likewise, an extended foraging season may reduce the importance of extensive food storage, thereby allowing colonies to construct smaller amounts of comb. In contrast, temperate climate colonies must amass large food reserves for winter survival, which favors larger colonies, the construction of large amounts of comb, and an emphasis on food storage over brood production (Seeley 1985, Oldroyd et al. 1994).

The characteristics observed for *A. m. scutellata* nests in the current study were similar to those reported for a smaller sample of Okavango colonies observed by Schneider and Blyther (1988). However, compared with the current study the colonies observed by Schneider and Blyther (1988) contained smaller total comb areas, a greater proportion of comb devoted to brood rearing, and less comb allocated to food storage. These authors examined primarily newly founded colonies, which typically are smaller and devote most all effort to brood production and rapid growth (Schneider and McNally 1994). Thus, the data reported by Schneider and Blyther (1988) may reflect *A. m. scutellata* nesting biology during only 1 portion of the annual colony cycle in the Okavango Delta.

Comparisons between the Okavango and neotropical African colonies revealed only 1 consistent difference in nesting biology. Compared with the Okavango colonies, the neotropical colonies were more likely to build exposed-comb nests and less

likely to occupy wooden cavities. This difference may simply reflect a greater availability of wooden cavities (and nest cavities in general) in the Okavango Delta. Conversely, colonies in the different habitats may have different nest site preferences. For example, predation rates on honey bee colonies are higher in the Okavango Delta than in the neotropics (Otis 1991, Schneider and Blyther 1988), and this in turn may contribute to a greater frequency of wooden cavity nests in the Okavango. Cavities located high in trees may be less detectable and more easily defended against predators. However, at present the factors underlying the difference in nest cavity types observed in the different habitats are unclear.

No differences were observed between Okavango and neotropical colonies in the other nest characteristics examined. In all environments, colonies exhibited similar densities, occupied similarly sized nest cavities (except in Peru), constructed similar amounts of comb, and devoted virtually identical proportions of comb area to brood production, food storage, and drone rearing. Comparisons among the different areas must be interpreted with caution, however, because of different methodologies used in the various studies. Nevertheless, the available data suggest that the aspects of nesting biology examined in this study may have undergone few substantial changes from the ancestral African condition during the colonization of Central and South America. This is consistent with recent mitochondrial and nuclear DNA analyses which suggest that, despite hybridization with European bees in some regions, the bee advancing northward is predominantly African in genetic composition (Rinderer et al. 1991; Sheppard et al. 1991; Smith et al. 1989; Hall 1991, 1992; Hall and Smith 1991).

Acknowledgments

We thank H. V. Daly and H. G. Hall for identifying honey bee samples collected in Botswana and Costa Rica, respectively. In Botswana, we thank the Office of the President, the Department of Wildlife and Tourism, and the National Museum and Art Gallery for their assistance. In Costa Rica, we thank G. Frankie and the Stewart Ranch for their support and assistance in locating a study site. We give special thanks to our local assistances in Botswana, Longwan and James, and to Neyar Campos in Costa Rica for help in locating and dissecting bee colonies. The research was funded by Fulbright Grant No. 85-42174, a grant from the Whitehall Foundation, U. S. National Science Foundation grant BSR 8906997, and U. S. Department of Agriculture Seed Grant No. 92-37106-7990.

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Received for publication 31 October 1995; accepted 26 February 1996.