Original article

Developmental patterns associated with founding and swarming in colonies of the African honey bee race, *Apis mellifera scutellata* Lepeletier

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Summary — The developmental patterns of naturally occurring, recently founded colonies of the African honey bee race, *Apis mellifera scutellata*, were examined in the Okavango River Delta, Botswana. Colonies moved into the study area beginning in mid-June. During the first 3–4 months after founding, colonies devoted most comb area to worker brood production, reared few or no drones, emphasized pollen collection, yet stored little food. Reproductive swarming occurred in October–November, at which time brood production declined, and food storage and drone production increased. Thus, the developmental strategy of newly founded colonies in the Okavango is geared towards rapid growth and the immediate channeling of harvested resources into worker brood, which culminates in a relatively brief period of reproductive swarming. The developmental patterns for the Okavango colonies are similar to those reported for the Africanized honey bee in South America, although the Okavango colonies may have a shorter swarming season.

Apis mellifera scutellata / swarming / colony founding / brood / Africa

INTRODUCTION

Newly founded colonies of social insects frequently pass through progressive developmental stages characterized by distinct patterns of growth and resource allocation. Such developmental patterns are hypothesized to maximize colony survival and eventual reproductive output (Oster and Wilson, 1978). Colonies of the honey bee, *Apis mellifera*, are founded by swarming, in which a queen and numerous workers leave an existing nest and establish in a new nest cavity. The swarm must quickly construct combs and gather resources to rear new workers to compensate for attrition in the founding worker force and to initiate colony growth. Once colonies reach sufficient size,

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drones (males) are produced, new queens are reared and swarming occurs (Seeley, 1985; Winston, 1987).

While all honey bees reproduce by swarming, temperate and tropical races exhibit marked differences in developmental and reproductive strategies. Temperate climate swarms must establish in early spring and summer to allow sufficient time to build up the colony population size and food reserves necessary to survive a prolonged winter (Seeley and Visscher, 1985; Lee and Winston, 1987). As a result, the swarming season in temperate regions is relatively brief, and newly founded colonies must focus their efforts on both brood production and food (primarily honey) storage. New temperate climate colonies typically do not swarm during their first year, and then subsequently produce 1–3 swarms per year (Seeley, 1978; Winston, 1980; Lee and Winston, 1987).

In contrast, tropical honey bee races, most of which occur in Africa (Ruttner, 1988), do not experience winter and have an extended foraging season that permits the establishment of colonies virtually year round (Fletcher, 1991; Otis, 1991; McNally and Schneider, 1992). Also, tropical colonies experience high rates of predation, which may further favor high rates of reproductive swarming (Schneider and Blyther, 1988; Winston, 1992). Thus, colonies often produce multiple swarms during a prolonged period, and newly established colonies frequently swarm during their first year (Winston, 1979; Winston et al, 1983; Otis, 1991). Increased swarm output, in conjunction with an extended availability of forage, favors an emphasis on brood production and little food storage (Winston et al, 1981; Schneider and Blyther, 1988; McNally and Schneider, 1992).

A knowledge of the developmental and swarming processes of tropical honey bees is essential for understanding the population dynamics of A mellifera in Africa, and the rapid spread and colonizing success of the Africanized honey bee (descendants of introduced colonies of the African race, A m scutellata) in the neotropics. Much of what we currently know about tropical colony development comes from a limited number of studies on Africanized colonies in South America (Winston, 1979, 1981; Winston and Taylor, 1980). In contrast, patterns of growth and development for naturally occurring tropical honey bee colonies in their native African environment have only recently been investigated (McNally and Schneider, 1992; Schneider and McNally, 1992a,b, 1993), and to date there have been no detailed investigations of the developmental patterns associated with founding and swarming. Such information is necessary to evaluate the extent to which the swarming behavior observed in the neotropics reflects 'natural' behavior or responses to a new environment.

The purpose of this study was to investigate colony developmental patterns associated with founding and swarming in the African honey bee race, A m scutellata, in Africa. Where possible the results of this study are compared to existing data for the Africanized bee in the neotropics.

MATERIALS AND METHODS

Study site

The study was conducted in the Okavango River Delta, Botswana. Descriptions of the study site are given in Schneider and Blyther (1988) and McNally and Schneider (1992). The annual colony cycle of A m scutellata in the Okavango consists of 3 seasons or periods (McNally and Schneider, 1992; Schneider and McNally, 1992a). The establishment period (June–September), which occurs primarily during the period of peak floral abundance, is a time when large numbers of swarms move into the study area, establish in nest cavities, and rapidly grow. The establishment period is followed by the reproductive swarming sea-

son, which occurs during October and November at the end of the peak bloom period. The swarming season is followed by the absconding season (November–May), during which large numbers of colonies emigrate from the study area when the availability of floral resources is reduced and variable. The distinct annual cycles of founding and swarming make *A m scutellata* in the Okavango well suited for a study of colony developmental strategies in tropical bees.

Determining colony developmental and swarming patterns

Colony developmental patterns were examined by dissecting in the field 10.5 ± 5.0 (mean ± SD) naturally occurring nests each month (range 3–17). All dissections used for the present study were conducted between mid-June and November, the establishment and swarming periods. The following were recorded for each colony, using a grid of 5 x 5 cm squares when necessary: (1) date of dissection, expressed as Julian day; (2) total comb area (cm²); (3) proportion of total comb area that contained brood (eggs, larvae, pupae), food, or that was empty; (4) proportion of food comb area that contained honey and pollen; (5) proportion of total comb area that was drone comb; and (6) the proportion of drone comb that contained drone brood (see McNally and Schneider, 1992, 1994, and Schneider and McNally, 1992a,b, for further details of measuring comb areas and identifying drone comb). Correlation analysis was subsequently used to examine changes in the different comb areas over time. Proportional data were arcsine transformed prior to analysis. Because numerous correlation coefficients were generated simultaneously, we used the sequential Bonferroni adjustment to determine table-wide levels of significance (Rice, 1989).

Additionally, each dissected nest was categorized as newly established, swarming, thriving, or associated with seasonal absconding. A colony was considered to be newly established if at least 75% of the combs consisted of new, white wax. A colony was classified as swarming if it contained developing queen cells (preparation for swarming) or cells from which new queens had recently emerged and a reduced worker population (evidence of recent swarming). A thriving colony was considered to be one containing dark combs, indicating several cycles of brood

rearing, and no evidence of swarming or absconding. Colonies associated with seasonal absconding were identified based on brood rearing patterns and amounts of empty comb. Several weeks before seasonal absconding the laying activity of the queen is reduced and workers begin consuming young larvae and food reserves (Woyke, 1976; Winston *et al*, 1979; Schneider, 1990a,b; Schneider and McNally, 1992b). Older larvae and pupae are usually not eaten. As a result, colonies preparing for seasonal absconding contain few eggs, no young larvae, and increasing amounts of empty comb. Departure from the nest is delayed until the sealed brood has emerged. The remaining food stores are consumed before the nest is abandoned, and thus absconding colonies leave behind mostly empty combs (Winston *et al*, 1979; Schneider, 1990a; McNally and Schneider, 1992). Hence, if a dissected nest was found to have been abandoned it was considered to have undergone seasonal absconding if the combs were undamaged but contained little or no brood or food. A colony was classified as preparing for seasonal absconding if at the time of dissection the nest was occupied, but at least 50% of total comb area was empty, less than 25% of total comb area contained brood, and the brood consisted mainly of older larvae and pupae (McNally and Schneider, 1992). ANOVA and *t*-tests were subsequently used to compare different comb areas among the differen types of colonies, and between *A m scutellata* colonies in the Okavango Delta and the Africanized bee in South America. Proportional data were arcsine transformed prior to analysis. Unless otherwise stated, all values are reported as the mean ± 1 SD.

RESULTS

A total of 60 colonies were dissected from mid-June through November. Of these, 22 were newly established, 13 were associated with reproductive swarming, 19 were thriving, and 6 were associated with seasonal absconding (fig 1). When examining total comb areas we excluded 2 of the newly established colonies because they contained no combs. Additionally, when examining worker brood, drone brood, and food comb areas we excluded: (1) the absconding colonies, because of their reduced brood
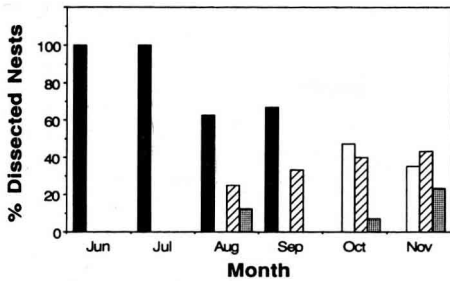
Fig 1. The proportion of colonies dissected during each month of the study period that were newly established (closed bars), swarming (open bars), thriving (hash-marked bars), or associated with seasonal absconding (stippled bars).

rearing and food storage activity; and (2) 3 swarming colonies that failed to requeen and contained no brood. The analyses for total comb area were therefore based on 58 colonies; those for worker brood, drone brood and food comb areas were based on 49 dissected nests.

All colonies dissected between mid-June and July, and 78% of the colonies examined during the first 4 months of the study, were newly established (fig 1). We did not observe thriving colonies until mid-August, and swarming was observed only in October and November. These data suggest that the vast majority of the dissected colonies were founded during the early part of the study, and that the observed comb areas reflected the growth and development occurring during 1 establishment and swarming cycle. Nevertheless, we cannot rule out the possibility that some of the swarming and thriving colonies observed in the later months had persisted in the study area from the preceding year.

Colony size (inferred from total comb area) increased fairly steadily throughout the establishment and swarming period, although the colonies dissected in November tended to be somewhat smaller (fig 2a). When viewed over all 58 nests that con-
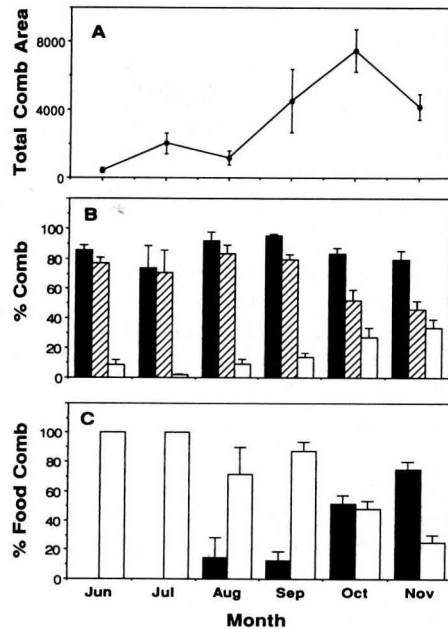

Fig 2. (A) Mean ± SD total comb area (cm²) for the nests dissected during each month. (B) The mean ± SD percentage of total comb area utilized each month (closed bars), and the proportions devoted to worker brood production (hash-marked bars) and food storage (open bars). (C) Mean ± SD percentages of the total food comb area devoted to pollen (open bars) versus honey (closed bars) storage each month.

tained comb, there was a highly significant, positive correlation between total comb area and data of excavation ($r = 0.373$; $P < 0.01$).

The proportion of total comb area utilized for either brood rearing or food storage remained fairly constant (75–95%) throughout the study period (fig 2b), and there was no correlation between proportion of comb utilized and date of dissection ($r = 0.10$; $P > 0.05$). However, as the study progressed the allocation of comb to worker brood production declined, while that for food storage increased. There was a highly significant, negative correlation between the proportion of comb area containing brood

and date of dissection ($r = -0.490$; $P < 0.01$). Worker brood accounted for 78.8 ± 13.6% of total comb area throughout the establishment period (June–September), but then declined to 48.9 ± 22.7% during the swarming season (October–November; t-test; $P < 0.01$; fig 2b). There was a significant, positive correlation between the proportion of comb area containing food and date of dissection ($r = 0.495$; $P < 0.01$). Food storage accounted for only 9.8 ± 8.8% during the establishment period, but increased to 30.5 ± 20.1% during the swarming season (t-test; $P < 0.01$; fig 2b).

The allocation of food comb to honey *versus* pollen storage also changed during the study period (fig 2c). There was a highly significant, negative correlation between the proportion of food comb area containing pollen and the date of dissection ($r = -0.762$; $P < 0.01$). The correlation between the proportion of food comb containing honey was significantly and positively correlated with date of dissection ($r = 0.662$; $P < 0.01$). During June–September, 87.4 ± 29.0% of food comb area consisted of pollen, while 8.6 ± 22.7% contained honey (1 newly established nest contained no stored food). In contrast, during the swarming season, pollen storage declined to 36.6 ± 21.8% (t-test; $P < 0.01$), and honey storage increased to 63.4 ± 21.8% of food comb area (t-test; $P < 0.01$; fig 2c).

Both drone comb areas and drone brood production increased during the study period, and peaked in the swarming season (fig 3). However, there was no correlation between date of dissection and drone comb area ($r = 0.315$) or date of dissection and the proportion of drone comb containing drone brood ($r = 0.178$; $P > 0.05$ for both correlations). The proportion of total comb area that consisted of drone comb remained low throughout the study period (2.5 ± 2.2%). Drone comb was observed primarily from September–November (fig 3). Drone brood production occurred primarily in
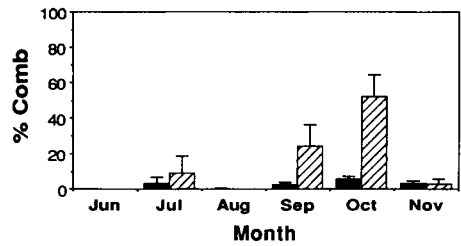

Fig 3. The monthly means (± SD) for the percentage of total comb area that was drone comb (closed bars) and the proportion of drone comb that contained drone brood (hash-marked bars).

association with swarming. Of the 16 colonies dissected from June–August, only one (in July) contained drone brood (fig 3). Drone production occurred almost entirely during September and October, and declined sharply in November at the end of the swarming season.

There were no distinct differences between the different comb areas of the swarming and non-swarming colonies (comparisons were restricted to the 32 nests dissected during the 2 months of the swarming season). The 13 swarming colonies and the non-swarming colonies did not differ with respect to total comb area (6 905.9 ± 5 052.0 vs 4 895.6 ± 3 608.2 cm^2; t-test; $P > 0.05$). Comparisons of brood, food and drone comb areas were restricted to the 4 colonies preparing for swarming and the 13 thriving colonies examined during the swarming season; colonies that had recently swarmed and the absconding colonies examined during October–November were excluded because of their reduced brood rearing activity. The swarming and thriving colonies did not differ in any of the comb areas examined (table I; t-tests; $P > 0.05$ for all comparisons).

We also found no distinct differences when comparing the swarming colonies observed in the Okavango with 10 swarming Africanized colonies observed by Winston

Table I. Mean (± SD) proportions of total comb area devoted to worker brood, food storage, and drone production in the 4 colonies preparing for swarming and the 13 thriving colonies dissected during the swarming period.

Comb area (%)	Swarming	Thriving
Total comb area utilized	89.0 ± 10.9	85.9 ± 15.6
Comb area with worker brood	67.0 ± 21.1	50.4 ± 18.5
Comb area with food	17.7 ± 9.6	33.5 ± 18.7
Food comb area with honey	49.0 ± 18.8	67.0 ± 20.6
Food comb area with pollen	51.0 ± 18.8	33.0 ± 20.6
Total comb area drone comb	7.7 ± 4.6	3.5 ± 4.4
Drone comb with drone brood	56.0 ± 44.1	33.5 ± 41.9

All comparisons were non-significant (t-tests; $P > 0.05$).

and Taylor (1980) in French Guiana. The total comb area of the swarming colonies in the Okavango (6 905.9 ± 5 052.0 cm^2) did not differ from the 8 288 ± 304 cm^2 reported for the Africanized colonies (t-test; $P > 0.05$). Likewise, the proportions of total comb area utilized for brood production and food storage (89 vs 86% for the Okavango vs Africanized colonies) and the proportions of comb containing worker brood (67% for both colony groups) did not differ ($P > 0.05$ for both comparisons). Data are not available for the comb areas of swarming Africanized colonies allocated to pollen and honey storage.

DISCUSSION

Oster and Wilson (1978) described the growth of social insect colonies as consisting of 2 main stages. Newly founded colonies, which are typically small, pass through an ergonomic stage characterized by: (1) growth and an emphasis on brood production; (2) reduced defensive behavior, because defense against predators may reduce the already small worker force; and (3) smaller worker size, because the small size of founding colonies may limit the harvesting of resources and thus the availabil-

ity of food for developing brood. As the ergonomic stage progresses, colony population, defensive behavior and worker size increase. The ergonomic stage is followed by the reproductive stage, in which worker brood production plateaus or declines, and colony efforts are redirected towards raising reproductive males and females.

The Oster and Wilson model provides a good conceptual framework for evaluating the developmental patterns observed for colonies of A m scutellata in the Okavango Delta. Colonies immigrated into the study area beginning in June, presumably to capitalize on the abundance of forage that occurs from August–October (see also Schneider and Blyther, 1988; McNally and Schneider, 1992). Newly established colonies grew rapidly, devoted most available comb space to raising worker brood, and stored little food. What food was stored consisted almost entirely of pollen, which provides the proteins and fats necessary for brood production (Danka et al, 1987; Winston, 1987). Foraging activity during the establishment period is concentrated predominantly on pollen collection (Schneider, 1989; Schneider and McNally, 1992b) and large amounts of pollen may be gathered each day. Thus, the low levels of pollen stor-

age observed in the present study suggested that the harvested resources were almost immediately diverted into brood production.

The defensive behavior and worker size observed for newly founded A m scutellata colonies are also consistent with the Oster and Wilson (1978) model. Newly established colonies exhibit little or no defense behavior (Schneider and McNally, 1992c). Indeed, when recently founded colonies are disturbed workers flee the combs and may abandon the nest (Schneider and Blyther, 1988; Schneider and McNally, 1992c). Thus, during the early stages of colony development few workers are likely to be lost in defense, which may help maintain a larger number for foraging, nest construction and brood care. The initial workers raised by recently established colonies may be somewhat smaller than those reared later in colony development, because cells in the central (older) regions of the combs tend to be slightly smaller than those in the outer, newer regions (Winston, personal communication). Smaller size may allow a greater number of workers to be produced from the resources that can be initially harvested. Thus, the early developmental stages of A m scutellata in the Okavango appear to be geared almost entirely towards rapid increases in colony population size.

The period of rapid growth in A m scutellata colonies was followed by the production of reproductives, at which time worker brood rearing declined and food storage increased. In general, in the present study colonies delayed the construction of drone comb and the rearing of drone brood until total comb area was 4 000–5 000 cm^2 (figs 2 and 3). Maximum drone production occurred during the swarming season, although drones may be reared at low, sporadic levels throughout much of the year (McNally and Schneider, 1994). The rearing of virgin queens and the production of swarms were observed only during October and November. Defensive behavior is greatest at this time, which may reflect larger colony size and increased ability to mount attacks, or greater levels of investment in colony growth and reproductive output (Schneider and McNally, 1992c).

The decreased worker brood production during the swarming season may have resulted from 2 interacting factors. First, the laying activity of swarming queens declines (Allen, 1955, 1960; Schneider, 1990a). Second, there may have been a shift in emphasis towards food storage during the swarming season. During October and November, food comb increased to approximately 30% of total comb area, and much of this consisted of honey. Forage availability in the study area is reduced and variable from mid-November through May (McNally and Schneider, 1992). Some colonies persist within the region throughout this period, and may virtually deplete their food stores before forage availability begins to increase (McNally and Schneider, 1992; Schneider and McNally, 1992a,b). However, many colonies emigrate during these months and consume all remaining honey stores prior to departure (Schneider and McNally, 1992a). The build-up of honey reserves during October and November may simply reflect a greater availability of nectar during these months. However, the increased honey stores may also represent preparations for surviving the period of reduced floral resources or fueling the long distance travel that may occur in response to a deteriorating foraging environment.

There were no differences between swarming colonies of A m scutellata in the Okavango and the Africanized honey bee in French Guiana. In both habitats, swarming occurred in colonies of comparable size which exhibited similar patterns of brood production. The developmental patterns associated with swarming in both environments are characterized by rapid colony growth, little food storage, and (by inference) the immediate channeling of

resources into brood production (Winston, 1979; Winston and Taylor, 1980; Winston *et al*, 1983). The developmental patterns of Africanized colonies in the neotropics therefore appear to have been little modified from those of the ancestral African population. Furthermore, while resource availability undoubtedly influences the developmental patterns of honey bee colonies, the observed similarities in the African and neotropical environments suggest that the growth patterns may reflect an inherent developmental strategy, and are not only opportunistic responses to local resource conditions. Despite their similarities, colonies in Africa and the neotropics may differ in the length of the swarming season (McNally and Schneider, 1992) and thus the annual swarming rate per colony. However, at present the swarming behavior of honey bees in Africa is too poorly understood to allow for direct comparisons of swarming duration and rate in the 2 environments. Future studies of *A m scutellata* in Africa should be focused on clarifying the population-level dynamics of swarming activity.

ACKNOWLEDGMENTS

Résumé — Développement des colonies de l'abeille *Apis mellifera scutellata* Lepeletier en fonction de la fondation et de l'essaimage. La croissance et le développement de colonies d'abeilles de race africaine récemment fondées ou en cours d'essaimage ont été étudiés chez une population naturelle dans le delta de l'Okavango au Botswana. Chaque mois de mi-juin à novembre (périodes de fondation et d'essaimage), on a étudié sur place en moyenne 10,5 nids naturels ± 5,0. Pour chaque colonie on a mesuré la surface totale des rayons (en cm^2) et les surfaces de couvain d'ouvrières (œufs, larves et nymphes), de rayons de nourriture (miel et pollen), de rayon de mâles et de couvain de mâles. En outre on a classé chaque colonie en colonie nouvelle, en essaim, en essaim déserteur saisonnier ou en colonie en développement. Sur les 60 colonies étudiées, 22 étaient nouvellement fondées, 13 se reproduisaient par essaimage, 19 se développaient et 6 désertaient. 78 à 100% des colonies examinées de juin à septembre étaient nouvellement fondées ; les colonies essaimantes n'ont été observées qu'en octobre et novembre (fig 1). La surface globale des rayons a augmenté très régulièrement tout au long de la période d'étude (fig 2). De mi-juin à septembre, les colonies nouvellement fondées ont consacré la grande majorité de leurs rayons à la production de couvain d'ouvrières, ont élevé peu ou pas de mâles, ont privilégié la récolte de pollen par rapport à celle de nectar mais n'ont stocké que peu de nourriture (figs 2 et 3). Pendant la période d'essaimage (octobre-novembre) la production de couvain d'ouvrières a baissé tandis que les réserves de nourriture, principalement de miel, se sont accrues (fig 2). La production de couvain de mâles a été maximale en septembre et octobre (fig 3). L'utilisation des rayons par les colonies essaimantes ne diffère pas significativement de celle des colonies en développement examinées pendant la saison d'essaimage (tableau I). De même la croissance et la production de couvain observées chez les colonies de l'Okavango étaient semblables à celles des colonies africanisées d'Amérique du Sud. Dans le delta de l'Oka-

vango la stratégie de développement des colonies d'*A m scutellata* nouvellement fondées est donc orientée vers une croissance rapide de la colonie et la transformation immédiate des récoltes amassées en production de couvain. Cette croissance rapide culmine pendant la période d'essaimage qui est relativement brève. Les ressemblances entre les colonies d'*A m scutellata* et les colonies africanisées d'Amérique du Sud suggèrent que le mode de développement s'est peu modifié dans le milieu néotropical. Pourtant la période d'essaimage pourrait être plus courte dans la région de l'Okavango.

Apis mellifera scutellata / essaimage / fondation de colonie / dynamique population / Afrique

Zusammenfassung — Volksentwicklung der afrikanischen Honigbienenrasse *Apis mellifera scutellata* Lepeletier (1836) in Abhängigkeit von der Nestgründung und vom Schwärmen. Das Wachstum und der Entwicklungsverlauf von neugegründeten und von schwärmenden Völkern der afrikanischen Bienenrasse *Apis mellifera scutellata* wurde in der freilebenden Population im Delta des Okavango Flusses in Botswana untersucht. Jeden Monat wurden von Mitte Juni bis einschließlich November (Reproduktionssaison) im Mittel 10,5 ± 5,0 Nester in der Umgebung untersucht. Die Gesamtfläche der Waben, die Fläche der Arbeiterinnenbrut (Eier, Larven und Puppen), der Futterwaben (Honig und Pollen), der Drohnenwaben und Drohnenbrut wurde bestimmt. Zusätzlich wurde jedes Volk nach verschiedenen Charakteristika klassifiziert: als Neugründung, als Volk in Schwarmstimmung als Volk in Vorbereitung zum saisonalen Wanderschwarm oder als Volk in der Wachstumsphase. Insgesamt wurden 60 Völker untersucht, von denen 22 gerade neu gegründet waren, 13 stammten aus reproduktiven Schwärmen, 19 waren in der Wachstumsphase und 16 stammten von Wanderschwärmen. Von Juni bis September bestanden 78–100% der Völker aus Neugründungen, Schwärme wurden nur im Oktober und November beobachtet (Abb 1). Die Gesamtfläche der Waben nahm während der ganzen Versuchszeit stetig zu (Abb 2). Von Mitte Juni bis September bauten die meisten Völker Arbeiterinnenwaben, sie zogen nur wenig oder keine Drohnen auf und sammelten bevorzugt Pollen im Vergleich zu Nektar, lagerten jedoch nur wenig Futter ein (Abb 2, 3). In der Schwarmzeit (Oktober–November) nahm die Produktion der Arbeiterinnenbrut ab, während die Futtervorräte (vor allem Honig) zunahmen. Die größte Drohnenproduktion erfolgte im September und Oktober (Abb 3). Die verschiedenen Wabenflächen der schwärmenden Völker unterschieden sich nicht signifikant von denen der sich aufbauenden Völker, die während der Schwarmzeit untersucht wurden (Tabelle I). Es wurde ein ähnlicher Verlauf des Volkswachstums und der Brutproduktion in Okavango wie bei den afrikanisierten Bienen in Südamerika beobachtet. Die Entwicklungsstrategie bei Nestgründungen im Okavango Delta ist auf eine sehr schnelle Volksvergrößerung ausgerichtet und die Tracht wird in die Brut investiert. Dieses schnelle Volkswachstum gipfelt in einer relativ kurzen Schwarmperiode. Die Ähnlichkeiten zwischen *A m scutellata* Völkern in Okavango und den afrikanisierten Bienen in Südamerika lassen vermuten, daß sich das Entwicklungsmuster im neotropischen Lebensraum wenig geändert hat. Die Schwarmzeit scheint in Okavango jedoch kürzer zu sein.

Apis mellifera scutellata / Nestgründung / Populationsdynamik / Afrika

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