

Intra-Colony Demography and Reproductive Rate of the Africanized Honeybee in South America*

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Received March 28, 1978

Summary. 1. Demography and growth patterns of Africanized honeybee colonies in South America are described, and the influence of worker survivorship, rate of worker production, age structure, and colony growth patterns on their reproductive rate (swarm production) is discussed.

2. During a reproductive cycle, a colony passes through four phases: pre-emergence, post-emergence, pre-swarming, and post-swarming. Growth in the worker population approximates a sigmoid curve, but swarming occurs before high growth rates peak. Colonies swarm at a small size, with sufficient workers to produce viable prime swarms and afterswarms, as well as to continue the parent colony.

3. The timing of adult worker emergence influences the number of afterswarms, as well as the number of adults maintained in the original colony when swarming is completed.

4. Patterns of survivorship for both brood and adult workers shift during swarming cycles, with high brood mortality and reduced adult longevity early in the cycle, in contrast with lower brood mortality and increased longevity of adults as colonies mature.

5. Survivorship appears to be related to the age structure of colonies, with high mortality at points in the swarming cycle at which there is a high mean worker age and a low proportion of young workers. The age structure of colonies also shifts during swarming cycles with a progressive increase in the proportion of young workers. A consequence of this shift is that swarms are populated predominantly by young workers. Patterns of survivorship and age structure influence colony growth rates, and thus partly determine the rate of swarm production.

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Introduction

In a social insect such as the honeybee, population growth rates are determined at the colony level, and thus intra-colony demography is important in determining the growth rate of populations. Reproductive rate in highly social insect colonies is the rate of queen production (=swarms for honeybees), and such intra-colony demographic parameters as worker survivorship, rate of worker production, age structure, and colony growth patterns might affect reproductive rate (Wilson, 1971). However, the role of these factors in determining colony reproductive rate is poorly understood, and data are lacking.

In 1956, 26 queens of the African honeybee subspecies *Apis mellifera scutellata* (formerly *adansonii*, Ruttner, 1976) which had been brought to Brazil for breeding purposes escaped in swarms near São Paulo and established feral colonies that hybridized with local races of honeybees. The resulting hybrid or 'Africanized bee', retaining most of the original African characteristics, has spread throughout much of South America, often exhibiting high colony densities (Anonymous, 1972). The rapid expansion of the Africanized bee is partly due to the high reproductive rate of feral colonies, with colonies characterized by such 'r-selected' traits as small size at reproduction (Taylor et al., in preparation), rapid growth to reproductive age, short intervals between reproductive efforts, and relatively large clutch size (Otis, in preparation). The purpose of the present study is to determine how intra-colony demographic parameters such as worker survivorship, rate of worker production, age structure, and colony growth patterns might influence the reproductive rate of Africanized honeybees.

Methods

General Information. The study was conducted during the swarming season near Kourou, French Guiana, South America (5°10'N, 52°40'W) from August 1976 to February 1977. Although hybridization between European and African honeybee races may have occurred in other areas of South America, no hybridization occurred in the study area, as there were fewer than 15 colonies of European bees in all of French Guiana when the Africanized bee arrived in 1974 (Otis, personal communication). The Africanized bees in French Guiana are morphometrically (H.V. Daly, personal communication) and behaviorally (Fletcher, 1978) extremely similar to bees from South Africa.

Study Colonies. A total of 16 colonies were used for this study. (Additional data from Otis, in preparation, were used in calculating swarming intervals, the total comb area in pre-swarming colonies, and the number of afterswarms. Places where such data were used are indicated in the text by sample sizes greater than 16). Bees were captured as swarms or transferred from colonized swarm boxes or from feral colonies in cavities. Data from transferred bees were not used until colonies had swarmed at least once. In order to simulate natural conditions and allow internal examination, 22-liter study hives (42 × 22 × 24 cm) were constructed from eight and nine mm plywood. The volume chosen (22 L) is comparable to the comb volume of feral colonies in French Guiana and elsewhere in South America (Taylor et al., in preparation). Each box had a three cm entrance hole and a telescoping hive cover. Boxes contained six movable wooden top bars with one cm wide starter strips of wax foundation along the bottom edge, along which bees built their own comb. Hives were placed at forest edges in the savannah region near Kourou, and kept well-shaded. Except for inspections and the introduction of marked bees (see below), colonies were not manipu-

lated in any way. Thus, the colonies represent, as closely as possible, feral colonies of Africanized honeybees.

Colony Growth. Data on colony growth were obtained weekly (and more frequently as colonies approached swarming) by measuring the areas of comb, unsealed brood (eggs and larvae), sealed brood (pupae), nectar, honey, and pollen with a centimeter ruler. Each of the six combs in a colony was removed and measured on one side (the same side each time), and then replaced in its original location and orientation. Since comb has two sides, usually almost identical, measurements were doubled to obtain the approximate total areas. Occasionally the two sides of comb would be clearly different, particularly on the outer frames; here both sides were measured individually. Only data from the average-sized study colonies of Africanized bees are presented here. Although these results may not apply to feral colonies which are larger or smaller than study colonies, observations of feral colonies in French Guiana and Peru suggest that most colonies are similar to those of the present study.

Brood Survivorship. Brood mortality was measured by following cohorts of unsealed brood and groups of 100 newly-laid eggs to determine survivorship to the sealed brood or pupal stage. For the unsealed brood cohorts, the total area of eggs and larvae was measured in each colony eight days after laying began, when the first brood was being sealed; the area of sealed brood was measured on day sixteen, when all of the unsealed brood of the first eight days should be sealed (the egg and larval stages are three and five days long, respectively). Thus, the difference in the area of unsealed brood on day eight and sealed brood on day 16 reflects the amount of brood mortality at this point in the colony cycle. Area cohort measurements were also used to determine brood mortality post-swarming by a similar technique.

Cohorts of 100 eggs (marked by counting cells from fixed reference points on comb) were followed to determine brood mortality at other times in the swarming cycle. Cells with eggs which were not sealed eight days later were recorded as deaths. Non-sealed cells were either empty, contained eggs, or had very young larvae; the eggs and young larvae represented replacement brood laid after the original brood died.

Mortality during the pupal (sealed brood) stage was assumed to be zero for survivorship and age structure calculations, since it is impossible to examine the condition of pupae sealed under pupal caps. Fukuda and Sakagami (1968) have shown that mortality at this stage is usually negligible, and less than two percent sealed brood mortality was observed.

No bee diseases were seen during this study.

Adult Survivorship. To determine adult longevity, marked cohorts of 100 newly emerged worker bees were placed into study colonies at ten-day intervals, beginning on the twentieth day after a colony was established, when the first new young adult workers emerged. Cohorts were obtained by removing combs from other hives in the apiaries, allowing workers to emerge from the sealed pupal cells, and introducing the newly emerged workers into the study hives within one to two hours after marking. Workers were marked with colored and numbered labels glued onto their thoraces. Acceptance of marked workers and tag retention were determined by examining colonies the day after the introduction of a cohort; any marked workers not located were excluded from further analysis.

The numbers of surviving marked workers from each cohort were determined at least every five days by removing and carefully searching each frame, and recording all marked workers. After the frames and hives had been inspected, the frames were rechecked before being replaced into the hive. The longevity of each bee was calculated as the midpoint between the last day the bee was observed and the first day it was absent (i.e., if a bee was found on day five but not day ten or subsequently, its longevity would be 7.5 days). From these data, survivorship curves were constructed, and mean longevities calculated.

Age Structure. The mean age of workers during the first swarming cycle (from the time a swarm was introduced to an empty hive until swarming was completed) was calculated in three colonies for which there were complete survivorship and colony growth data. The number of workers in the swarms establishing these colonies was known (Otis, personal communication), and the age structure of those swarms estimated using data from Winston and Otis (1978). The number

of workers emerging daily from the time of first emergence until the completion of the first swarming cycle could be calculated from the sealed brood curves for those colonies. Survivorship of each day's emergence was calculated using the survivorship curves obtained from the cohorts of marked bees introduced into colonies. From these data for any given day, the mean age, number of living workers, and the proportion of young workers (eight days old or less) could be determined. This parameter gives an estimate of the proportion of nurse bees present, since it is largely workers less than nine days old which feed larvae and teneral adults (Free, 1965; Smith, 1974).

For more detailed methods, see Winston (1978).

Results

1. Colony Growth and Rate of Worker Production

The swarming cycle of the Africanized honeybee can be divided into four periods: pre-emergence, post-emergence, pre-swarming, and post-swarming (Fig. 1). These phases are described below for the first and second swarming cycles.

a) First Swarming Cycle

Pre-Emergence. This period begins with colony establishment and terminates twenty days later, with the emergence of the first adults (development time from egg to adult is 20 days (Kerr et al., 1972)). Workers generally begin foraging and building comb within an hour after colonization. Much of the comb building occurs early in the swarming cycle, with well over half of the colony's final comb area completed during the first 16 days (Fig. 1).

The queen usually begins laying eggs in the newly completed cells only a few hours after colonization. These first eggs hatch in three days, with the first larvae becoming pupae five days later, and subsequent larvae pupating over the next 8 to 12 days. The first days of the swarming cycle are characterized by increasing quantities of unsealed brood, peaking at a mean of 3313 cm² ($n=7$, Fig. 1), followed by pupation from day 8 to day 20, with sealed brood area peaking just prior to the first new worker emergence on day 20 ($\bar{x}=2502$ cm², $n=7$, Fig. 1).

There is a period of relatively little activity from day 16 to day 20, when rates of comb building, brood rearing, and probably foraging decrease (Fig. 1). Here the adult population is at its lowest level, with an average of only 43 percent of the original colonizers alive at first worker emergence (Fig. 2).

Post-Emergence. This phase of the swarming cycle begins with the first worker emergence 20 days after colonization, and lasts about seven days, at which time rapid growth to swarming strength (the pre-swarming period) begins. The post-emergence period is characterized by increasing numbers of workers, although growth in the adult population is relatively level (Fig. 2). Little comb building takes place during this period (Fig. 1).

Pre-Swarming. The pre-swarming period, lasting a mean of 25.8 days ($n=6$), is characterized by increasing amounts of sealed brood (Fig. 1) and numbers

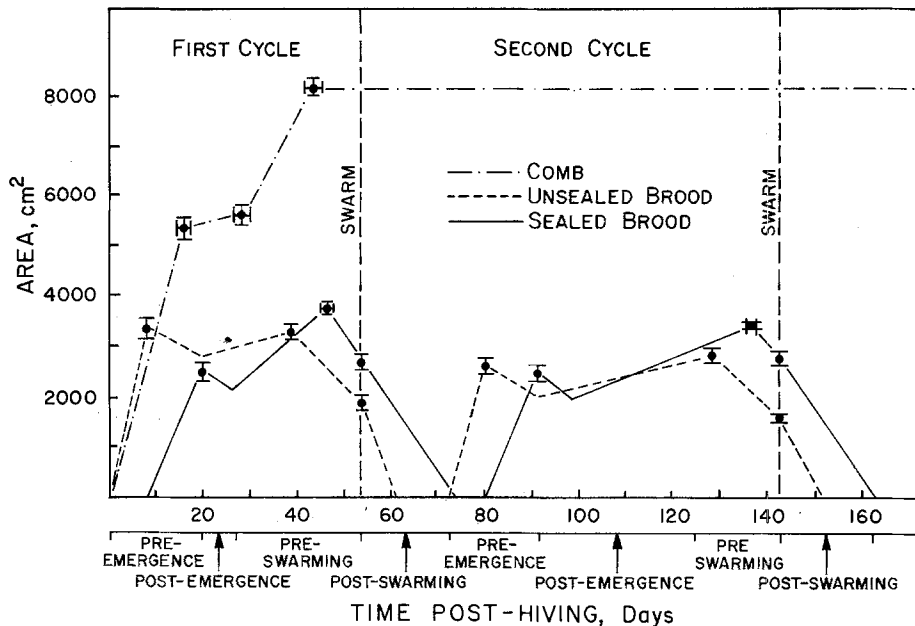


Fig. 1. Timing of colony cycles and areas of unsealed brood, sealed brood, and comb for two swarming cycles of a model colony of Africanized bees. Vertical error bars show standard errors for area measurements, and horizontal error bars show standard errors for timing of colony events. For sample sizes, see text. Note the difference in area of unsealed brood on day 12 and sealed brood on day 20, reflecting high brood mortality

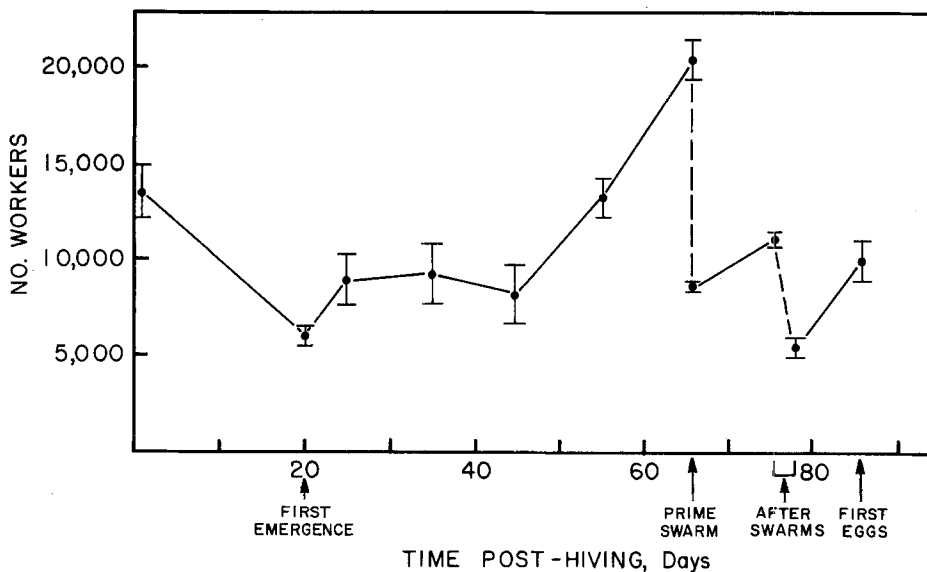


Fig. 2. Mean number of workers and standard errors for three study colonies throughout the first swarming cycle. Dotted lines connect points before and after swarms. Dates of swarming have been synchronized for clarity

of adult workers (Fig. 2). Colonies also complete comb-building, with hives reaching a final mean comb area of 8144 cm^2 ($n=21$) an average of 17 days ($n=6$) before swarming (Fig. 1).

Colony growth in this period is reflected by rapidly increasing sealed brood in pre-swarming colonies, peaking at a mean of 3745 cm^2 ($n=6$) an average of 6.5 days ($n=6$) before swarming (Fig. 1). Both unsealed and sealed brood decrease from the peak just prior to swarming, with means of 1853 cm^2 ($n=6$) of unsealed brood and 2714 cm^2 ($n=6$) of sealed brood present at the time of swarming (Fig. 1), both significantly lower than the pre-swarming peak ($P < 0.01$, *T*-Test). The amount of sealed brood and the timing of the peak (Fig. 3) is correlated with the number of afterswarms (Fig. 4) and will be discussed in the following section.

The increase in sealed brood results in a rapidly growing worker population 12 days after the sealed brood area begins to increase (since this stage lasts 12 days). The result is a rapid increase in the number of workers before swarming. At swarming, the worker growth curve has not begun to asymptote; that is, colonies swarm during a period of rapid population growth (Fig. 2).

Post-Swarming. This period lasts from the day of swarming until the colony has a new laying queen, an average of 18.9 days ($n=20$, Fig. 1). At the time of swarming, about 60% of the workers in the colony, particularly young workers (Winston and Otis, 1978), issue with the old queen (Fig. 2). The old colony is left with sealed and unsealed queen and worker brood, nectar and pollen stores, and approximately 40% of the workers (most of which are from the older age classes). During the post-swarming period queens mature and emerge; zero to four afterswarms issue with these virgin queens 9 to 16 days after the prime swarm has issued (Otis, in preparation).

As previously mentioned, the precise timing of the peak in sealed brood area in pre-swarming colonies (Fig. 3) is a factor in determining the number of afterswarms. The number of cells containing sealed brood when the prime swarm issues is correlated with the number of afterswarms ($r=0.547$, $P < 0.05$), (Fig. 4). If colonies from which no afterswarms issued are excluded, the correlation between the number of afterswarms and the amount of sealed brood at swarming is even stronger ($r=0.777$, $P < 0.01$). This latter correlation may be more accurate, since the production of afterswarms may be dependent on other factors besides the amount of sealed brood.

b) Second Colony Cycle

The second swarming cycle (and probably subsequent cycles as well) is similar to the first cycle, but is longer from the commencement of egg-laying until swarming (Fig. 1, 73.1 days, $SE=6.4$, $n=20$, for the second cycle, compared to 52.5 days, $SE=4.7$, $n=18$, for the first cycle). The increased length of the second cycle is likely due to the presence of fewer workers at the beginning of the second pre-emergence period (7–10,000) than are present in a newly colonized swarm (10–15,000). Other factors differing between the first and second

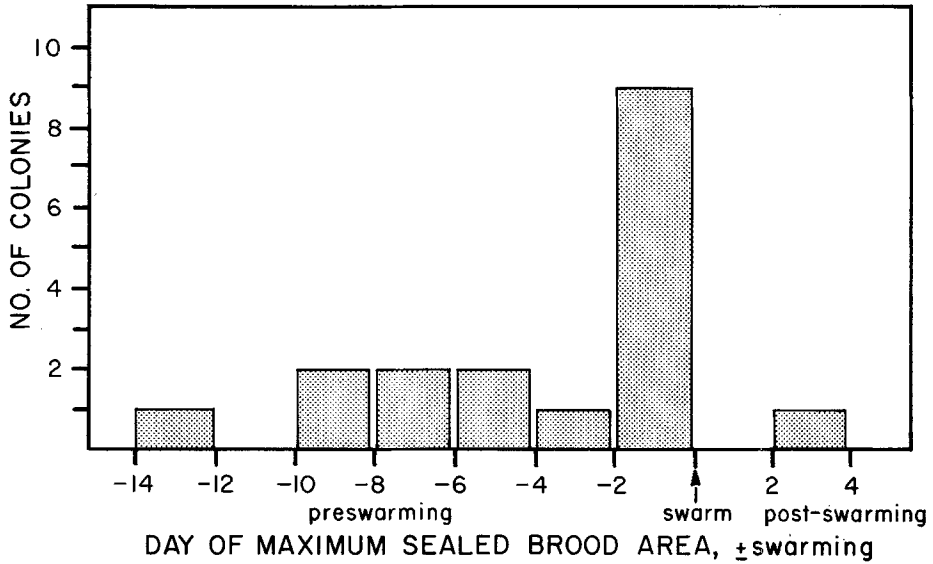


Fig. 3. Timing of the maximum sealed brood area in pre-swarming colonies, shown as the number of colonies with the peak area of sealed brood in the colony occurring in a given two-day interval before or after the prime swarm issued

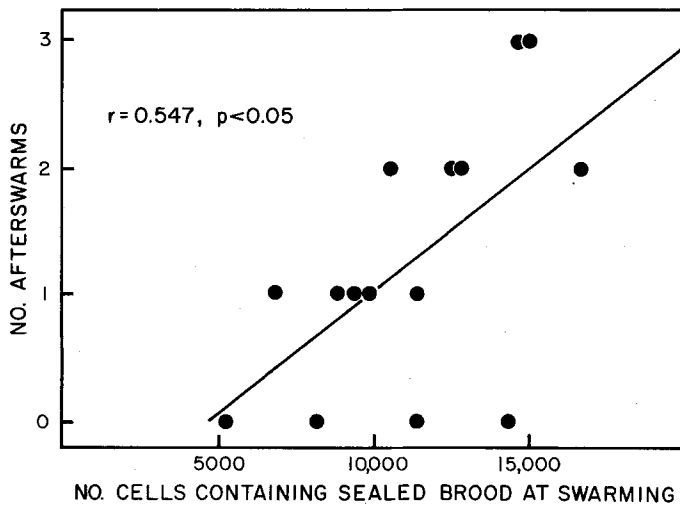


Fig. 4. The relationship between the number of afterswarms issuing from colonies and the amount of sealed brood present in colonies when the prime swarm issued. Data on number of afterswarms is from Otis (in preparation)

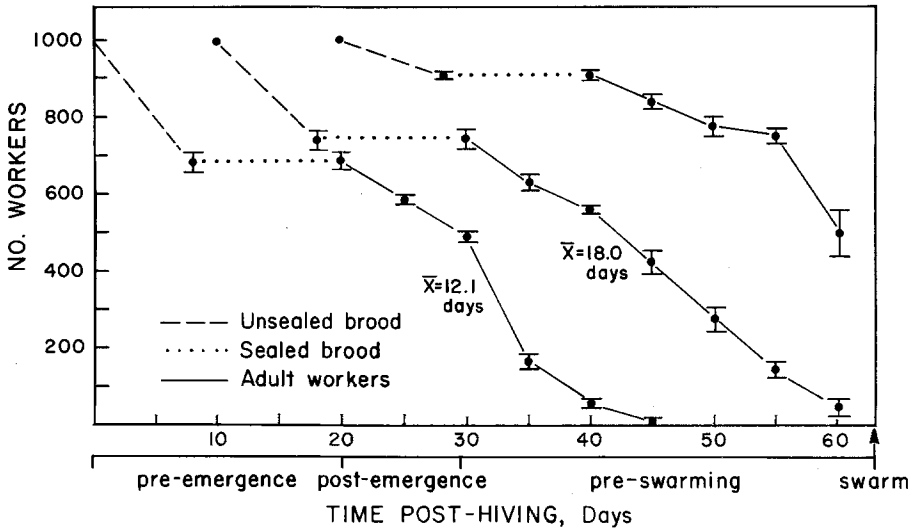


Fig. 5. Survivorship curves for three cohorts of workers during the first swarming cycle. All data have been converted to an initial population of 1000 individuals. Error bars are standard errors; for sample sizes, see text

cycles are the presence of comb. (Fig. 1), and nectar and pollen at the beginning of the second cycle; these factors may act to conserve the already-low worker population.

2. Survivorship

a) Brood Survivorship

Mortality of the first unsealed brood is relatively high during the pre-emergence period, averaging 32.4 percent ($n=6$) between egg and pupae (Fig. 5). In contrast, mortality of unsealed brood is considerably lower during the post-emergence and pre-swarming periods, when new workers have emerged, averaging 10.4% ($n=11$) during these periods. Post-swarming, brood mortality is again high, averaging 44.4% ($n=18$); thus, almost half of the unsealed brood remaining in a colony after the prime swarm issues is not sealed successfully. Brood mortality reaches its lowest point at the beginning of the second colony cycle, averaging only 5.2% ($n=9$) for the first brood cycle.

b) Adult Survivorship

Adult longevity follows the same pattern as brood mortality, with longevity improving as colonies grow. The first newly emerged workers on day 20 are short-lived, with a mean life span of 12.1 days ($n=3$, Fig. 5). The survivorship

schedule of these workers approaches a Type II curve (Pearl, 1928), with constant mortality at all ages.

Adult survivorship schedules shift considerably as the colony approaches swarming. Cohorts of adults introduced just ten days after the first emergence of new workers show greater longevity ($\bar{x}=18.0$ days, $n=5$, Fig. 5) than the first emerged adults ($\bar{x}=12.1$ days). The mortality schedules of adults late in the pre-swarming period result in a Type I survivorship curve (Pearl, 1928), with low worker mortality until day 15, and higher mortality subsequently. Since colonies swarmed before these cohorts were completed, it was not possible to calculate an accurate mean age for these workers, but the estimated mean longevity is about 20 days.

Longevity of emerged adults post-swarming is initially low, averaging 14.3 days ($n=3$, $SE=2.07$) for workers emerging two to three days after the prime swarm issues (these cohorts only include workers which did not issue with afterswarms, and thus survivorship data may not be as accurate as for other cohorts). However, workers emerging when afterswarming is completed show relatively high longevity, 21.8 days ($n=3$, $SE=3.07$).

3. Age Structure

Two components of age structure were examined, the mean age of workers and the percentage of young workers eight days old or younger (most nurse bees, which produce larval food in their hypopharyngeal glands, are of this age). In a newly issued swarm, the mean age of workers is low, about 9.3 days, and the percentage of young workers is high, about 60%. The mean age rises during the pre-emergence period, since no new workers emerge until day 20; the mean age is 25.8 days at that time (from Winston and Otis, 1978), with no workers younger than 21 days old (Fig. 6).

After the first worker emergence, the mean age of workers decreases rapidly, with a corresponding rise in the percentage of young workers. After the rapid post-emergence shifts in age structure, the colony reaches a stable age distribution 20 to 25 days before swarming (Fig. 6), although the overall number of workers in the hive is rapidly increasing (Fig. 2). Just prior to swarming, the mean age of workers is 10.0 days ($n=3$, $SE=0.10$), and the mean percentage of young workers is 46% ($n=3$).

Due to the high probability of young workers issuing with prime swarms (Winston and Otis, 1978), the mean age of workers in the hive rises immediately after swarming, from 10.0 days to 10.6 days ($n=3$, $SE=0.09$), and the proportion of workers eight days and younger decreases correspondingly. However, the emergence of young workers in the period between the prime swarm and the first afterswarm lowers the mean adult age and increases the proportion of young workers. Large numbers of young workers issuing with afterswarms slightly shifts the age structure of the colony towards older bees immediately post-afterswarming (Fig. 6). When afterswarming is completed, the mean age is again lowered due to emerging young workers. Twenty days after the prime swarm, when all the brood has emerged and a new queen is present, the mean age reaches its lowest point, 6.1 days ($n=3$, $SE=0.23$), and the percentage of young workers is at its highest level, 75% ($n=3$).

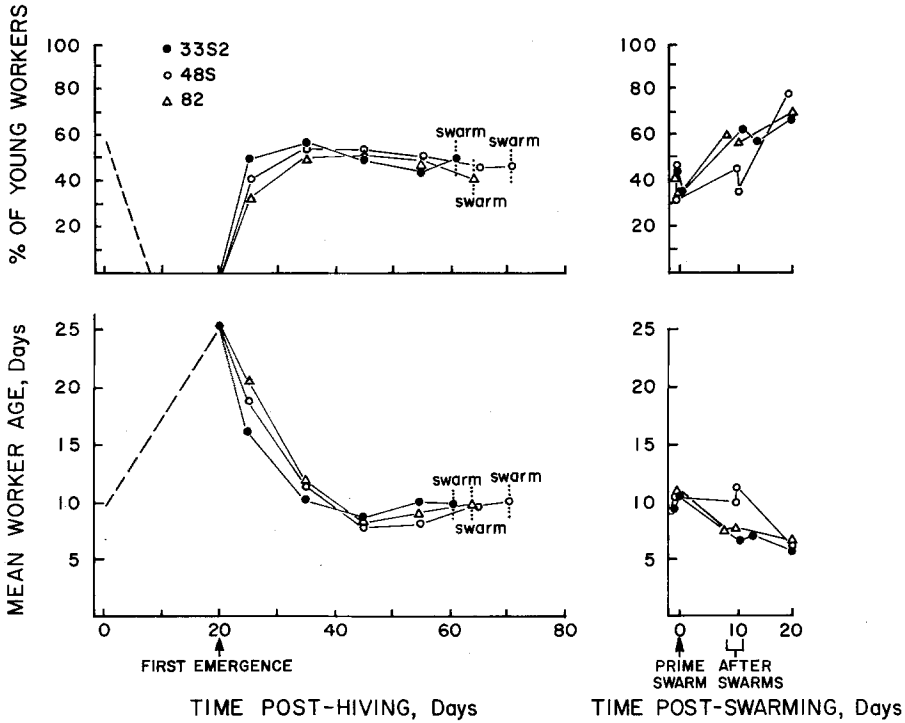


Fig. 6. The mean ages and percentages of young workers eight days old or less in three colonies during the first swarming cycle. Post-swarming data has been separated from the pre-swarming data for clarity. The shifts in mean age and percentages of young workers at the time of swarming and afterswarming reflect determination of these values before and after swarms issued. One afterswarm issued from 48S, and two from 82 and 33S2. Dotted lines are estimates

Discussion

Reproductive rate in eusocial insects can be considered to be the replacement rate of queens (=colonies), and has two components, productivity of new colonies and their survivorship. Wilson (1971) has suggested that intra-colony demographic parameters which increase these two factors would be selected for. In honeybees, selection could act on such attributes as the rate of worker production, patterns of colony growth and survivorship, the age structure of workers, and the timing and composition of swarms (Fig. 7).

In order to increase reproductive output, colony growth patterns should be designed to decrease the intervals between swarming and increase queen survivorship (=swarms and the parent colony). Under these conditions, colonies would be expected to swarm at a small size, with sufficient workers to produce viable prime and afterswarms, as well as to continue the parental colony. This seems to be the case in Africanized bee colonies; swarm intervals are short (50 to 90 days), colonies are small at swarming (20,000 workers, ± 5000), and swarms contain sufficient workers to survive ($12,500 \pm 2500$ for prime swarms;

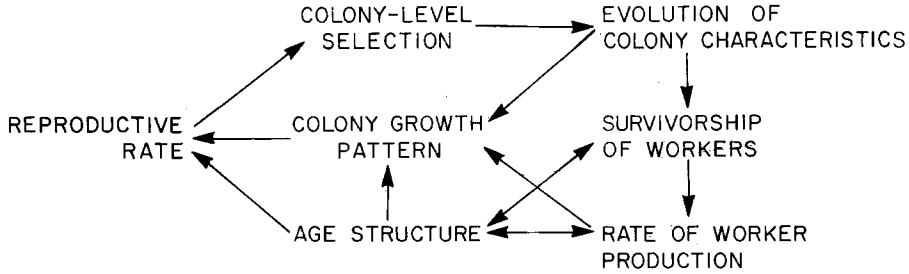


Fig. 7. A model showing how intra-colony demographic parameters could influence reproductive rate in a eusocial insect such as the honeybee (adapted from Wilson, 1971)

6000 \pm 4000 for afterswarms). When all swarming is completed, 7–10,000 workers remain in the parent colony (Fig. 2), which is sufficient for growth to swarming strength in about 70 days under favorable conditions.

The timing and amount of worker emergence after the prime swarm issues are also important for increasing reproductive rate. If the peak of sealed brood (Fig. 3) occurs prior to the prime swarm, many of the young workers will have emerged and issue with the prime swarm, and fewer workers will be available for afterswarming. Conversely, if the number of cells containing sealed brood is high when the prime swarm issues, the number of workers emerging between the prime swarm and the afterswarm(s) will also be high, and more workers will be available for afterswarming. The number of afterswarms is, in fact, correlated with the number of cells containing sealed brood at swarming (Fig. 4). For the parental colony, brood which is unsealed at the time of swarming and subsequently sealed will usually begin emerging 12 days after the prime swarm, at a time when afterswarming is usually completed. These bees (about 4000, Fig. 2) together with a few thousand remaining older bees serve as the nucleus for the parent colony and its new queen.

Survivorship patterns partly determine rates of colony growth, and thus ultimately reproductive rate. High brood mortality during the pre-emergence period (32 percent) limits the potential number of emerging workers during the post-emergence period, and low adult longevity (12 days) of the first new workers results in slow initial growth in the colony population. The colony does not regain the number of workers in the colonizing swarm (12,500 \pm 2500) until day 50 to 55, during the pre-swarming period (Fig. 2). At this time, rapid growth in the worker population corresponds to a shift in survivorship patterns, with increased longevity of adults (18 to 20 days), and low brood mortality (10 percent). Improved survivorship of brood and adults not only acts directly to increase the colony population by resulting in more and longer-lived workers emerging at that time, but probably also acts to further increase the rate of worker production by providing greater numbers of workers to perform brood rearing and foraging tasks.

The age structure of colonies, particularly the availability of young workers, affects reproductive rate through its effect on survivorship of both immatures and newly emerged adults. Two age-related parameters of colonies have been

studied; the mean age of workers and the proportion of young workers, eight days old or less. Young workers are needed to feed unsealed brood and teneral workers (see review by Free, 1965), and increased brood mortality (Smith, 1974) and decreased adult longevity (Haydak, 1937; Maurizio, 1950) would be expected at points in the colony cycle when the proportion of young workers is low and the mean age of all workers is high. For Africanized bees, low survivorship is indeed found for brood and adults during the pre-emergence and post-swarmling periods, when the proportion of young workers is low (zero to 35 percent) and the mean age is high (up to 26 days old). Conversely, survivorship is improved when the proportion of young workers is high (45 to 80 percent) and the mean age low (6 to 10 days old), such as in the pre-swarmling period and when afterswarmling is completed (Fig. 6).

The age structure of colonies may also be important in determining the survivorship of swarms (Winston and Otis, 1978) and the parental colony when swarmling is completed. High numbers of young workers in swarms would increase the number of surviving workers which can forage and feed teneral bees before the first emergence of new workers. Africanized bees swarm at a point in the swarmling cycle when there are many young workers in the hive (Fig. 6), and the probability of young workers issuing with swarms and afterswarms is much higher than for older workers (between 80 and 100 percent for three to eight-day old workers, Winston and Otis, 1978). When afterswarmling is completed, the mean age of workers in the original colony decreases due to continued worker emergence (Fig. 6), and the proportion of young workers in the colony when the new queen begins laying is high (70 to 80%). Although the number of workers is low at this time (less than 10,000), the high brood survivorship (95%) found when the new queen begins laying might be attributable to the favorable age structure in the colony, as well as to the presence of comb (Fig. 1) and some nectar and pollen stores.

The life-history traits of Africanized bee colonies are particularly striking when compared to similar characteristics in temperate races. Colonies in tropical areas, without the restriction of needing large colonies to overwinter, might be expected to have traits resulting in a higher rate of increase than temperate races. Comparison of data from Africanized and temperate races suggests that this is the case. For example, Africanized bees swarm two to four times per year, including the first year a colony is established (present study; Otis, in preparation), while temperate races rarely swarm the first year, and swarm only 0.92 to 0.96 times yearly in subsequent years (Seeley, 1978). Colonies of Africanized bees in South America are smaller (mean comb area of 7900 cm², Taylor et al., in preparation) than those of feral colonies in New York, USA (mean comb area of 23,400 cm², Seeley and Morse, 1976), and likely produce smaller prime swarms and more afterswarms (Otis, in preparation) than temperate races (Burgett and Morse, 1974; Avitable and Kasinkas, 1977), although data exactly comparable to Otis (in preparation) are not available.

Comparison of demographic data for Africanized and temperate races suggests that intra-colony demography of Africanized bees is adapted for their relatively higher rate of increase. Development time for workers of Africanized bees is shorter (20 days from egg to adult, Fletcher, 1977; Kerr et al., 1972)

than for temperate races (21 days,, Jay, 1963), as is the mean longevity of adult workers (rarely greater than 20 days for Africanized bees; rarely less than 25 days for temperate workers, Fukuda and Sekiguchi, 1966 and references cited therein). Also, a much higher proportion of young workers issue with swarms of Africanized bees (Winston and Otis, 1978) than for temperate races (Butler, 1940; Meyer, 1956), which likely results in more rapid initial colony growth and shorter swarm to swarm intervals. However, since intra-colony demographic data for temperate races has not been obtained simultaneously with information on colony dynamics, it is not yet possible to examine the role of demography in determining reproductive rate of temperate honeybee colonies.

The present study has shown how intra-colony demography is important in determining the high reproductive rate characteristic of Africanized honeybees. The production of large numbers of swarms has no doubt been important in their phenomenal rate of spread in South America, and demographic factors of age structure, survivorship, and patterns of colony growth strongly influence the swarming biology of Africanized bee colonies. These data provide insights into the initiation of swarming (to be presented in a future paper, see also Winston, 1978), as well as the necessary framework for an experimentally testable theory concerning the effects of intra-colony demography on life-history characteristics in honeybees. Changes in such traits as colony growth rates, size at initial and subsequent reproductions, swarming intervals, and clutch size (afterswarm production) should be inducible by manipulating age structure of colonies and swarms, rate of worker production, and survivorship of immatures and adults. Such experiments, with comparative data for other races and species of honeybees, might provide a falsifiable theory concerning the effect of colony demography on reproductive rate in honeybees and perhaps other groups of social insects.

Acknowledgements. I would like to thank O.R. Taylor and G.W. Otis for their invaluable encouragement and assistance during all phases of this study, and G. W. Otis for the use of additional data concerning timing of the swarming cycle. I am grateful to G. J. Gamboa and P.F. Kukuk for their detailed reviews of this manuscript, to N. Gary for generously sharing honeybee techniques and loaning bee labels, and to the Centre Spatial Guyanais, Kourou French Guiana, for permission to establish apiaries on their property. This work was supported by USDA grant #12-14-7001-36 (O.R. Taylor, principal investigator) and NSF Improvement of Dissertation Award #22386, and was submitted as part of a dissertation in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Kansas.

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