POPULATION BIOLOGY OF THE AFRICANIZED HONEY BEE

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SUMMARY

The birth rate, death rate, and population growth rate of unmanaged colonies of Africanized honey bees were determined in French Guiana. The study was undertaken to better understand the factors contributing to the rapid range expansion of the Africanized bee in South America. Colony fecundity was high. Colonies produced a mean of 2.82 swarms (range of 1-5) per swarming sequence. Mean swarm-to-swarm intervals were short : 49.9 days (n = 19) for colonies undergoing their first swarming sequence, and 72.4 days (n = 19) for colonies in their second or third swarming sequence. Because generation lengths were generally short, colonies founded early in the reproductive season underwent several swarming sequences per year. Losses of study colonies were also high due to predation (30 % loss of established colonies per year ; high mortality of small swarms immediately after colonization), loss of queens on mating flights (7.8 % per swarming sequence), and absconding (30 % per year). The median survival of established colonies was only approximately 7 months. With the aid of a computer simulation, colony births and deaths were integrated to yield a realized annual population growth rate of 16, a particularly high rate for honey bees. Historically, Africanized honey bees have attained high colony densities only 2-3 years after colonizing new regions. This pattern can now be more readily interpreted.

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RESUMEN

Biología de Poblaciones de la Abeja Africanizada

Se determinó la velocidad de nacimiento, velocidad de muerte y velocidad de crecimiento de colonias no manejadas de abejas africanizadas en Guayana Francesa. Se hizó este estudio para una mejor comprensión de los factores que contribuyen a la rápida expansión del rango de la abeja africanizada en Sudamérica. La fecundidad de la colonia fué alta. Las colonias produjeron un promedio de 2.82 enjambres por secuencia de enjambrazón.

Los intervalos promedio de enjambre a enjambre fueron cortos : 49.9 dias (n = 19) para colonias que experimentaron su primera secuencia de enjambrazón, y 72.4 días (n = 19) para colonias en su segunda o tercera secuencia de enjambrazón. Las colonias fundadas tempranamente en el período reproductivo experimentaron varias secuencias de enjambrazón por año, debido a que los períodos de duración de las generaciones fueron generalmente cortos. Las pérdidas en las colonias de estudio fueron también altas debido a predación (30 % de pérdida en colonias establecidas por año ; alta mortalidad de pequeños enjambres inmediatamente después de la colonización), pérdida de reinas en vuelos nupciales (7.8 % por secuencia de enjambrazón), y evasión (30 % por año). La sobrevivencia media de colonias establecidas fué de aproximadamente sólo 7 meses. Con la ayuda de una simulación en computadora, se integraron nacimiento y muerte de las colonias para producir una velocidad de crecimiento poblacional anual de 16, velocidad particularmente alta para abejas melíferas. Historicamente, las abejas africanizadas han alcanzado altas densidades de colonias sólo después de 2 a 3 años de haber colonizado nuevas regiones. Este patrón, ahora, puede ser más facilmente interpretado.

INTRODUCTION

This paper summarizes research conducted on the population biology of the Africanized honey bee. African honey bees (*Apis mellifera scutellata* Ruttner, 1976) escaped from an apiary near Rio Claro, Brazil, in 1957, and the swarms produced by them and possible hybrids with European honey bee races have colonized most of South America (Kerr, 1967 ; Taylor, 1977), reaching very high densities in some areas. In order to better understand the rapid spread and growth of this feral population, unmanaged feral colonies were studied to document rates of swarming, absconding, mortality, and to determine generation lengths. This information has been used to model growth rates for a feral population in the savannas of coastal French Guiana.

Methods

This study was conducted from February 1976 to June 1977 in the savannas near Kourou, French Guiana, 5°10'N, 52°40'W. Hoock (1971) described the climate and flora of the region. Feral Africanized honey bee colonies were founded by trapping swarms with pressed-pulp swarm-boxes baited inside with a thin coat of beeswax (Taylor and Otis, 1978). These colonies were transferred to 22 litre hives that contained 6 movable top bars. Alternatively, some colonies were initated by placing swarms in 22 litre hives containing top bars fitted with a median strip of foundation that served as a guide for comb building. Otherwise, colonies built all their own comb. After successful establishment, colonies were left unmanaged except for hive inspections. The hives were placed along forest-savanna interfaces, usually in shade. No more than 10 colonies were ever located in an apiary, and each of the 11 apiaries was a minimum of 2 km from the next.

All colonies were inspected every 1-3 weeks for survivals, absconding, and swarming. Detailed swarming histories and swarm-to-swarm intervals were obtained by inspecting hives every day, or occasionally every second day, from the time first eggs were laid in queen cups until all queens had emerged from queen cells or had been destroyed naturally. The condition of each queen cell was recorded during inspections. Each comb was searched twice for queens, and all queens were marked with a numbered, color-coded label (Honig Mungesdorff, Postfach 290292, West Germany). The hive was weighed. When possible, swarms that issued from study colonies were caught, their sizes determined, and they were used to initate new study colonies. If not observed directly, swarms were determined to have issued by the loss of a marked queen and a concurrent reduction in hive weight ; usually there was also an obvious reduction in the worker population of the hive. This method detected all but a few of the smallest swarms (0.1-0.2 kg, 1,000-2,500 bees). After the completion of swarming, the parent colony was checked to determine if the new queen successfully mated and when she initated oviposition. More detailed methods are presented by Otis (1980). The choice of the 22 litre hive design proved to be fortuitous. The mean volume occupied by feral colonies in Peru which had initated queen rearing or had swarmed once was 23.3 litres ($n = 10$; Winston and Taylor, in press). Feral nests measured in French Guiana were comparable in size.

All bees studied were Africanized. Feral honey bees were not present in French Guiana prior to the arrival of Africanized bees in 1974 (Otis and Taylor, 1980). The only colonies of European honey bees had been located in Cayenne, 48 km southeast of Kourou. All 15 of these colonies had become Africanized by the time this study was initiated (determined behaviorally through personal observations and confirmed by morphometric analyses by H. V. Daly). No other managed colonies of honey bees were maintained within 200 km of the study area. Morphometric analyses of workers taken from many study colonies confirmed that the bees were Africanized with no evidence of recent hybridation (H. V. Daly, pers. com. ; Daly and Balling, 1978).

RESULTS

Honey bees reproduce by swarming. In a normal swarming sequence, fertilized eggs are laid in special queen cups. Six to 30 days later, usually after at least one queen cell has been sealed, the queen leaves with a large group of workers from the colony. Approximately eight days after the first queen cell has been sealed, the first virgin queen emerges. She then either destroys the remaining queen cells, mates and initiates ovipositions, or she leaves with a smaller group a workers in what is known as an afterswarm (cast). The after-swarming process can be repeated with new virgin queens several times before one of the last queens to emerge kills the remaining queen brood (in cells), mates, and initiates egg laying.

A non-reproductive swarm is produced when a colony absconds, or abandons its hive. This is also sometimes referred to as a migratory swarm (Chandler, 1976). Absconding differs from reproductive swarming in that the colony produces no new queens and the entire population of workers leaves its nest with the mated queen. Reproductive swarming was common from August 1976 through February 1977. Nearly all colonies swarmed at least once during this period. As swarming frequency declined in March, absconding frequency increased, reaching a maximum in mid-April and declining again in May. A minor period of absconding also occurred in early October. Subsequent to this study, swarming and absconding continued at a lower level from July to December 1977 (P. Kukuk, pers. obs.). In the 39 detailed swarming sequences studied, each colony produced from one (prime swarm only) to five swarms (prime swarm and four afterswarms). The frequency distribution of afterswarm production is given in Table I. Colonies produced a mean of 1.85 afterswarms per swarming cycle. Three colonies (3 % n = 84) failed to produce prime swarms, but produced virgin queens and underwent a normal afterswarming process. On the average, a colony that swarmed produced 0.97 prime swarms and 1.85 afterswarms, as well as continuing to exist itself, thereby yielding a gross total of 3.82 colonies and swarms per swarming sequence.

During the swarming season from August 1976 to March 1977, colonies had rapid growth rates and short generation lengths (Table III). Colonies founded by swarms with 10,000 or more workers in empty hives produced reproductive swarms a mean (harmonic) of 49.9 days later (n = 19). A few swarms reproduced in less than 35 days. Colonies which had already swarmed at least once had a mean prime swarm to prime swarm interval of 72.4 days (n = 19). Part of this latter interval was spent in completing the afterswarming process and in queen mating. Excluding the time involved in afterswarming and mating, the mean interval from the resumption of oviposition until issue

Table I – Numbers of afterswarms produced in 22 liter hives by Africanized honey bee colonies per swarming sequence.

Tabla I – Número de enjambres secundarios producidos por colonias de abejas africanizadas en colmenas de 22 litros por secuencia de enjambrazón.

Number of afterswarms	0	1	2	3	4	
Frequency	5	10	14	6	4	$\Sigma = 39$
Total afterswarms produced	0	10	28	18	16	$\Sigma = 72$
Mean afterswarm production						1.85 ± 0.186

Table II – Mortality of recently colonized swarms of differing sizes resulting from attacks of ants (*Camponotus* sp.).

Tabla II – Mortalidad de enjambres de diferentes tamaños recientemente colonizados resultante de ataques por hormigas (*Camponotus* sp.).

Swarm Size	Probability of death	n
1.00 + kg	0.00	13
0.75 - 0.99 kg	0.20	5
0.50 - 0.74 kg	0.33	3
0.25 - 0.49 kg	0.50	6
0.0 - 0.24 kg	0.66	3

of the next prime swarm was 59.7 days (n = 19). These short generation lengths allowed some colonies to undergo as many a four swarming sequences per year. Smaller swarms (e.g., many afterswarms) required more time to attain the conditions that induce swarming.

In conjunction with a high colony birth rate, colonies also had a high death rate. The period of greatest risk for a colony was during and just after swarming, when the worker population was low and the queen was mating. The sources and magnitudes of mortality are enumerated below. At the end of a swarming sequence, the remaining virgin queen leaves the colony to mate. During mating flights, queens are vulnerable to predation by birds (e.g., tyrant flycatchers), dragonflies, and other bee predators. In this study, 7 of 90 (7.8 %) queens disappeared at the time of mating. Virgin queens in afterswarms may sustain a similar rate of mortality leading to the «death» of their swarms. After having issued from the parent colony, a swarm scouts for and colonizes a new domicile. Many swarms undoubtedly die through starvation or predation by ants before successfully establishing new nests, but quantifying this source of mortality is difficult. Mortality occurring between swarm issue and colonization could not be estimated. Swarm mortality from ant attacks (*Camponotus* sp.) immediately after colonization was quite high and related to swarm size (Table II). For example, no swarm weighing more than 1.25 kg died at this time, but 50 % of colonies between 0.25 and 0.50 kg were killed.

Table III – Frequency distributions of generation lengths (in days) for Africanized honey bee colonies during the swarming season. A, from colonization to swarming intervals for newly founded colonies ; B, prime swarm to prime swarm intervals for established colonies in their second or third swarming sequence ; C, oviposition to prime swarm intervals for colonies in their second or third swarming sequence. X = harmonic mean, n = number of colonies observed.

Tabla III – Distribución de frecuencias de duración (en días) de generaciones para colonias de abejas africanizadas durante el período de enjambrazón. A, intervalos desde colonización hasta enjambrazón por colonias recien fundadas ; B, intervalos desde enjambre primario hasta enjambre primario por colonias establecidas durante la 2da o 3ra secuencia de enjambrazón ; C, intervalos desde oviposición hasta enjambre primario por colonias durante la 2da o 3ra secuencia de enjambrazón. X = medio armónico, n = número de colonias observadas.

Midpoint of Interval (days)	A	B	C
30	1	0	0
35	1	0	0
40	4	0	1
45	2	0	1
50	1	0	1
55	2	2	3
60	4	3	6
65	1	1	3
70	1	3	1
75	0	2	1
80	0	2	1
85	0	1	0
90	0	1	0
95	1	3	1
100	0	1	0
105	1	0	0
$\bar{X}$	49.9	72.4	59.7
n	19	19	19

A few established colonies were attacked by army ants or animals such as armadillos and tamanduas. Such colonies either died or were able to abscond, after which they again had to attempt to establish a new nest. The probability of such attacks on established colonies was 0.001 per day, or 30 per cent loss per year. Finally, 31 % of the colonies (n = 65) absconded between August 1976 and August 1977. During the major absconding period from March to May, absconding appeared to be a response to poor food resource conditions, but was also influenced by the recency of swarming (Winston et al., 1979). Three colonies which received direct sunlight absconded in early October, apparently as a result of colony overheating. The majority of colonies that absconded had the additional problem of having to establish a new nest during an unfavorable season.

A survivorship curve was constructed for established colonies. The periods survived by each colony, computed in half months, were determined from the time of successful colony establishment until the time of colony loss due to death or absconding. The proportion of colonies surviving in each age class after colony establishment was then determined and plotted (Fig. 1). Because of the duration of the study (1 1/2 years), longer colony survivorship are slightly under-represented ; the dotted line estimates the survivorship curve adjusted for this factor. Colonies generally were short-lived. After 7 months, only half the established colonies were extant. This survivorship curve is for established colonies only and does not include mortality that occurs in the nest-founding period.

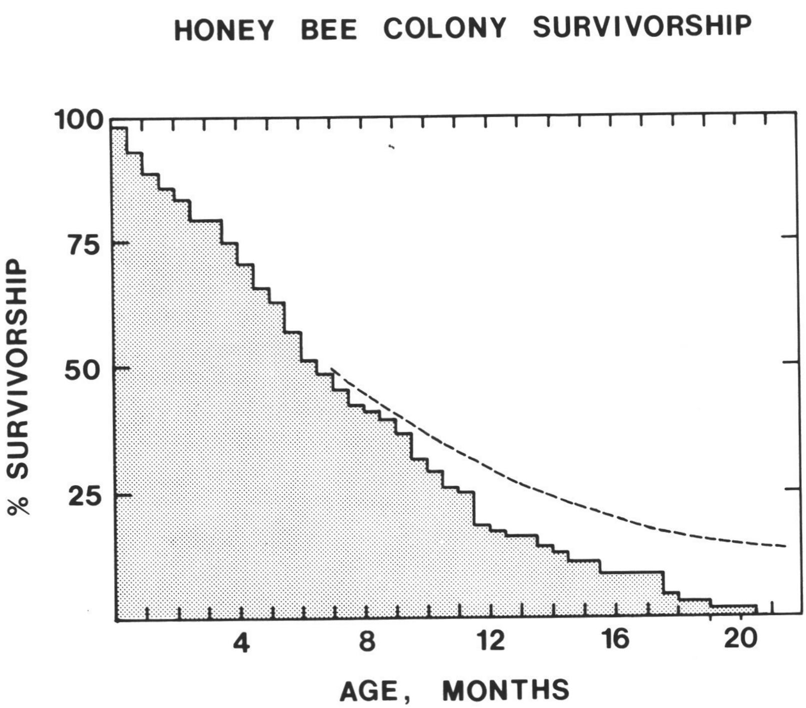

Fig. 1 – Survivorship curve for established colonies of Africanized honey bees. Losses were due to predation, absconding, and queen loss. Broken line represents an estimated survivorship curve based on the assumption that survivorship of longer lived colonies was underestimated during the study.

Fig. 1 – Curva de sobrevivencia de colonias establecidas de abejas africanizadas. Las pérdidas se debieron a predación, evasión y pérdida de la reina. La línea punteada representa una curva estimada de sobrevivencia basada en la suposición que la sobrevivencia de colonias de mayor longevidad fué subestimada durante el estudio.

It is evident that Africanized bees have both high reproductive rates and high mortality. In order to estimate the population growth rate, it was necessary to integrate births and deaths. Standard life table analyses were not applicable. It was not possible to accurately age many colonies, and swarming and absconding were not age-related events ; thus it was impossible to construct a current (time-specific) life table. It was also not possible to follow a cohort of colonies and construct an age-specific life table. Population projection matrix approaches could not be used because probabilities of some colony events (e.g. swarming) varied over time, and reproduction had neither an annual or constant-generation basis. Because of these difficulties, a unique computer simulation was developed. The simulation began with a single, established Africanized bee colony. That colony and all swarms derived from it were followed over a 318 day period analagous to the actual study interval for which sufficient data were available. The outcomes of all colony events and the time intervals between events were selected at random from the appropriate data sets generated in the field studies. The simulation outcome was the number of colonies alive at the completion of the simulation. Complete details of the simulation are given by Otis (1980).

The nature of the simulation was such that a nearly infinite number of patterns were generated. For example, the original colony could die before producing swarms, yielding a net number of colonies of 0. Alternatively, the initial colony could swarm early in the simulation, ultimately producing many surviving daughter and granddaughter colonies by the end of the simulation. A frequency distribution of the outcomes from 1,000 independent simulations is given in Fig. 2. A few simulations yielded more than 50 colonies, but most resulted in few surviving offspring. The mean outcome from these simulations was 15.17 (S.E. = 0.358) ; meaning that on the average, a colony started at the beginning of the study period would give rise to over 15 new colonies in 318 days. It was estimated that a population of 1,000 feral colonies would increase to 16,000 colonies during one year. This is an extremely high rate of increase.

In addition, the simulation was programmed to return the number of colonies alive at the beginning of each month in each simulation. The mean of these monthly values were plotted (Fig. 3). The resulting pattern parallels the general swarming and absconding pattern already described. The simulated population grew steadily throughout the swarming season (August through February) although the minor absconding period in October caused the slight reduction in growth. A peak of about 17 surviving colonies per colony was reached just prior to the major absconding season, after which the simulated population declined about 15 %. The gradual resumption of swarming in June caused the population to increase to the value of 15.2 colonies at the end of the study period.

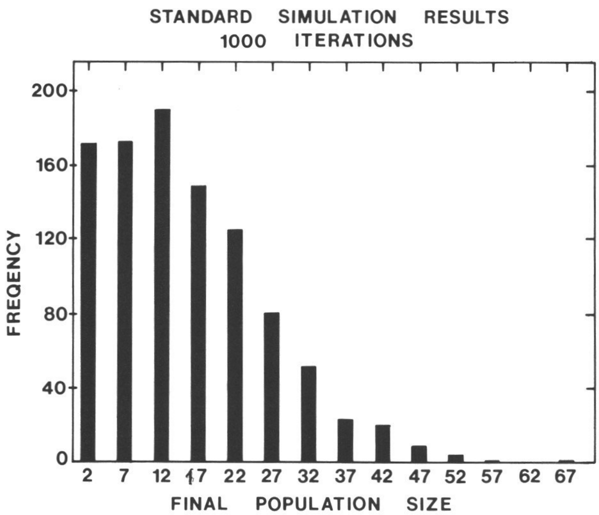

Fig. 2 – Frequency distribution of the colony population growth rates computed in 1,000 independent iterations of the simulation. The simulation was developed to analyze the population growth rate and pattern of feral Africanized bees.

Fig. 2 – Distribución de frecuencias de la velocidad de crecimiento de la pobalción de la colonia computada en 1,000 repeticiones independientes de la simulación. La simulación se desarrolló para analizar la velocidad y patrón de crecimiento de la población de abejas africanizadas silvestres.

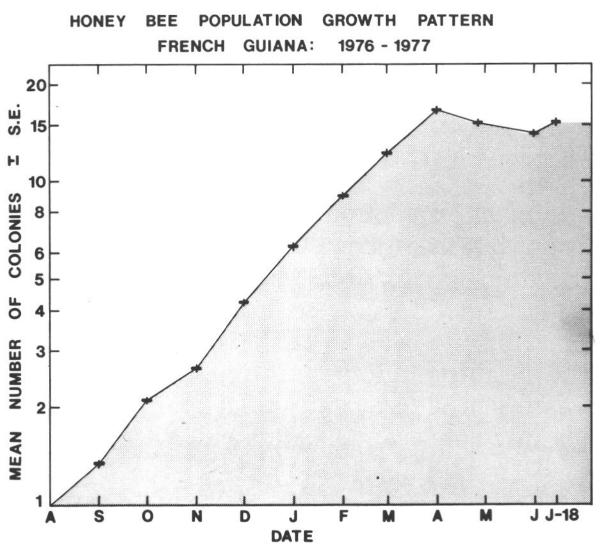

Fig. 3 – The simulated pattern of growth of the Africanized honey bee population for the 318 days interval of intensive study.

Fig. 3 – Patrón simulado de crecimiento de la población de abejas Africanizadas durante 318 días de estudio intenso.

DISCUSSION

The Africanized honey bee population in French Guiana was characterized by rapid intra-colony growth rates (Winston, 1979), small colony size, frequent swarming, production of numerous afterswarms, reproductive swarming during most of the year, absconding during adverse conditions, low colony survivorship, and an annual growth rate of 16 colonies per colony. The life history attributes of European races of honey bees in temperate regions (New York and Kansas, U.S.A.) contrast with this. Feral colonies of European bees are considerably larger ; mean comb area was 23,400 cm^2 (Seeley and Morse, 1976) vs. 8000 cm^2 for feral Africanized colonies in Peru (Winston and Taylor, 1980). They undergo one, or occasionally two, swarming sequences per year (Seeley, 1978 ; Winston, 1980). Slightly fewer afterswarms are produced (mean of 1.5 ; Winston, 1980), and few of these survive their first winter (Otis, unpublished data). Mean colony longevity was quite long, 2.1 years, and considerably longer, 5.6 years, for colonies that had successfully survived the first winter. The net reproductive rate was approximately equal to 1.0 (Seeley, 1978). The major selective force shaping these traits is the prolonged cold of winter. Relatively large colony size and good honey storage capabilities are selected for. Small swarms that cannot store much honey before winter have a low probability of survival (Otis, unpublished data).

The life history «tactics» of Africanized bees may be largely a response to predation, the major mortality factor observed in this study. In addition, colonies were free of the limitations imposed by a cold winter and did not require large stores of honey to survive. Under these conditions, frequent swarming at small colony size and the production of large numbers of swarms is a more successful strategy. Absconding, a rare behavior among European bees (Martin, 1963), then becomes a viable option during periods of resource scarcity.

In general, a consistent pattern of population increase has been observed for Africanized bees over most of South America. Initially, small numbers of swarms colonize regions, but within two or three years the feral colony density becomes very high. It has not been possible to understand this population phenomenon on the basis of our knowledge of the swarming process among European bees. Now, with the information concerning the frequency of swarming, numbers of afterswarms produced, and the annual population growth rate for Africanized bees in French Guiana, this growth process is more readily interpreted.

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