Flight Times of Africanized and European Honey Bee Drones (Hymenoptera: Apidae)

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ABSTRACT Flight activities of Africanized honey bee (*Apis mellifera* L.) drones were compared with those of two color morphs of European drones in Venezuela. European drones departed from colonies 19 ± 2 ($\bar{x}$ ± SEM) min earlier, and flight times were more variable than those of Africanized drones. Mean flight time differences decreased as the drones aged and were similar whether drones were flying from Africanized or European colonies. Overlap of their flight distributions was >70%, which suggests that interbreeding of the two types of bees will be substantial under most natural conditions. Black and yellow European drones flew at similar times with similar variances, which precludes the idea that flight time differences are due to body color.

KEY WORDS Insecta, *Apis mellifera* drones, Africanized bees, mating

AFRICAN HONEY BEE QUEENS, *Apis mellifera scutellata* (Lepeletier), were imported to Brazil in 1956 with the objective of developing a strain of bees better adapted to Brazilian beekeeping conditions than were previously imported European bees (Kerr 1957, Michener 1975). Descendants from these African bees have hybridized to varying degrees with European subspecies (primarily *A. m. iberica* (Goetze), *A. m. mellifera* L., and *A. m. ligustica* (Spinola)) to form an "Africanized" type. These Africanized bees have spread over much of South America, Central America, and Mexico and will probably spread into southern Texas in 1990 (Taylor 1988). The rapid change of European populations into Africanized populations could come from a mating advantage of Africanized bees. Such an advantage could be numerical in origin (i.e., there are more feral Africanized drones than managed and feral European drones), it could be related to behavioral differences between Africanized and European queens and drones, or it could be both numerical and behavioral.

In the polyandrous honey bee, mating is a complex process wherein queens and drones mate while in flight up to several kilometers from their colonies (Koeniger 1986). A queen takes up to three 5- to 30-min mating flights (Oertel 1940, Woyke 1960), obtaining a lifetime supply of spermatozoa from 7 to 17 drones (Taber & Wendel 1958, Woyke 1960, Kerr et al. 1962, Adams et al. 1977). The large volume of possible mating territory makes it clearly beneficial for reproductives to coordinate mating flights in space and time to reduce risks of predation and disorientation loss. For instance, mating flights normally occur only during a 3-h period in the afternoon (Oertel 1940, Koeniger 1986). Taylor (1985) suggested that a temporal separation of mating flights of the two bee types could play a role in the remarkable success of Africanized bees.

The work presented here provides detailed information on distributions of flight times of Africanized drones and two subspecies of European drones. Biological implications of these distributions, especially as they relate to the success of Africanized bees, are considered.

Materials and Methods

An apiary with 10 colonies each of Africanized and European honey bees was established near Sarare, Lara, Venezuela. Africanized colonies were derived from local Africanized swarms. European colonies were headed by queens imported from the United States. Colonies predominately from two subspecies, Carniolan bees, *Apis mellifera carnica* (Pollman), and Italian bees, *A. m. ligustica* (Spinola), were used to produce European drones. Body color of the Carniolan drones was mostly black (i.e., all gastral tergites were ≥90% black). Body color of the Italian drones was mostly yellow (i.e., gastral tergites 1–4 were ≥90% yellow). Africanized drones used in the experiment were not visibly distinguishable from the black European drones.

Approximately 2 wk before the initial observations, and again shortly after the observations were begun, frames with sealed cells of immature drones were collected from several Africanized and European colonies. Drones were held until eclosion in an incubator (35°C, 50% RH). Within 24 h after eclosion, each drone was marked on the thorax with two dots of enamel paint to denote eclosion date

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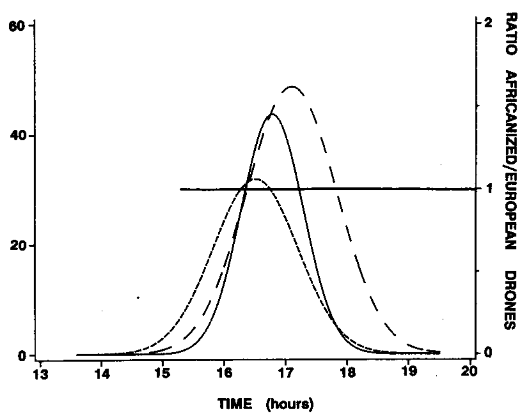

Fig. 1. Estimated percentage of mature (age >10 d) Africanized (——) and European (- - -) drones flying of total drone flight for each type, and ratio (% Africanized/ % European, — — —) of drones flying at any time throughout the afternoon. Equal numbers of Africanized and European drones are assumed. The portion of the ratio above A/E = 1 represents times during the day when the relative number of Africanized drones is greater than that of the Europeans.

and drone type (i.e., black European, yellow European, or Africanized). Drones of each type then were introduced into both Africanized and European test colonies. Drones were introduced into 10 Africanized and 10 European colonies, first for 5 consecutive d and again a week later for 6 consecutive d. Approximately 50 black European drones, 50 yellow European drones, and 100 Africanized drones of various ages were introduced into each colony during each of the two introduction periods. Weekly colony inspections were made to count and categorize all drones according to type and age. The number of drones in individual colonies varied throughout the experiment depending upon mortality and drifting. Colonies that did not have representatives from all three drone types were not observed.

Observations began when the first drones introduced into the colonies were 8 d old. Each colony was observed by one person between 1300 and 1800 hours. The time to the nearest minute when a drone left a colony was recorded along with its color markings. Four or five colonies were observed each day; nine sets of daily observations (a total of 4,029 drone departures) were made over a 20-d period. The experiment was conducted during the dry season in February and March.

Least squares analysis was used to compare drone flight times. A randomized complete block design with a factorial treatment arrangement was used; colony type, drone type, and age groups of drones were treatment groups; examination day was a blocking factor. Because drones younger than 10 d are often not sexually mature (Harbo 1985), drones were divided into "immature" (age ≤10 d) and "mature" (age >10 d) age groups. Data for individual drones were pooled within drone type and age group each day for each colony.

Maximum likelihood estimates (Milliken & Johnson 1984) of flight time variance for each drone type were obtained from the mixed model:

$$Y_{ijkl} = \mu + \alpha_i + B_j + \alpha B_{ij} + C_{k(ij)} + \epsilon_{ijkl}$$

where α_i is the i^{th} colony type, B_j is the j^{th} examination day, αB_{ij} is the interaction of colony type and examination day, and $C_{k(ij)}$ is the k^{th} colony for the i^{th} colony type and j^{th} examination day. Between $[C_{k(ij)}N(O, \sigma^2 b)]$ and within $[\epsilon_{ijkl}N(O, \sigma^2 w)]$ variances were added for the total variance.

Results

European drones flew 19 ± 2 min ($\bar{x}$ ± SEM) earlier than Africanized drones ($F = 109.34$; df = 1, 84; $P < 0.0001$) (Table 1). The departure time differences were similar whether drones were flying from Africanized colonies or European colonies ($F = 1.21$; df = 1, 84; $P > 0.20$). Flight time differences between the two drone types decreased significantly as the drones aged ($F = 13.93$; df = 1, 84; $P < 0.0001$). Immature European drones flew 28 ± 3 min earlier than immature Africanized drones, whereas mature European drones flew 11 ± 3 min earlier than mature Africanized drones. Black and yellow European drones within each age group departed colonies at similar times: immature black European 1603 hours ± 3 min, immature yellow European 1606 hours ± 3 min; mature black European 1619 hours ± 3 min, mature yellow European 1618 hours ± 4 min.

Departure time variances of black and yellow European drones were similar within each age group (Table 1). However, departure times of the two European drone types were more variable than those of the Africanized drones for both immature

Table 1. Mean departure times for Africanized and European drones by age group, and maximum likelihood estimates of variances and 95% CL for departure times of "immature" (age ≤10 d) and "mature" (age >10 d) Africanized, black European, and yellow European drones

Age group	$\bar{x}$ ± SEM, hours ± min		Variance (min²) ± 95% CL		
	Africanized (*n*)	European (*n*)	Drone type	Immature	Mature
Immature	1633 ± 67 (1,185)	1605 ± 67 (1,117)	Africanized	836 ± 70	717 ± 71
Mature	1630 ± 58 (1,199)	1619 ± 57 (528)	Black European	1,472 ± 160	1,119 ± 192
Overall	1631 ± 61 (2,384)	1612 ± 60 (1,645)	Yellow European	1,664 ± 209	1,060 ± 218

and mature groups. Variability in flight times appears to decrease as drones mature (Table 1).

The mean and variance differences result in distinctive distributions of flight times for mature Africanized and European drones (Fig. 1). This results in a greater percentage of Africanized drones flying than European drones between 1620 and 1750 hours. Otherwise, when drones are flying, there is a greater percentage of European drones.

Discussion

The tendency for Africanized drones to fly later with less variability than European drones could result in a slight tendency for drones to mate with queens of their own type. Such positive assortative mating of the two subspecies was found by Kerr & Bueno (1970) in Brazil (E × E, 65%; A × A, 58%) and by Taylor et al. (in press) in Venezuela (E × E, 58%; A × A, 60%). The importance of this positive assortative mating, however, to the success of Africanized bees in South and Central America and Mexico is ambiguous. In the first instance the mating advantage slightly favors European bees, and in the second it slightly favors Africanized bees.

In either case, these advantages are probably insignificant compared with the numerical advantages resulting from higher swarm and drone production rates. Studies in French Guyana indicate that, if resources are available, Africanized bees swarm 6 to 12 times annually (Winston et al. 1981, Otis 1982). In contrast, European colonies swarm 1 to 3 times in New York (Seeley 1978) and fewer times in French Guyana (Winston et al. 1981). This represents a minimum 2- to 11-fold reproductive advantage for Africanized bees in at least one part of South America. Additionally, Africanized colonies in one apiary in Venezuela produced nine times more drones than a similar number of European colonies (Rinderer et al. 1987). Other research in Venezuela indicates that these differences are not always this high but are commonly in the 2- to 4-fold range (unpublished data).

Gene flow between Africanized and European populations will occur as long as there is not complete temporal isolation. Complete isolation is unlikely under any natural conditions because flight times of the two drone types overlap considerably (>70% when drones are 11 d or older, Fig. 1). As a result, flight time differences will decrease and eventually disappear as the two types of bees interbreed and become increasingly homogeneous.

Another factor to consider is weather. Changing weather conditions will alter both time and variability of drone flight. Drones whose flight has been delayed by an afternoon thunderstorm, for instance, depart colonies in large numbers when the sky clears (Taber 1964). Such weather was not a factor in this study because weather conditions were consistently favorable for flight. Yet, flight time differences between Africanized and European drones will be affected during seasons or in regions where weather is more variable.

Departure differences were the same whether the two types of drones were in Africanized colonies or European colonies. This suggests that flight time differences were due to the drones themselves rather than the influence of the colony. Perhaps Africanized and European drones respond differently to environmental cues, colony cues, or both. Thermodynamic difference due to body color was one possibility. This, however, does not appear to be important because black and yellow European drones flew at similar times with similar variances.

Flight time differences between Africanized and European drones appear to contribute little to the overwhelming success of the Africanized bee. Consequently, efforts to reduce Africanized bee influence should focus on activities to reduce swarm and feral colony numbers and methods to control the genetics of managed bees (e.g., queen replacement and enhanced drone production).

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