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Social reproductive parasitism by Africanized honey bees

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INTRODUCTION

Africanized honey bees (*Apis mellifera scutellata* hybridized with various European honey-bee subspecies) have been colonizing South and Central America for 31 years. Social reproductive parasitism has probably contributed to the success of these bees, and particularly to the general displacement of previously existing honey-bee populations of European origin.

Parasitism is widely known among the Apoidea. It ranges from cleptobiosis (food robbing) to cleptoparasitism (typically involving solitary bee species) to true social parasitism, wherein a reproductive female usurps the position of the queen of a parastized host colony (Michener 1974, Wilson 1971). Social parasitism can be facultative or obligate, temporary or permanent, intraspecific or interspecific (Wilson 1971). Both queens and drones of Africanized honey bees have been observed to parasitize conspecific colonies. Queens engage in temporary facultative parasitism, a phenomenon first described by Wheeler (1904) for ants. A queen which is normally free-living invades a conspecific nest; the parasitism is temporary in that the usurped nest is eventually inhabited only by offspring of the parasite. Such parasitism is regarded evolutionarily as the least specialized form of social parasitism (Taylor 1939). Drone (male) parasitism has not been reported for other social insects, and does not fit into Taylor's (1939) evolutionary scheme. The behavior is best described as permanent facultative parasitism, since the host queen continues to produce offspring while the colony supports the drone parasites.

PARASITISM BY QUEENS

Female social reproductive parasitism has long been an activity associated with Africanized bees, but the phenomenon has not been studied on a rigorous experimental basis. Anecdotal reports (Michener 1972, 1975) typically cite a small cluster of a few to several hundred worker bees, including a mated Africanized queen, landing near the entrance of a hive. Workers from the swarm enter the hive, and may eventually kill the resident queen, permitting the parasitizing queen to assume the egg-laying role in the nest. Thus, the usurped colony becomes fully Africanized (i.e., all the bees are Africanized, and no further hybridization with European bees has occurred) after only about nine weeks. It must be noted that Africanized colonies are also sometimes parasitized, and that European queens have been observed to parasitize (unpublished observations).

Reports suggest that the frequency of this phenomenon is highly variable. Early surveys (Michener 1972) indicate widespread parasitism in some regions of Brasil but little parasitism in other areas. Gonçalves *et al.* (1974) reported that they had never observed the phenomenon in 18 years of work in Brasil. Taylor (1985) points out that colony invasions are often subtle and indistinguishable from hybridization. Other experience in Venezuela has been that the frequency of queen parasitism increases when colonies are queenless or have failing queens, are small, or have been stressed by manipulation. In one small experiment (unpublished observations), queenless colonies of either Africanized or European bees usually accepted both Africanized and European queens when the queens, in small artificial swarms, were placed at the colony entrances. Queenright colonies never accepted foreign queens. European colonies whose queens were confined in cages accepted queens of either type, but similarly prepared Africanized colonies generally did not accept queens.

The sources of parasitizing queens are unknown. It is possible that the small clusters of invading bees are absconding swarms or afterswarms. An observation of parasitism in Baton Rouge in the autumn suggests an absconding swarm as the source. In Africa, migrating swarms of *A. m. scutellata* amalgamate and then cast off extra queens with small groups of workers (Kigitiira 1984); if similar swarm mechanics occur in the neotropics, cast queens may also parasitize colonies.

PARASITISM BY DRONES

Parasitism by Africanized drones has been the subject of much greater experimental attention than has queen parasitism (Rinderer *et al.* 1985, 1987). Originally, inspections of an experimental apiary of genetically marked European colonies in Venezuela revealed that the majority of drones in the colonies were Africanized. This observation led to a series of experiments to study the causes and magnitude of this parasitism and its effects on host-colony drone production.

Experiment 1

In the first experiment, an apiary in Venezuela was used with 10 Africanized and 10 European colonies standardized to fill two-story 10-frame Langstroth hives. Distinctive orientation marks painted on hive fronts and the placement of the colonies in a serpentine row near a wood lot were used to reduce the movement of drones between colonies arising from errors in orientation known to occur infrequently with European drones (Butler 1939, Livenetz 1951). In addition, the Africanized and European colonies were alternated along the row, with Africanized colonies facing north and European colonies facing south, to further reduce orientation errors (Jay 1965, 1966, 1968).

Africanized and European drones were reared in these and other colonies from eggs obtained from queens usually caged on drone comb. All adult drones were emerged in an incubator and, within 2 days, were marked with paint and introduced into experimental colonies. The paint markes indicated age, bee type, and colony into which the drones were introduced (home colony). Each colony received approximately 100 drones of each bee type from several different sources over a 5-day period. Two weeks later we introduced a similarly raised and marked group of approximately 200 drones to each colony. At 2- to 3-day intervals after the first drones were introduced, each colony was thoroughly inspected, and all drones seen were recorded by paint-mark classification. When drones had moved to different colonies, their 'host colony' was also recorded. These colony inspections were made only in the morning.

Chi-square analysis was used to determine equality of responses of the drones according to drone type and colony effects. All χ^2 values are calculated from numbers collected when the adult age of drones was 12 days. The same drones were seen repeatedly throughout the experiment, which violates the additivity assumptions necessary to calculate sums of χ^2s for drones of different age groups and χ^2s for sums of drones from all age groups. Day 12 was chosen because it is the first day in the experiment after which the drones were all old enough to fly. The χ^2 values calculated for older drones are, in all cases, consistent with the values and conclusions presented.

Africanized drones established in Africanized colonies migrated to European colonies in large and vastly disproportionate numbers when compared to drones in any other category of drone type, home colony, and host colony (Fig. 1). Three factors contributed to the migration of these Africanized drones. First, European colonies hosted the large majority of those drones that left their home colony (95% by day 21) (Fig. 2). Second, a greater proportion of drones placed in Africanized home colonies migrated (Fig. 3). Finally, a greater proportion of Africanized drones migrated (Fig. 4).

Experiment 2

In the second experiment the effects of the direction that colony entrances faced were estimated. Half the Africanized colonies and half the European colonies, selected randomly, were turned at intervals during the course of 10 days so that the direction of their entrances was reversed. One additional group of drones was reared, paint-marked, and introduced into the 20 colonies. Again, each colony received approximately 100 Africanized and 100 European drones from several different sources. These colonies were inspected as before.

The effects of the direction of colony entrances were minimal. Nearly equal proportions of drones migrated from colonies with north-facing and south-facing entrances (χ^2=1.6; df=1; p=*ns*) and nearly equal proportions of drones from colonies facing these two directions migrated to Africanized and European colonies (χ^2=2.15; df=1; p=*ns*). A larger proportion of drones in Experiment 2 migrated by day 12 (Exp. 1, 33.4%; Exp. 2, 40.6%; χ^2=9.15; df=1; $p < 0.001$) probably because all but two colonies had at least one adjacent colony facing in the same direction.

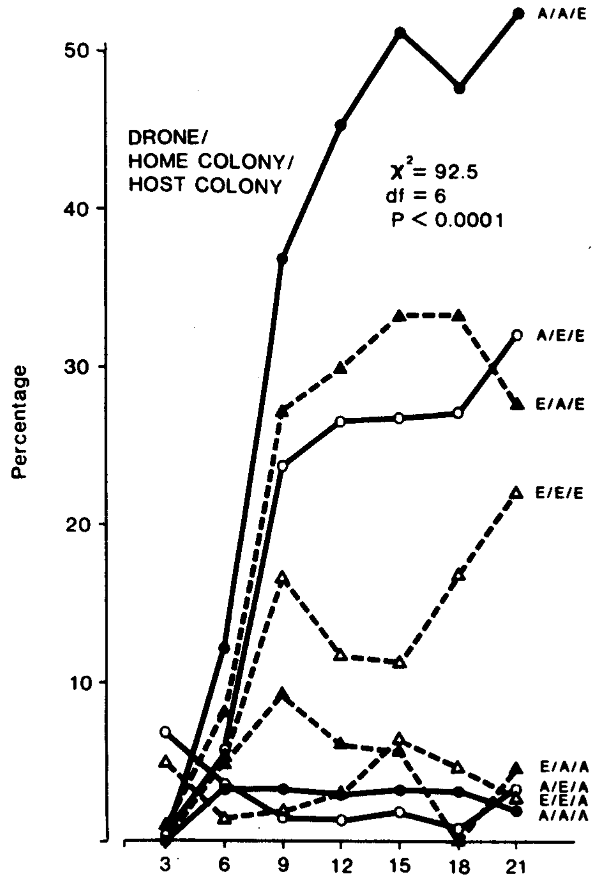

Fig. 1 — The migration of adult drones (ages 3 to 21 days) among European and Africanized colonies in Experiment 1. The percentages of drones in four categories of drone type and home colony, that migrated to other colonies (host colonies) of both types. A, Africanized; E, European; categories represent drone/home colony/host colony.

The major effects of the bee type of colony seen in Experiment 1 were seen also in Experiment 2. The large majority of those drones that left their home colony entered European colonies ($\chi^2=80.1$; df=1; $p<0.0001$), and a greater proportion of drones originally placed in Africanized colonies migrated ($\chi^2=60.7$; df=1; $p=0.001$). In Experiment 2, similar proportions of Africanized and European drones migrated ($\chi^2=0.21$, df=1; $p=ns$).

Experiment 3

The simple movement of drones between colonies is relatively unimportant unless their presence or absence influences the reproductive potential of the colonies. For Experiment 3, we prepared an apiary of European bees in Baton Rouge, Louisiana, in order to estimate these possible influences. This apiary contained large colonies (50–60 000 bees) with laying queens, no immature drones, and three frames of empty

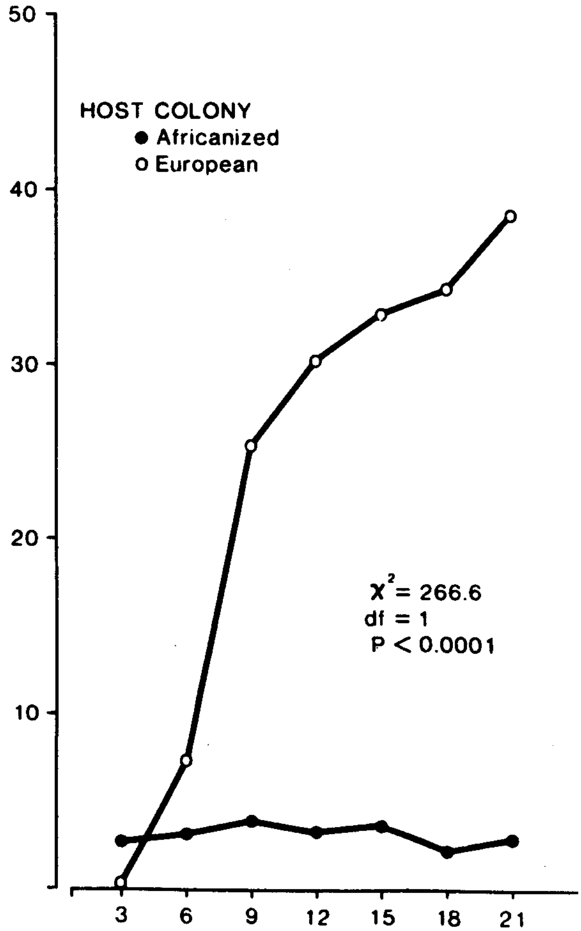

Fig. 2—The percentages of all drones that migrated to European and Africanized host colonies during Experiment 1.

drone comb. Adult drones were reared in other colonies and added to experimental colonies when they were 1 to 6 days of age in groups of 0, 500, 1000 or 2000. These four treatments were used with four, seven, seven, and eight colonies, respectively. Hive entrances were screened to confine drones to the hives but permit normal worker-bee activity. On the 14th day after the apiary was prepared, the number of immature drones being reared by each colony was counted.

A statistically significant inverse linear relationship ($b=-0.648\pm0.287$) between the number of drones reared by the colonies and the number of drones added to them was found (Fig. 5). The estimated slope implies that an adult drone in a colony has a depressing value of about −0.65 drones on the regulatory system which governs the production of additional drones. It also suggests that the loss of an adult drone stimulates the additional production of 0.65 drones. The migration of a single drone results in a numerical reproductive advantage of about 1.3 drones for the parent colony when both factors are considered.

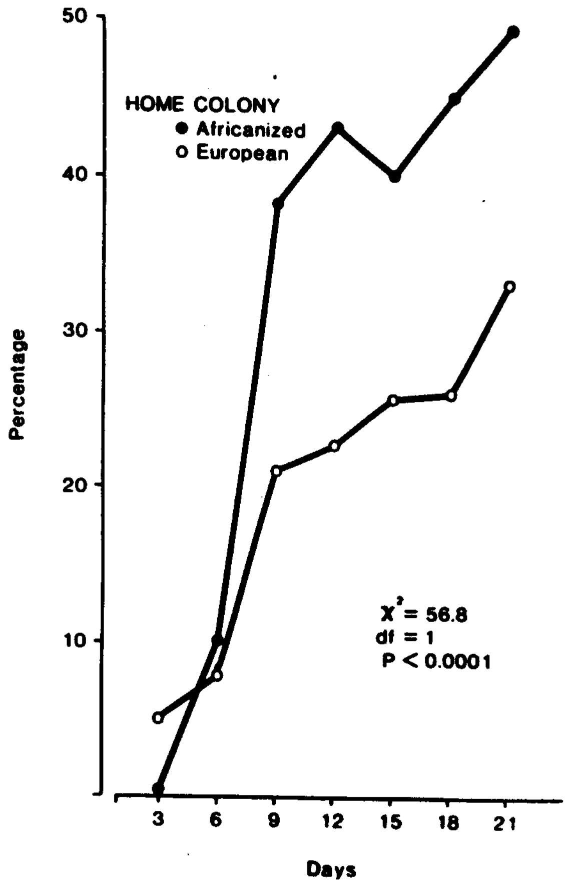

Fig. 3 — The percentages of drones in Africanized and European colonies that migrated during Experiment 1.

PARASITISM AND THE AFRICANIZATION PROCESS

Social reproductive parasitism can contribute to the Africanization process in several ways. Complete Africanization soon occurs when an Africanized queen usurps a European colony. An invaded colony may then contribute to further Africanization through swarms, drones, and additional queens. Recently parasitized colonies may unknowingly be transported to previously uninfested areas; frequent colony inspections and marked European queens are required to prevent such occurrences. Africanized queens may be able to overwinter in European colonies in regions with harsh winters, and subsequently contribute to wider Africanization during the spring and summer. Thorough investigations are needed to determine the frequency and importance of queen parasitism in the Africanization process. If parasitism is contingent upon identifiable environmental conditions, knowledge of those conditions can be used in regulatory activities against Africanized bees.

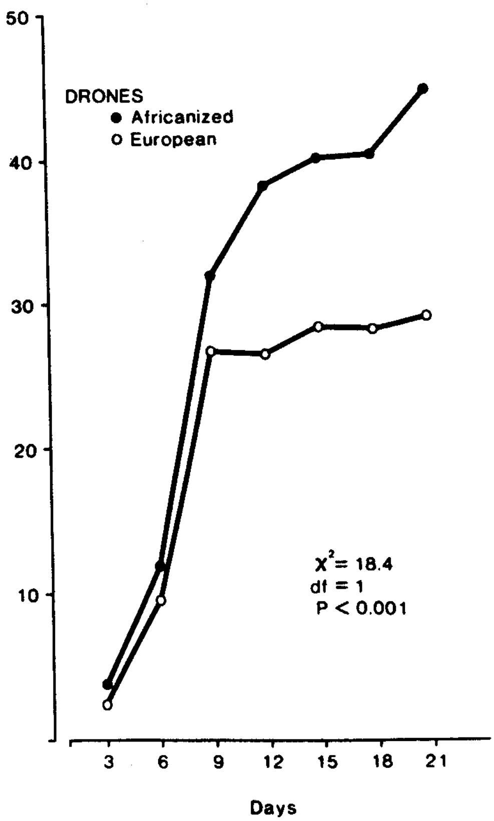

Fig. 4 — The percentages of Africanized and European drones that migrated during Experiment 1. Numbers of drones in each category of drone type and home colony are between 229 and 361.

Social parasitism by drones is also important. Since Africanized colonies export half or more of their Africanized drones to European colonies and accept almost no foreign drones, Africanized colonies can minimally contribute a disproportionately large share of a mixed drone population. In one experiment the drone population was 91% Africanized in an apiary containing equal numbers of colonies of each bee type (Rinderer *et al.* in press). This would enhance the positive assortative mating tendencies (Kerr & Bueno 1970) of Africanized bees and impair those of European bees. Over several generations this condition alone would result in complete Africanization. Maximally, a few Africanized colonies could produce all or nearly all of the drones in a mating area if they produce large numbers of drones earlier in the season, as certain of our observations suggest. In this case, complete Africanization would result in two to three generations. Where populations of drones rest on this continuum as a result of reproductive parasitism probably varies as Africanization proceeds. Throughout the Africanization process, however, reproductive parasitism by drones probably results in a strong mating advantage for Africanized colonies.

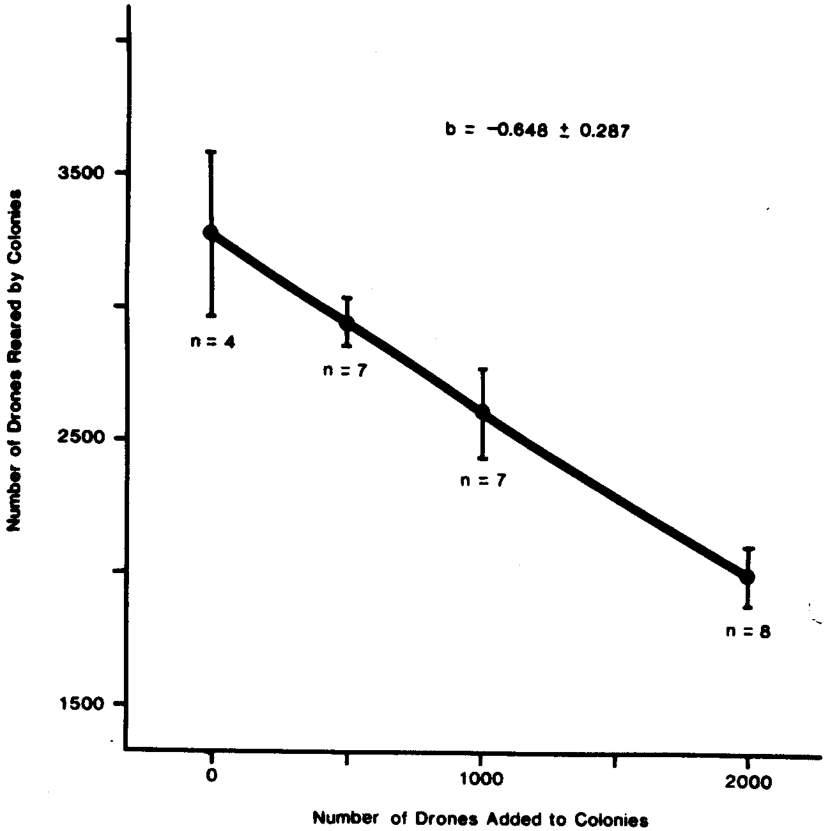

Fig. 5 — The relationship between numbers of adult drones in colonies and the production of immature drones during 14 days in Experiment 3. The slope and the means (± standard error of each mean) are shown for the four points that are collinear.

Knowledge of social reproductive parasitism by Africanized queens and drones suggests that the control of this parasitism can contribute to a continuing supply of commercial European bee stocks despite Africanization. The availability of such bee stocks will substantially reduce the costs of Africanization for American agriculture (McDowell 1984). Social parasitism should be considered in research and control programs designed to stop or slow the large-scale spread of Africanized bees.

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