Swarming Behavior of Honey Bees (Hymenoptera: Apidae) in Southeastern Louisiana

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ABSTRACT Reproductive swarming phenology, swarm sizes, and cavity selection were studied in a European-derived population of *Apis mellifera* L. in southeastern Louisiana before and immediately after the initial detection in 1992 of *Varroa destructor* Anderson & Trueman (Acari: Varroidae). Frequency of swarms was highest between early April and early May in each of 6 yr. Swarm weight averaged 1.42 kg (range 0.17–4.30 kg) and did not change significantly the year after detection of *V. destructor*. Swarms spent an average of ≈20 daylight hours scouting for a new nest-site from a temporary location and moved more frequently to cavities of 30-liter than to those of 13-liter volume. Swarms were random in direction of movement. Dance tempos at the time of swarm departure indicated movement to cavities at distances from 200 m to ≈10 km. The genetic composition of this honey bee population is likely to change after natural and artificial selection for resistance to new parasites, such as *V. destructor* and *Aethina tumida* Murray (Coleoptera: Nitidulidae), and as Africanized bees expand their range. Swarming characteristics are also likely to change both from direct effects of parasites on colony reproduction, and by changes toward bee populations with differing life histories.

KEY WORDS *Apis mellifera*, swarming, colony founding, cavity selection

BY1804, A FERAL POPULATION OF European honey bees had been reported in Louisiana (Oertel 1976). These feral bees probably were self-sustaining and capable of surviving independently of managed bees introduced later by beekeepers. The two types of bees most likely introgressed during the last century, but some degree of genetic separation between feral and managed bees has persisted (Schiff and Sheppard 1995). The survival of this and other feral or native honey bee populations results from a number of traits commonly perceived as adaptive, many of which are related to reproductive swarming.

Colonies must grow early in the year to allow division into parent colony and swarm(s) that will attain adequate populations and surplus stores to reach the next yearly cycle of reproduction. More than 80% of the swarms observed in north temperate regions (32–50° N) were produced during periods of ≈2 mo in early spring (Mitchener 1948, Burgett and Morse 1974, Fell et al. 1977, Caron 1979, Page 1981, Schmidt and Thoenes 1987, Seeley and Visscher 1985). The size of swarms is also important. In British Columbia, larger swarms produced more workers and had longer survival (Lee and Winston 1985). Documented swarm sizes range from 0.3 to 5.3 kg (mean 1.5 kg) in central New York (Fell et al. 1977) and from 0.2 to 2.2 kg in southern Louisiana (mean 0.9 kg) (Rinderer et al. 1982). Some of the restrictions on the timing of colony growth and reproduction seem to be less stringent in subtropical areas of North America (Rubink et al. 1996).

European honey bees scout and evaluate potential nesting cavities before and immediately after colony division, and their dances typically converge on a consensus, indicating a single location before movement of the swarm (Lindauer 1951). The distance traveled by a swarm to a selected cavity, inferred from the dance tempo of scouts, ranges from ≈300 to >4,000 m, suggesting the need for swarms to move away from competition with the parent nest (Lindauer 1951, Seeley and Morse 1977). However, a high proportion of observed swarms may move relatively short distances: half of the swarms in the above-mentioned two studies had consensus dances to cavities <1 km away, and swarms provided with arrays of "swarm traps" at different distances readily occupied these artificial cavities at distances <800 m away (Jaycox and Parise 1980, 1981; Gould 1982; Schmidt 1995; Seeley and Morse 1977). "Swarm traps" might cause deviations from natural movement distances (e.g., contradictory results on distance preferences of Italian bees and of northern European bees were obtained using bait hives (Jaycox and Parise 1981, Gould 1982).

Other aspects of cavity choice by European swarms are better understood. Most occupied tree cavities in

New York range from 30 to 60 liters and have small bottom entrances (Seeley and Morse 1976). Choice experiments have indicated a preference for intermediate volume cavities (≈20–50 liters) when presented as alternatives to smaller (5–10 liters) or larger cavities (100–120 liters) (Seeley 1977; Jaycox and Parise 1980, 1981; Rinderer et al. 1982; Schmidt and Hurley 1995). Italian swarms prefer cavities from 10 to 30 liters, whereas more northern European bees prefer to occupy cavities from 40 to 80 liters (Jaycox and Parise 1980, 1981; Gould 1982). However, in a test in Florida, when given no alternatives, European swarms occupied cavity volumes of 10–13 liters (Morse et al. 1993).

Comparisons of tropical African and Neotropical African-derived (Africanized) honey bees to European bee swarming characteristics are sparse because simultaneous testing of the two bee types in the same area is difficult. In the only study of both types of bees in two different areas, both European and Africanized bees ceased swarm production in December and January in southern Texas, but swarmed all months in northern Mexico with higher intensities in the spring and fall (Rubink et al. 1996). African and Africanized colonies occupied high proportions of cavities smaller than 20 liters (Ratnieks et al. 1991, Schmidt and Hurley 1995, McNally and Schneider 1996). However, Rinderer et al. (1982) found no clear preference for smaller cavities by Africanized bees in Venezuela compared with European bees in Louisiana. Consensus dances of Africanized swarms in Costa Rica indicated movements to cavities on average 4.7 km away (Schneider 1995), which is beyond the longest distance reported for European bees.

I report observations and experiments conducted from 1989 to 1994 on the phenology of swarming, sizes of swarms, and choices of nest cavity distance and volume by European honey bees in southeastern Louisiana. These studies were prompted by the predicted imminent arrival of Africanized bees to document changes in reproductive parameters that would affect beekeeping and public safety. Movement of Africanized bees along the Gulf Coast east of Texas has stopped, possibly due to parasitism by *Varroa destructor* Anderson & Trueman (Villa et al. 2002). However, the baseline information collected during these studies currently allows 1) comparisons with European-derived bees in other areas, where they are either native or feral, to deduce the roles of genetics and environment in shaping colony reproduction; and 2) contrasts with African and African-derived bees in regions where they are native (Africa) or introduced (New World). The data will also make it possible to observe in the future whether in the southeastern United States, 1) newly introduced parasites such as *V. destructor* and *Aethina tumida* Murray produce changes in the number, timing, size, or health of the local feral population; and 2) varying levels of resistance in local or selected European bees (or in advancing Africanized bees) affect the degree of introgression into the existing managed and feral European population.

Materials and Methods

Observations were made on 176 swarms between February 1989 and June 1994. These swarms had different origins: 94 were captured in bait hives in East Baton Rouge and Iberville parishes of Louisiana, 66 were moved to a new observation site after being reported to the laboratory, and 16 were prepared as artificial swarms (Seeley and Morse 1977). Depending on the number of swarms being monitored, and on the need for increasing sample sizes of different observations at the time, varying amounts of data were collected on each one of these swarms. The numbers used for different swarm characteristics are described below.

Swarming Phenology. Numbers of new swarms during the first 6 mo of each year from 1989 until 1994 were recorded. Anecdotal evidence indicated that swarms in the second part of the year were very infrequent, so no data were collected after 30 June. In 1989, only 27 swarms, captured in bait hives arranged inside a radius of 1 km, were recorded. In 1990 and 1991, both swarms reported by the public around metropolitan Baton Rouge ($n = 20$ and 60, respectively), and swarms directly observed or captured ($n = 30$ and 32, respectively) were recorded. In 1992–1994, captures in bait hives were used (11, 36, and 20 swarms, respectively). Initially, parent colonies that produced these swarms were most likely feral. Managed colonies were the most likely sources in the last 2 yr, due to the adverse effects of parasitic mites on feral colonies, but the origin of each individual swarm is impossible to discern.

Weights of Swarms. Weights of swarms were measured in 1989–1991, and 1993 ($n = 16$, 30, 19, and 33 swarms, respectively). Weights were obtained to the nearest 10 g after subtracting the weight of the hive, and of comb, stores, and brood (in cases where comb construction had started inside bait hives).

Scouting and Movement to New Nest Sites. Sixty-six natural swarms and 16 artificial swarms (Seeley and Morse 1977) were placed on stands in 1990 and 1991 for experiments on distance attraction to Nasonov-baited hives. All queens were tagged with plastic numbered discs. The dances of scouts and the departure times were recorded whenever possible. A distance and direction of movement was arbitrarily deemed as reliable for 14 swarms when scout dances converged on a single pattern of distance and direction, the swarm departed within 30 min from the last reading, and the swarm did not move into a provided bait hive. The actual movement of one of these swarms and that of two others (for which consensus dances were not observed) was confirmed by the presence of the tagged queen. Because the genetic origins and resulting dance tempos of these swarms were unknown, I used data summarized by von Frisch (1967) from data on Carniolan honey bee, *Apis mellifera carnica* Pollman, which covers distances up to 10 km. Scouting time (time between installation and departure in daylight hours) was recorded for 47 swarms of different origins.

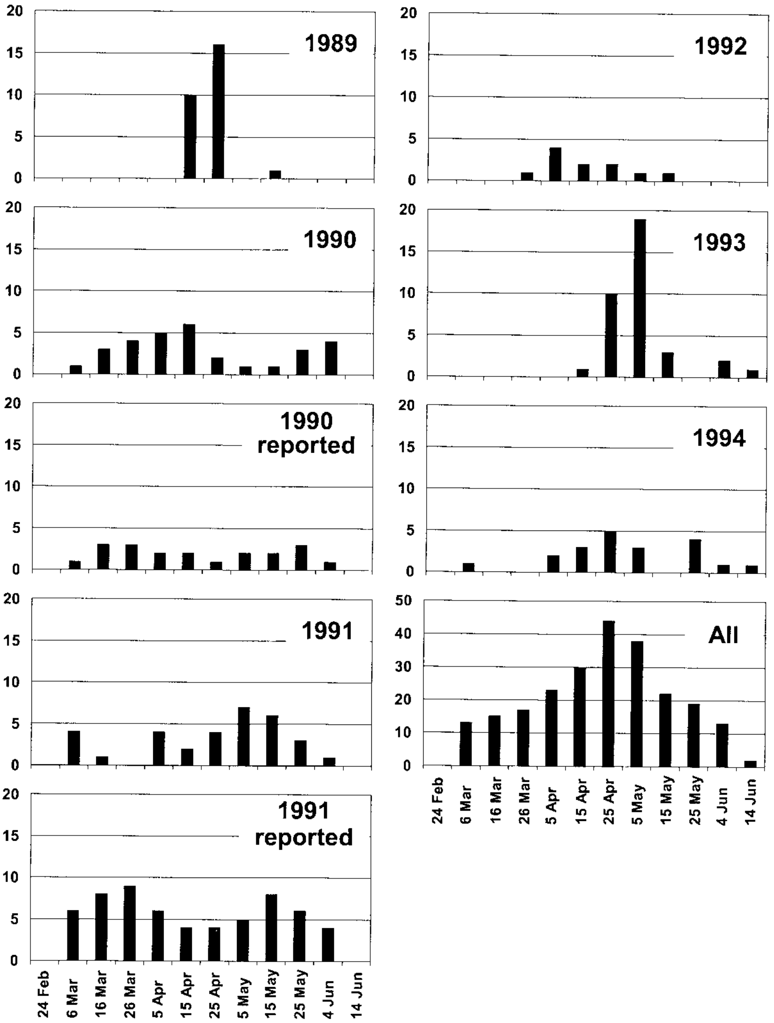

Fig. 1. Number of swarms at 10-d intervals that were directly observed (1989–1994) or reported by the public (1990 Reported, 1991 Reported), and total number of swarms observed or reported per interval in all years (All). The labels on the *x*-axis indicate the midpoint of the 10-d time interval.

Volume of Nesting Cavities. In springs 1993 and 1994, 20 sites were established with a 13- and a 31-liter wood pulp cylindrical hive (Schmidt and Hurley 1995) baited with a mixture of 30 μl each of citral, geraniol, and nerolic/geranic acid. At each site, two similar locations between 10 and 50 m from each other were identified and the two hives of different volumes assigned at random. Half of the sites were near apiaries (within 100 m), and half were considered independent of apiaries. A maximum likelihood model, incorporating the effects of location (apiary versus nonapiary) and time in the spring (categorized as before or after 30 April), was used to analyze swarm choice of cavity volume (PROC CATMOD, SAS Institute 1990).

Results

Eighty percent of swarms occurred within a span of 70 d centered around the period with most intense swarming; nearly 20% of the swarms occurred in the last 10 d of April (Fig. 1). The yearly 10-d period of most intense swarming was as early as 1–10 April in 1992, and as late as 1–10 May in both 1991 and 1993.

Swarm weights ranged from 0.17 to 4.33 kg (1.42 ± 0.08 kg, mean ± SE, $n = 95$; Fig. 2). The mean weight in each year ranged from 1.27 ± 0.14 kg in 1993–1.67 ± 0.22 kg in 1989, but yearly means did not differ ($P = 0.42$). The mean weight of all swarms from years before the discovery of *V. destructor* (1989–1991: 1.48 ± 0.10 kg, $n = 62$) did not differ from the weight of

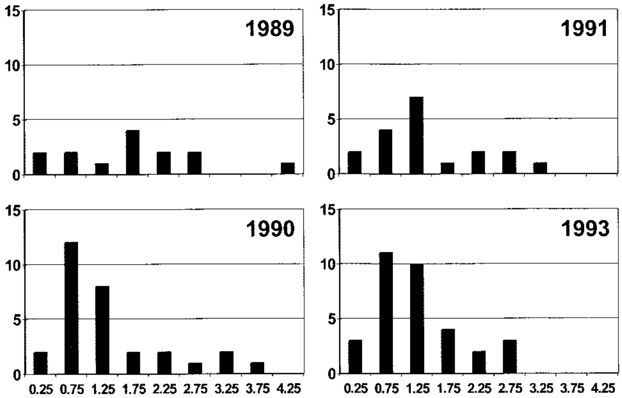

Fig. 2. Weight distribution of swarms (kilograms) captured in each of 4 yr in southeastern Louisiana. The labels on the x-axis indicate the midpoint of the interval.

swarms in the year after the discovery of the parasite (1993: 1.27 ± 0.14 kg, $n = 33$) ($P = 0.22$).

Nest site distances indicated by either consensus of dancing scouts ($n = 13$) or by the observation of a tagged queen ($n = 3$) ranged from 200 m to ≈10 km (mean = 3.36 ± 0.72 km; Fig. 3). The distribution of distances was not distinct (four <1 km, six between 1 and 4 km, five between 4 and 7 km, and one ≈10 km). Two swarms with tagged queens were discovered in empty hives at 200 m, and one was later located in the wall of a house at 2.2 km. Consensus dances of workers from one of the swarms found at 200 m were within 5° of the hive eventually occupied and indicated distances from 300 to 800 m. The flight direction of eight swarms observed at the moment of departure corresponded with the direction indicated by consensus dances in swarms within half an hour before leaving. Consensus dances in swarms ($n = 14$) indicated no preferred direction of movement. The mean time spent scouting did not differ between natural relocated swarms (19 ± 3 daylight hours, $n = 31$) and artificial swarms (24 ± 5 daylight hours, $n = 16$).

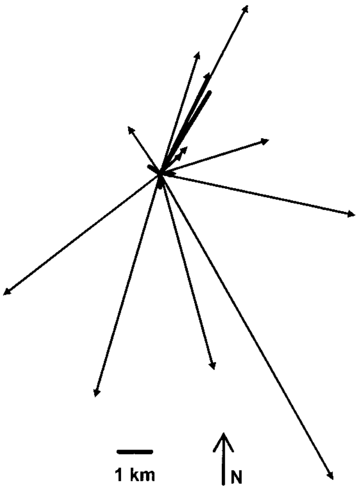

Fig. 3. Distances and directions of movement from a central release area indicated by consensus dances in 13 swarms and confirmed by verification of individually tagged queens in three cavities (shown by lines with no arrows).

Swarms preferred 31-liter cavities over 13-liter cavities (37 versus 16 occupations in two years of testing, $\chi^2 = 4.33$, df = 1, $P = 0.037$). Weights of swarms measured in the second year of the experiment (1993) did not differ according to the volume of cavity occupied (1.37 ± 0.17 kg in 31-liter traps versus 1.11 ± 0.20 kg in 13-liter traps, $P = 0.33$). There was also no effect of location (apiary versus nonapiary, $\chi^2 = 1.91$, df = 1, $P = 0.17$) and no effect of time in the season (early versus late, $\chi^2 = 0.16$, df = 1, $P = 0.69$) on the preference for a cavity size.

Discussion

This characterization of reproduction in a European honey bee population from the southern United States produced useful comparisons and contrasts with other introduced populations in North America and with populations in Europe. As has been reported for other honey bees of European origin, this honey bee population has a peak of swarming activity in the spring, a preference for cavities of 30 liters over smaller cavities, and a well defined process of scouting for new nest sites from a temporary location. However, some observations suggest that aspects of reproduction in this region differ from those described for European bees in other areas.

Life history characteristics of honey bees evidently are variable across climatic gradients. Colonies in areas with long and intense winters swarm during a very short period of time (Mitchener 1948, Burgett and Morse 1974, Fell et al. 1977, Caron 1979) and clearly prefer larger nesting cavities (Seeley and Morse 1976; Jaycox and Parise 1980, 1981). The population studied in Louisiana has similar behavior, but responses seem to be more plastic. Although the overall swarming intensity was rather peaked when averaged over several years, in some years it seemed to be diffuse and more similar to the phenology reported in southern Texas and northern Mexico (Rubink et al. 1996). The preference for larger volumes of cavities was also less pronounced than reported in New York (Seeley and Morse 1976), Illinois (Jaycox and Parise 1980, 1981), and Arizona (Schmidt and Hurley 1995). Morse et al. (1993) found occupation of 10–13-liter bird nesting boxes by another population of honey bees in the south.

The mean and maximum inferred swarm movement distances observed in this study are significantly greater ($P > t$ on ranked distances = 0.009) than those reported for temperate European bees (Lindauer 1951, Seeley and Morse 1977). Movement distances seem more similar to those found for Africanized bees in Costa Rica (Schneider 1995). The use of Carniolan dance tempos could have inflated estimates of distances if other races had been predominant (von Frisch 1967, Gould 1982). In an extreme case, had all swarms been of pure *Apis mellifera ligustica* Spinola origin, and the tempo relationship between Carniolan and Italian bees shown for distances of up to 1 km continue up to 10 km, estimated distances would have to be reduced by about one-third. In this case, the difference between my observations and those of temperate European bees would be greatly reduced (one-tailed t-test on ranked distances, $P = 0.047$).

Several factors could explain the differences observed in some of the reproductive characteristics of this population. The most parsimonious explanation is that honey bees respond at a very proximate level to local conditions and that the observed differences are nothing more than the expression of a fairly plastic behavioral repertoire present in honey bees of all origins. Alternatively, this feral European population could have different origins and possibly more diverse origins from those of other North American feral populations. This area has had active beekeeping for many years, including research with different lines of honey bees, e.g., lines derived from Africanized semen introductions (Taber 1977). Thus, diverse genetic origins could explain the less defined phenologies and cavity preferences of this population. A third possible explanation is that natural selection on the original population and on later introductions could have produced a modification in life history traits molded to the particular conditions of this region.

The future characteristics of a feral honey bee population in this area are difficult to predict. *V. destructor* spread rapidly after its detection in 1992; brood infestations in October 1993 in colonies derived from swarms captured in the spring ranged from 2 to 43%. Thirty-three swarms captured in the spring of 1993 had not shown a significant decrease in size. Phenologies in 1993 and 1994 had not changed noticeably. The characteristics of swarms in this area will be determined ultimately by the relative intensity of the following factors: natural and artificial selection for resistance to parasites, introgression of the European and African-derived bees, and parasitism by new introductions such as *A. tumida.* If parasitism is high and swarms are mostly derived from feral colonies, proportion of early swarms, total numbers, and size of swarms should decrease. Alternatively, if feral European bees disappear due to parasitism, only treated managed hives would produce swarms, and only the characteristics of managed bee genotypes would be observed. If the relative influence of managed hives is minimal and if Africanized bees or new genotypes of European bees possess or evolve resistance to parasitism, the feral population could change. With Africanization, characteristics such as broad swarming phenologies, small swarm sizes, preference for smaller cavities, and longer distances of swarm movement should become more common. The most likely scenario incorporates more complex interactions between parasites, the resistance of different bee genotypes to these parasites, as well as life history traits (including swarming) that contribute to the differential survival of distinct bee types in the feral population.

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