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SIZE OF NEST CAVITIES SELECTED BY SWARMS OF AFRICANIZED HONEYBEES IN VENEZUELA[1]

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Summary
Most feral swarms of Africanized honeybees (*Apis mellifera*, South American ecotype) in Venezuela selected cavities with a volume of 80 litres as nest sites when presented with a choice of 10, 20, 40 and 80 litres. Agonistic behaviour between scout bees inspecting nest boxes was common, indicating that nest cavities were a limited resource for this population of feral honeybees.

Introduction
Honeybees (*Apis mellifera*) reject very small cavities as nest sites when given choices (Lindauer 1955, 1961; Seeley 1977; Jaycox & Parise 1980). Seeley's (1977) data suggested that under certain conditions bees may also reject larger cavities, and he offered the hypothesis that selection of nest-cavity volume 'may regulate mature colony size at an optimum between small colonies with low survivorship and large colonies with low fertility'.

If that hypothesis is correct, natural selection would operate in two ways. First, choices of cavity sizes too small to allow colonies to grow large enough to survive predictable adverse periods would be selected against, particularly in cold climates. Second, choices of cavity sizes too large to maximize colony reproduction would also be selected against. With natural selection operating in both these ways, bees that evolved in different ecosystems would predictably choose different nest cavities, the optimum size in any case being somewhat larger than minimally acceptable cavities. Bees in ecosystems with comparatively long and severe periods of adverse conditions would choose comparatively large nest cavities. Alternatively, bees in ecosystems with shorter and less severe periods of adverse conditions would predictably choose nest cavities of comparatively smaller optimum and minimum sizes.

Bees primarily of European origin, in a temperate region of the United States with reasonably severe winters, selected cavities with a median volume of about 40 litres (Seeley & Morse 1976, Seeley 1977). Bees primarily of African origin (Africanized bees) in a tropical savanna region of French Guyana occupied swarm boxes of 12·4 and 22 litres at a low rate: 1·4 occupancies per 100 swarm-box months (Taylor & Otis 1978). Because Taylor and Otis (1978) did not offer larger nest boxes, their data did not show that smaller nest boxes were optimally selected by Africanized bees.

Our study was designed to measure the cavity size that feral swarms of Africanized bees in Venezuela optimally chose for home sites.

Materials and Methods
The study site was near Maturin, Venezuela, in a tropical dry forest (*sensue* Holdrige Life Zone; Ewel & Madriz, 1968). In the last 40 years portions of the forest have been replaced by pasture.

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Nest boxes with volumes *c.* 10, 20, 40 and 80 litres were constructed: 10-litre boxes from 5-frame Langstroth hive bodies with half-depth false floors; 20-litre boxes from 5-frame Langstroth hive bodies; 40-litre boxes from 10-frame Langstroth hive bodies; 80-litre boxes from two 10-frame Langstroth hive bodies. Each nest box had removable inner and outer covers and an entrance hole 1·5 cm in diameter through one of the narrow box surfaces, 1 cm above the floor. To increase their attractiveness to swarms, all boxes had been occupied by bees and comb until 4 days before they had been placed at the study site. Olfactory attractiveness of the units was further equalized with melted beeswax painted on a section of the interior surface of each box, 6 × 30 cm, just above the entrance hole.

Sixteen nest boxes, 4 of each size, were arranged at intervals of 10-20 cm in random order along a partially shaded wall of a building, at a height of 2·5 m. Half of the boxes never received direct sunlight, and half were in direct sunlight from 12.00 h until sunset. At least one box of each size was in each area. The building and adjacent trees were isolated in a pasture that was *c.* 2 km from a wooded stream bed known to contain feral honeybee colonies and *c.* 7 km from the nearest managed apiary.

The boxes were established on the study site on 24 December 1979, and were inspected at least twice daily until 10 January 1980. When a swarm was captured, the nest box was removed from the site shortly after sunset, the bees were transferred to a nucleus hive body without comb or foundation, and the nest box was returned to its position at the study site the next morning. During transfer, the swarm was weighed, and samples of drones and workers were taken. Three groups of ten workers were weighed to determine their average weight. The average width of 10 worker cells produced by the swarm in either the nest box or the nucleus hive body was also determined.

Results

All the swarm boxes attracted scout bees. During 5 periods when scouts were visiting the site, we made a systematic inspection of all entrances, and observed bees entering and leaving. During one inspection the time interval between bees entering a single box was slightly less than 20 sec, and all boxes were inspected at about the same frequency.

Agonistic behaviour between scout bees was common. Often, bees meeting at entrances or in the air space near them would grasp one another, fall to the ground, and attempt to sting. Sometimes, these encounters would result in the death of one of the agonistic pair. On 3 occasions such death was observed directly, and dead bees could be easily seen on the ground immediately under the nest box entrances. Many agonistic episodes were seen during any period when scouts were observed at the location.

Seven swarms that had full opportunity to choose between nest boxes were collected; these supplied the data in Table 1. Five swarms occupied 80-litre nest boxes and two occupied 40-litre nest boxes. These choices of nest box volume were non-random ($P<0{\cdot}025$; $\chi^2 = 9{\cdot}57$, 3 df), demonstrating a preference for nest-box volumes in excess of 40 litres. Swarm weights ranged from 0·3 to 3·0 kg and were apparently not related to volume chosen. Four swarms occupied boxes in shade, and 3 occupied boxes exposed to afternoon sun. Only the 3 smallest swarms contained no drones. Mean weights of worker bees ranged from 65 to 95 mg. The two swarms with the lightest bees (average 65 mg) occupied 40-litre boxes, and all the other swarms occupied the 80-litre boxes. The distance spanned by 10 cells of comb built by the swarms ranged from 4·7 to 5·0 cm.

TABLE 1. Cavity choice and characteristics of swarms of Africanized honeybees. Equal numbers of boxes of 10, 20, 40 and 80 litres were provided; only those listed were occupied.

Date collected	*Size of cavity occupied (litres)*	*Swarm weight (kg)*	*Presence of drones*	*Distance spanned by 10 worker cells (cm)*	*Average worker weight (mg)*
25 Dec. 79	80	1·4	yes	4·8—4·9	85
26 Dec. 79	80	3·0	yes	4·9—5·0	95
28 Dec. 79	80	1·7	yes	4·9—5·0	80
29 Dec. 79	40	0·5	no	4·8—4·9	65
30 Dec. 79	80	1·1	no	4·9—5·0	70
31 Dec. 79	40	2·1	yes	4·7—4·8	65
5 Jan. 80	80	0·3	no	—	90

It was estimated that 8 swarms arrived at the study site on the day after a 3-day period of rain (4 January 1980). A mid-morning inspection revealed scout bee activity similar to activity previously observed before the arrival of a single swarm, and at that time no nest box contained a swarm. In anticipation of a swarm's arrival, one of us inspected the study site at 14.00 h. At this time, 3 80-litre nest boxes contained separate swarms; the fourth 80-litre nest box was unoccupied but had a swarm clustered under it, as did one of the 80-litre boxes already occupied. Also, one swarm was in the process of forming a cluster on a 40-litre box. Additionally, two flying swarms arrived simultaneously at the study site from opposite directions, and settled on and near 2 other 40-litre nest boxes. Within 1 h, all the swarms had aggregated in the two 40-litre nest boxes occupied by the two swarms that were the last to arrive. Because of the confusion caused by the aggregation of swarms, no further data were taken on these swarms.

Discussion

The bees in this study were Africanized. Measurements of cell widths and weights of workers were in the range reported for bees at low and moderate altitudes in East and Central Africa (Smith, 1961), and for bees in South America considered to be Africanized (Consenza & Batista, 1972). In behaviour similar to that for swarms of Africanized bees described by Otis (1980), the swarms did not readily become established in nucleus hive bodies when placed in them. However, once the swarms were established, the bees showed the defensive behaviour expected from Michener's (1975) descriptions of Africanized bees.

Contrary to predictions about tropically adapted bees based on Seeley's (1977) hypothesis, most swarms of Africanized bees in our study chose the nest boxes with a volume of 80 litres. (This was the only size above 40 litres that was offered to the bees.) Five of 7 swarms chose 80-litres nest boxes. Also, if initial observations of the 8 simultaneous swarms were included, 13 of 15 swarms chose the maximum nest box volume available. Therefore, we cannot calculate a precise average for choice of cavity volume. Nonetheless, it is clear that the average for cavity volume chosen was in excess of 40 litres.

Our interpretations of the biological implications of our results rest in part on a detailed understanding of the studies of Seeley (1977) and Seeley and Morse (1976). Seeley and Morse determined a median volume of 45 litres for nest cavities by measuring the volume of naturally occurring cavities occupied by European bees. Seeley determined a model value of 35 litres for nest cavities chosen by European bees, by adding data from measurements of man-made cavities occupied by bees (but not designed for them) to data in the previous study. Seeley (1977) also caught feral swarms in experiments designed to provide a choice of volumes. In the first experiment, he offered feral swarms cavities of 10, 40, 70 and 100 litres and obtained 0, 4, 3, 4 occupancies, respectively. In a second experiment, he offered cavities of 40 and 100 litres and obtained 7 and 0 occupancies, respectively. According to our analysis of the combined data from Seeley's experiments, the average volume occupied was 58 litres, and no significant difference ($\chi^2 = 0{\cdot}89$, 1 df, $P<0{\cdot}35$) existed between the classes of 40 litres and above 40 litres. Consequently, when given a choice of nest boxes, the European bees studied by Seeley tended to choose large-sized boxes, but without demonstrating that a specific size was preferred. The same is true for the Africanized bees in our study.

Although both European and African bees apparently tended to occupy similarly large nest cavities, and neither type of bees demonstrated a preferred size, African bees clearly have a higher rate of reproductive swarming (Fletcher, 1978; Otis, 1980). Therefore, it is unlikely that (in the usual course of events for feral colonies), nest cavity size, by governing colony size, is a primary regulator of the reproductive rate of feral colonies. Using different evidence, Winston et al. (1980) also advance this hypothesis. Certainly cavity size does have an influence. Common experience with managed colonies in beekeeping equipment shows that additional space reduces swarming and that colonies in nucleus hive equipment have a strong tendency to swarm. However, such observations only show that cavity size establishes limits within which the primary regulators of colony reproduction operate.

Suitable nest cavities appear to be a limited resource in the survival and spread of bee populations. The agonistic behaviour we observed at the nest box entrances supports this view. Behaviour, like morphology, cannot be expected to develop or to be maintained over evolutionary time without the operation of reasonably continuous natural selection. When given a choice, bees studied by Seeley (1977) chose nest boxes larger than the cavities occupied by feral colonies of the same population. Furthermore, the volumes of the smallest nest cavity acceptable to bees of different genotypes are apparently different (Jaycox & Parise, 1980). Natural selection establishing this difference could only have occurred when bees occupied cavities too small to support survival and successful reproduction. Since bees tend to occupy large cavities when they are available, the occupancy of small cavities would occur only when the choice of cavities was restricted by their availability.

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H70