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NEST CAVITY SELECTION BY SWARMS OF EUROPEAN AND AFRICANIZED HONEYBEES*

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Summary
The overall pattern of nest-box occupations by European bees in Louisiana indicated a minimum acceptable volume of *c.* 10 litres, a maximum acceptable volume of *c.* 40 litres, and no preference between these extremes. Africanized bees in Venezuela had a nest-box occupation pattern indicating a minimum acceptable volume of *c.* 20 litres, no maximum acceptable volume within the limits of the sizes available in the experiment, and no clear preference between volumes from 20 to 120 litres. These data suggest a model of nest-cavity selection formulated as a hierarchical set of choices.

Africanized swarms weighed more, although the individual bees in them weighed less, and they always built a smaller total area of comb and tended to include fewer drones, than swarms of European bees.

Introduction
Studies of the selection of cavities as nest sites by honeybees (*Apis mellifera*) have clearly indicated the rejection of very small cavities (Lindauer, 1955, 1961; Seeley, 1977; Jaycox & Parise, 1980; Rinderer et al., 1981). Some, but not all, of Seeley's data (1977) and Lindauer's observations (1955, 1961) suggest that bees also reject larger cavities. Alternatively, bees may reject larger cavities in such experiments only under specific conditions. Cavity volumes that are neither too small nor too large may range about some optimum acceptable size, or all may be equally acceptable.

Bees of different races may differ in their selection of nest-site cavities. Jaycox and Parise (1980) hypothesized that 'African races probably accept smaller cavities than the Italian race.' This could occur even though Africanized bees seem to prefer cavity sizes ranging at least up to 80 litres (Rinderer et al., 1981).

Because Seeley (1977) obtained dissimilar results in two experiments, it is unclear if there was a real difference in cavity size preference between his European bees and the Africanized bees studied by Rinderer et al. (1981), or if differences in selection were caused by differing arrays of nest-box sizes.

Our study was conducted to determine and compare the maximum, minimum and preferred cavity volumes chosen as nest sites by swarms of European bees in North America and Africanized bees in South America. It was also designed to evaluate the possible effects of differing arrays of nest-box sizes on size selection. The use of collections of feral swarms of the two populations permitted comparisons with respect to swarm weight, comb cell size, weight of individual workers, and the presence or absence of drones.

Such studies cannot distinguish differences due to genotype from those due to environmental differences. Nevertheless, differences between bees inhabiting different ecosystems, to which they are adapted, reveal general variation in bees. Such variation is useful in understanding more fully the biological consequences, induced directly or through natural selection, of environmental constraints that differ between ecosystems. Also, a lack of differences between bees of differing genotypes and environments is most likely to occur only for characteristics common to all honeybees.

Materials and Methods
The study sites in North America were near Baton Rouge, Louisiana, USA, and those in South America were near Acarigua, Venezuela. Both areas are composed of patches of deciduous forest interspersed with land devoted to agriculture. Louisiana has a temperate

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continental climate with hot, humid summers and brief, mild winters. Venezuela has a tropical climate with a rainy season from May to November.

The honeybee population in North America is a hybrid of many races imported in the past, primarily from Europe. Because most successful imports were from temperate zones, and because of both natural and artificial selection, these bees are well adapted to temperate climates. Also, because of commercial patterns of queen distribution, the population of bees studied by Seeley (1977) is probably quite similar to the population of European bees in Louisiana. The honeybee population in Venezuela is a hybrid of African bees *Apis mellifera scutellata*, formerly called *adansonii*, (Ruttner, 1976), imported into Brazil, and several European races imported into both Brazil and Venezuela. Population dynamics and selection pressures have made this population quite similar to those of *A. m. scutellata* in Africa described by Fletcher (1978). These bees are highly successful in tropical South America.

Nest boxes of *c.* 20, 40, 80 and 120 litres were constructed as previously described (Rinderer et al., 1981); boxes of 5 and 10 litres were made from 5-frame Langstroth hive bodies with internal partitions. All equipment was previously unused, except that used inner covers or (for boxes 5 and 10 litres) portions of used inner covers were put on the uppermost internal surfaces. Nest-box parts, with external surfaces painted dark green, were transported to Venezuela; this assured similar construction, materials, and visibility for nest boxes at both locations.

Stands to support nest boxes 3 m above the ground were constructed and placed in well-shaded forest edges at least 3 km away from the nearest stand. Stands were randomly assigned one of 3 size-groupings of nest boxes: two each of sizes 5, 10, and 20 litres; two each of 20, 40 and 80 litres; two each of 40, 80 and 120 litres. The 6 boxes assigned to each stand were arranged in random order, with entrances turned to the same direction. In Venezuela, each type of nest-box group was used at 2 stand locations, and in Louisiana at 8 stand locations.

This experimental design, using 3 size groupings, allowed some swarms to select among smaller boxes only, others among larger boxes only, and still others among mid-sized boxes. The restricted choices provided a basis for estimating minimally acceptable nest-box sizes, maximally acceptable sizes, and preferences within acceptable ranges. Also, because the arrays of boxes on stands were varied, the design had the ability to reveal changes in nest-box occupation caused by different arrays.

The boxes were placed at the stand locations in Venezuela between 4 January and 18 January 1981, and in Louisiana in February 1981. Each stand location was inspected about once a week until 1 June in Venezuela and until 1 August in Louisiana.

When a swarm was found, its choice of nest box was recorded, it was removed from the box and weighed, and samples of drones and workers were taken. Three groups of 10 workers each were weighed after removal of their proventricular contents (Gary & Lorenzen, 1976) to determine their average body weight. Three measurements of the width of 10 worker cells of comb produced by the swarm were also made.

Results

No type of nest-box grouping attracted significantly more swarms than other types ($\chi^2=2\cdot5$, 2 df; $P=0\cdot28$ for nest-box groups in Louisiana and $\chi^2=4\cdot3$, 2 df; $P=0\cdot12$ for nest box groups in Venezuela). The nest-box occupation patterns of the collected swarms showed that Africanized bees had a tendency to occupy larger nest cavities than European bees for all three types of nest-box groupings (Table 1).

The groups of nest boxes of 5, 10 and 20 litres were occupied by 11 Africanized and 8 European swarms. Ten Africanized swarms occupied 20-litre boxes and one a 10-litre box, demonstrating that 20 litres was nearer their acceptable minimum cavity volume than 10 or 5 litres (binomial probability of acceptance of volumes less than 20 litres=0·006). Five European swarms occupied 20-litre boxes, and three occupied 10-litre boxes. Thus, for these bees, 10 litres was nearer their acceptable minimum volume than 20 litres (binomial probability of acceptance of volumes less than 10 litres=0·004).

The groups of nest boxes of 20, 40 and 80 litres were occupied by 4 Africanized and 10 European swarms. Three Africanized swarms occupied 80-litre boxes, and one occupied a 20-litre box. This pattern of occupation did not demonstrate a clear preference by Africanized

TABLE 1. Nest-box cavity choice and characteristics of swarms of European and Africanized honeybees. Nest-box stations contained two each of the indicated volumes. Σ = Number of swarms occupying each cavity size.

Population	*Cavity sizes provided on stand (l)*	*Collection date*	*Cavity size occupied (l)*	*Swarm weight (kg)*	*Distance[1] spanned by 10 cells of comb (cm)*	*Mean worker wt (mg)*	*Presence of drones*
European	5, 10, 20	8 Apr	20	1·0	5·2 – 5·3	97	no
	Σ 0, 3, 5	14 Apr.	20	0·9	5·0 – 5·2	94	yes
		14 Apr	10	0·4	5·2 – 5·3	86	yes
		22 Apr	20	1·3	5·3	110	no
		22 Apr	10	—	5·2 – 5·3	111	yes
		22 Apr	10	0·8	5·2 – 5·3	109	no
		29 Apr	20	1·1	5·1 – 5·3	103	yes
		5 May	20	0·2	5·3 – 5·4	92	yes
	20, 40, 80	8 Apr	20	1·0	5·2 – 5·3	98	yes
	Σ 5, 5, 0	14 Apr	40	0·7	5·2 – 5·4	91	yes
		14 Apr	40	0·8	5·3 – 5·4	94	no
		14 Apr	20	0·7	5·2 – 5·4	83	yes
		14 Apr	20	0·2	5·2 – 5·3	94	yes
		22 Apr	40	1·0	5·3 – 5·4	114	yes
		22 Apr	20	1·1	5·2 – 5·4	103	no
		5 May	20	1·1	5·1 – 5·2	118	yes
		13 May	40	0·4	5·1 – 5·2	103	yes
		13 May	40	0·8	5·0 – 5·1	104	no
	40, 80, 120	14 Apr	40	1·0	5·0 – 5·4	115	yes
	Σ 3, 1, 0	14 Apr	40	0·5	5·3 – 5·4	92	yes
		14 Apr	40	1·6	5·0 – 5·1	116	yes
		27 May	80	2·2	5·2 – 5·3	108	no
Means (± SE) and % with drones			28	0·9 ± 0·1	5·2 ± 0·02– 5·3 ± 0·02	103 ± 1·4	68%
Africanized	5, 10, 20	31 Jan	20	0·8	4·8 – 4·9	65	no
	Σ 0, 1, 10	7 Feb	20	1·5	4·6 – 4·7	60	no
		7 Feb	20	1·2	4·9	65	no
		7 Feb	20	2·2	4·8 – 4·9	55	yes
		7 Feb	20	1·5	4·8 – 5·0	60	no
		14 Feb	20	1·6	4·9	65	yes
		21 Feb	10	0·1	4·8	65	no
		21 Feb	20	1·2	4·7 – 4·9	55	yes
		11 Apr	20	1·2	4·8 – 4·9	55	yes
		18 Apr	20	0·8	4·8 – 4·9	55	no
		25 Apr	20	0·2	4·5 – 4·8	55	yes
	20, 40, 80	7 Feb	80	0·9	4·7 – 4·9	60	no
	Σ 1, 0, 3	14 Feb	20	1·5	4·7 – 4·9	60	no
		21 Feb	80	0·4	4·5 – 4·6	60	no
		21 Feb	80	2·2	4·7 – 4·8	55	yes
	40, 80, 120	31 Jan	120	1·3	4·9	65	no
	Σ 2, 1, 2	7 Feb	40	2·7	4·8 – 4·9	65	yes
		14 Feb	40	1·2	4·7 – 4·8	60	no
		7 Mar	120	2·4	4·8 – 4·9	55	yes
		21 Mar	80	1·8	4·9	60	no
Means (± SE) and % with drones			44	1·3 ± 0·2	4·8 ± 0·02– 4·9 ± 0·02	60 ± 0·9	40%
Comparisons between populations			see text	$t=2{\cdot}38$ (39 df) $P<0{\cdot}02$	$t=15{\cdot}06$ (40 df)[2] $P<2{\cdot}2\times10^{-18}$	$t=16{\cdot}87$ (40 df) $P<4{\cdot}4\times10^{-20}$	$\chi^2=3{\cdot}36$ (1 df) $P<0{\cdot}07$

[1]Minimum and maximum of 3 measurements
[2]Comparison of average measurements

swarms for any of the nest-box volumes within this range. Of the European swarms, 5 chose 20-litre boxes and 5 chose 40-litre boxes; there was a clear rejection of nest boxes larger than 40 litres (binomial probability=0·001).

The groups of nest boxes of 40, 80 and 120 litres were occupied by 5 Africanized and 4 European swarms. Two Africanized swarms occupied 40-litre boxes, one an 80-litre box and two 120-litre boxes. Thus, the Africanized swarms did not show a clear preference for any volume of cavity in the range 40 to 120 litres. Three of the European swarms occupied 40-litre boxes and one an 80-litre box; this pattern showed a rejection of 120-litre boxes (binomial probability=0·06).

The overall pattern of nest-box occupation by European bees in Louisiana indicated a minimum acceptable volume of *c.* 10 litres, a maximum acceptable volume of *c.* 40 litres, and no preference between these extremes. Africanized bees had an occupation pattern indicating a minimum acceptable volume of *c.* 20 litres, no maximum acceptable volume within the limits of the sizes available, and no clear preference between volumes of 20 and 120 litres.

Weight ranges of Africanized swarms were similar (0·1-2·7 and 0·2-2·2 kg, respectively), but Africanized swarms were significantly ($P<0{\cdot}01$) heavier on average (Africanized, 1·3 kg; European, 0·9 kg) ; see Table 1. Also, Africanized bees weighed significantly less ($P<1{\cdot}2 \times 10^{-20}$) than European bees (Africanized, 60 mg; European, 103 mg); see Table 1. Thus, Africanized swarms had on average *c.* twice as many worker bees as European swarms.

Choice of cavity size was not highly correlated with swarm weight. A significant correlation ($r=0{\cdot}27$, $F=7{\cdot}15$, 1 and 19 df; $P<0{\cdot}05$) for European swarms resulted from the heaviest swarm entering a large cavity. Without the use of this swarm in the calculation, $r=0{\cdot}01$. The correlation coefficient for Africanized swarms was 0·08.

The cell size of Africanized bees was always smaller than that of European bees (span of 10 worker cells=4·8-4·9 cm and 5·2-5·3 cm, respectively; $P<7{\cdot}7 \times 10^{-19}$). More European swarms than Africanized swarms tended to have drones (European, 68%; Africanized, 40%; $P<0{\cdot}07$); see Table 1. Also, although drones were not counted, there seemed to be fewer in Africanized swarms.

Discussion

A general tendency of Africanized swarms to occupy larger cavities than European swarms, and to accept a wider range of cavity sizes, is apparent from the data. However, several nest-box occupations in this study are anomalous to the general tendencies of both populations of bees. One of 4 European swarms occupied an 80-litre box when these boxes were on stands with boxes of 40 and 120 litres, but not one of 10 European swarms occupied an 80-litre box on stands that included boxes of 20 or 40 litre. One of 11 Africanized swarms occupied a 10-litre nest box on a stand with 5-litre and 20-litre boxes, in apparent contradiction to the general tendency of Africanized swarms to occupy larger boxes.

Other studies have revealed similar anomalies. Seeley (1977) studied a feral population of European bees similar to ours, and possibly related to it, as a result of commercial queen distribution patterns in North America. When Seeley offered groups of nest boxes of 10, 40, 70 and 100 litres, he recorded 0, 4, 3 and 4 occupations, respectively. Yet, when he provided groups of nest boxes of 40 and 100 litres, 7 swarms chose 40-litre boxes and none chose 100 litres. Rinderer et al. (1981) found that 7 swarms chose 40-litre or 80-litre boxes in a group containing 4 boxes each of sizes 10, 20, 40 and 80 litres. In this circumstance, a volume of 20 litres or less appeared unacceptable (binomial probability=0·008).

Collectively, these anomalies suggest that the array of nest sizes on a stand influenced cavity choice by swarms. A swarm occupying one of a group of cavities close together probably has not entirely resolved its selection before it arrives at the site. While bees are still in a swarm cluster, dance language functions to guide the swarm (Lindauer, 1955). However, some scout bees may be dancing after inspecting one acceptable cavity at a location while others are dancing as a result of having inspected other acceptable cavities at the same location. The precision of dance language is not known to resolve distances differing by only 1 or 2 m, especially when the distances are great (von Frisch, 1967). Thus, where unacceptable cavity volumes are interspersed with acceptable ones, scout bees are, in effect, recruiting for undesirable as well as desirable locations. Final cavity selection probably occurs at the site.

Since in the various experiments (Seeley, 1977; Jaycox & Parise, 1980; Rinderer et al., 1981) all nest boxes were known to be visited by scouts, all cavity entrances were probably marked with 'foot-print' pheromone (Butler, 1966), and some swarm members may have begun a pheromone concert (Morse & Boch, 1971) at the entrance of unacceptably small nest boxes. More experienced scout bees may have responded to such an event by recruiting the swarm to the nearest cavity that was at least marginally acceptable. An analysis of the 5 swarms making anomalous choices in our study indicates that all of them occupied nest boxes next to unacceptable boxes, even though other acceptable boxes not adjacent to unacceptable ones were also available (probability = 0·11).

The pattern of the anomalies in both our own and other studies suggests a model of nest-cavity selection in tests where acceptable cavities were interspersed with unacceptable ones. Bees seemed to obey a hierarchial set of rules: (1) avoid cavities too small; (2) avoid cavities too large; (3) occupy cavities in an acceptable range at random.

Seeley's experiment (1977) with groups of nest boxes of 10, 40, 70 and 100 litres, the experiment of Rinderer et al. (1981), and our present results showing both the African and European swarms occupying nest boxes in groups of 5, 10 and 20 litres, are examples of a hierarchical operation of the first rule. Our experience with European bees occupying nest boxes grouped in sizes of 40, 80 and 120 litres, and Seeley's experiment with groups of nest boxes of 40 and 100 litres are examples of the operation of the second rule. Our experiences with Africanized swarms occupying nest boxes supplied in groups of 20, 40 and 80 litres, as well as in groups of 40, 80 and 120 litres, are examples of the operation of the third rule. Thus, the model accounts for all the anomalies that have occurred in these types of experiments.

Groups of cavities of different sizes, only some of which are acceptable as honeybee nests, probably are a special case in nature. While some large trees and some cave areas constitute such a special case, most cavities occupied by bees occur singly (Seeley, 1977). In these situations, the first rules probably still apply, and result in an acceptable choice when nest-cavity availability is limited. Whether the third rule applies (and it can only apply in situations where availability is less limited) in the more usual situation is not entirely clear, although the data of Jaycox and Parise (1980) suggest that it does.

The tendency for Africanized bees to select large cavities for nest sites is contrary to predictions of their preference based on the role of cavities in the survival through winter by European bees (Jaycox & Parise, 1980; Rinderer et al., 1981). Perhaps the function of cavity-nesting is somewhat different for tropical honeybees. The selection of larger cavities may limit the need for temperature regulation in uniformly warm climates. Mature colonies of Africanized bees may only partly fill a large cavity with their nest (O. R. Taylor, personal communication), and this would leave an insulating air space around the nest. Also, larger cavities may often be associated with larger thermal sinks surrounding the cavity. Nests preconditioned towards coolness may have added importance for Africanized bees, since the bees reduce nest entrances tightly with propolis, apparently as a defensive measure against smaller predators.

Bees of temperate climates may choose smaller cavities that are sufficiently large to store food reserves for winter survival but still small enough to be warmed passively in spring.

The larger number of bees in Africanized swarms most likely stems from a fundamental adaptive difference between the two populations of bees. Observations of swarms from both populations were made during periods of good nectar availability. Thus, absconding swarms with large numbers of bees, which are reasonably common in Africanized populations during periods of poor nectar availability, could not have been sufficiently represented in our study to account for the observed difference. Winston et al. (1981) found that European swarms from 40-litre hives and Africanized swarms from 20-litre hives had similar numbers of bees. This observation supports the conclusion that, under more natural conditions, Africanized swarms have more bees. The Africanized bees in the study by Winston et al. (1981) were at a disadvantage because they were forced to swarm from smaller rather than from equal-sized or large nest boxes, which they prefer, and yet their numbers equalled those of European swarms. More studies of the biology of swarms after they have left the parent colony may reveal the ecological factors confronting African and European bees that have resulted in observed differences in numbers of bees in swarms.

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