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Selection of nest cavities by Africanized and European honey bees

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Summary — Africanized honey bee swarms in Costa Rica displayed no size preference among pulp-based nest cavities molded to internal volumes of 13.5, 24 and 31 l. In a crossover experiment where only one cavity volume was available at a site, European honey bee swarms selected 68 cavities of 31 l volume and only 22 cavities of 13.5 l volume. When given a choice of either 31 or 13.5 l cavities, European swarms occupied the larger cavities in 84% of the choices. No correlations between swarm size, swarm date, and size of cavity inhabited by a swarm were observed among 82 European swarms measured in Tucson, Arizona during the 1993 spring swarming season. The results indicate that 13.5 l cavities are best for trapping Africanized bee swarms since they are rejected by most European swarms.

Africanized honey bee / *Apis mellifera* / swarm / feral bee / nest cavity / pheromone

INTRODUCTION

Nest cavities are of crucial importance in the biology of honey bees, *Apis mellifera* L. The cavity provides protection of the colony against predators and from extremes of heat and cold plus rain, wind, and dryness. The environmental differences between areas have led to speculations that honey bees in different areas, or of different genetics, should differ in their nest cavity choices (Lindauer, 1955; Seeley, 1977; Seeley and Morse, 1978; Jaycox and Parise, 1980, 1981; Rinderer *et al,* 1981, 1982; Winston *et al,* 1983; Morse *et al,* 1993). Two fundamental questions vis-à-vis swarms and nest cavity size are of interest: 1) what size is preferred by swarms; and 2) what size range of cavities will be tolerated by swarms. The first question asks what is the ideal preferred size of cavity for a swarm if a nearly unlimited selection is available. The second question asks what range of cavity sizes will be acceptable if no better choice is available. To investigate the first question one can place in each of several locations a group of swarm cavities differing only in cavity volume. The investigator records the number of swarms inhabiting each cavity size and from that can infer both a cavity size preference of swarms and a general nature as to how 'choosy' swarms are. The second question concerning size tolerance of cavities acceptable to swarms is experimentally more difficult to determine. To answer this question, only 1 cavity size can be available in a given location at a time, and the number of swarms inhabiting that cavity size is recorded. A major difficulty in this design is that the investigator does not know how many swarms were available and might have selected a more preferable cavity, had it been available. To overcome this problem, a crossover design can be used in which a known highly acceptable cavity is alternated with a test cavity on a regular basis in each location (see Schmidt *et al,* 1993). By comparing over time the numbers of swarms inhabiting the acceptable control cavities *versus* the numbers of swarms in the test cavities, one can obtain direct measures of the acceptability of given cavity sizes, the limits of cavity size that is acceptable, and a general measure of swarm 'choosiness'.

Differences in criteria for nest site selection of honey bees are not simply of academic interest, they also have economic and management implications. In the US, massive surveys and control efforts for Africanized honey bees using swarm trap lines have been implemented (Rubink *et al,* 1990; Rowell *et al,* 1993). Operating these trap lines is costly in both time and resources. In addition, many swarms of European honey bees are captured in these trap lines, resulting in the wasteful destruction of these bees. The goals of the research reported here were to test hypotheses of differences in cavity size tolerance and cavity size preferences of tropical Africanized and temperate European honey bees and to use this information to determine if cavities could be designed that were acceptable to Africanized bees, but were rarely acceptable to European bees.

MATERIALS AND METHODS

All artificial nest cavities were made of brown reinforced wood pulp manufactured and molded by Western Pulp Products of Corvallis, OR. Cavities were made in the shape of truncated cones and have 3 different internal volumes: 31 l (40 cm top diameter, 25 cm bottom diameter, and 40 cm high); 24 l (40 cm top diameter, 28 cm bottom diameter, and 26 cm high); and 13.5 l (30 cm top diameter, 22 cm bottom diameter, and 28 cm high). In the experiments with Africanized honey bees, cavities were assembled by attaching flat pulp lids with latex caulking and 2 strands of iron utility wire placed at 90° angles around the cavities and tightened (fig 1). Cavities were modified to improve assembly ease for the tests with European bees. Instead of caulking and wires, molded lids were manufactured to fit snugly into the cavity bodies. The lids were secured with 2 or 4 nails inserted through grommet holes near the top of the body and into the lid material (fig 2). All cavities contained a 3 cm diameter entrance hole at the bottom, and a pheromone attractant consisting a of 1:1:1 mixture of citral/geraniol/nerolic + geranic acids as described previously (Schmidt and Thoenes, 1992) was placed inside the cavity above the entrance hole.

Data were analyzed by χ^2 test, with Yate's correction factor applied in comparisons having 1 degree of freedom.

Experiments with Africanized honey bees

Fifty stations were established during the month of February 1987 in Lomas Barbudal National Park and around Hacienda La Pacifica and Finca Las Pumas (both near Cañas) in Guanacaste Province, Costa Rica. Each station contained a 31, 24 and 13.5 l nest cavity attached to a tree at a height of 3–5 m above ground (fig 1). The cavities were checked periodically during the next 4–6 weeks for honey bee swarms or other inhabitants. Any cavities containing non-honey bee inhabitants were removed, reconditioned, and replaced on the tree. Stations were surveyed in late September 1987 at which time all cavities were examined for defects, cleaned and the pheromone lures replaced. This reconditioning procedure was repeated in February–March 1989. Swarms were considered to have chosen a cavity if a colony was present or if abandoned comb was left inside or on the cavity.

Fig 1. Three sizes of artificial nest cavities (left to right: 31, 13.5, 24 l) attached to a tree in Guanacaste, Costa Rica. The 24 l cavity was inhabited by an Africanized honey bee swarm which had expanded and built combs beneath the cavity.

Fig 2. Two sizes of nest cavities used to test cavity acceptability and preference of European honey bee swarms. The cavity on the left is 31 l, the cavity on the right is 13.5 l.

Experiments with European honey bees

Twenty experimental stations containing 4 nest cavities each were established 15 March 1993 in and around Tucson, AZ, USA. The cavities were attached to the trunks and main branches of mesquite, or other suitable trees, at heights of 2–4 m. Most stations were separated by more than 3 km from other stations. Ten stations were randomly assigned to contain 31 l cavities and the remaining 10 stations received 13.5 l cavities. A weekly rotating system began 25 March in which the sizes of cavities at each site were interchanged after being surveyed. This design eliminated the effect of location and the frequent survey times reduced the temporal effects on the experiment. Swarm attraction was determined by the presence of a swarm inside a cavity when opened. Swarms attracted were visually scored as large, medium, or small. Occupied cavities were replaced with additional new cavities to maintain the same number of empty cavities at each station. Weekly surveys and cavity rotations continued until 20 May 1993 when the swarming season was nearly complete.

RESULTS

Africanized honey bees

Dry years occurred from 1987–1989 in Guanacaste, Costa Rica, with the result that few swarms were available during the spring swarming season. Thus, regular surveys during this time were not as productive as desired and were replaced by periodic surveys. Between these periodic surveys, cavities and stations were sometimes lost to fires, vandalism, or large animal damage. These factors account for the unequal numbers of cavities among which bees could choose. Despite these difficulties, the results of the survey reveal that Africanized honey bee swarms exhibit no preference ($P > 0.3$; χ^2 test) among pulp cavity volumes ranging from 13.5 to 31 l (table I). Both of the larger cavity sizes had swarm occupancy rates of 11%, whereas the smaller 13.5 l cavities were occupied at a rate of 18%.

European honey bees

The honey bees in Arizona were European in descent as no Africanized bees had been reported in the state. Swarm activity during 1993 was greater than during the previous 14 years in the Tucson, AZ area (Thoenes, 1992; and personal observations). The first swarms were captured during the week of 25 March. Numbers of swarms increased quickly until a peak on 15 April which was followed by high numbers of swarms for the next 3 weeks (fig 3). The swarming season lasted about 9 weeks. Throughout the season, the numbers of swarms captured in the 13.5 l cavities averaged about one third that of the 31 l cavities. There was no tendency during the early, mid, or late season for

Table I. Number of Africanized honey bee swarms inhabiting different sized nest cavities.

Cavity volume	*Cavities* [a]	*Swarms* [b]	*% capture*
31 l	83	9	10.8
24 l	75	8	10.7
13.5 l	77	14	18.2

[a] Cavity numbers are based on the combined existing cavities when surveyed in September 1987 and February 1989; [b] no significant difference in swarm numbers for different cavity volumes ($P > 0.3$; χ^2 test).

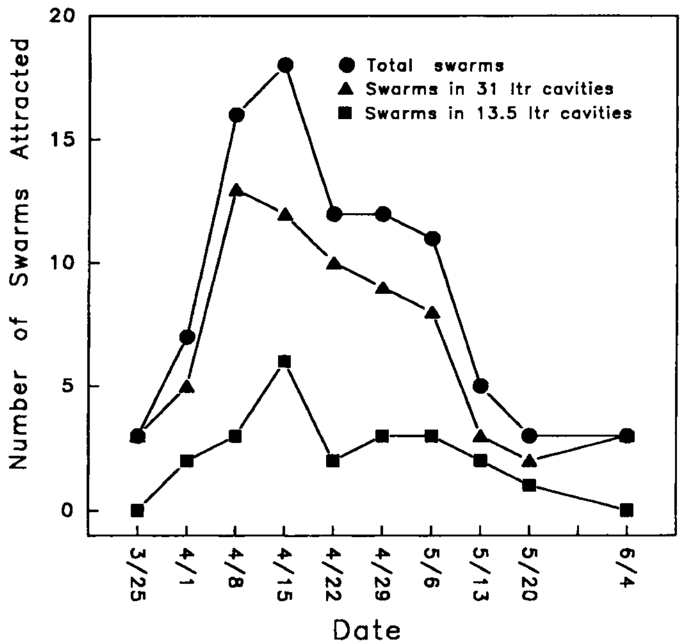

Fig 3. Phenology of European honey bee swarm attraction in spring 1993 in Tucson, AZ, USA.

swarms to change preferences between the 2 cavity sizes.

Seventy-six percent of all swarms occupied 31 l cavities ($P < 0.0001$, table II). Among the 14 stations that were isolated from the nearest station by at least 3 km a 72% preference for large cavities was observed. Six stations occupied 3 locations with each location consisting of 2 cavity stations within 100 m of each other. For these 6 stations, all but 3 swarms selected the 31 l cavities for a large cavity occupancy rate of over 86%.

Data for size of swarms that occupied nest cavities and could be measured, the cavity sizes they occupied, and the phenology of swarming relative to swarm size are shown in table III. Most of the swarms (39)

Table II. Number of European honeybee swarms inhabiting large and small nest cavities.

Cavity volume	*Number of attracted swarms* [a] *(number of stations)*		
	Total (20)	*Isolated sites (14)*	*Sites 100 m apart (6)*
31 l	68 [b]	49 [b]	19 [b]
13.5 l	22 [c]	19 [c]	3 [c]

[a] Figures within a column followed by different letters differ at the level of $P < 0.005$ or more (χ^2 test).

Table III. Swarm size, date of capture, and choice of nest cavity size among European honey bee swarms.

Cavity size	*Swarm size* [a]	*Swarms*	*%*	*Mean week of swarming* [b]	*Median week of swarming* [b]
31 l					
	Large	21	34.4	4.95	4
	Medium	13	21.3	4.85	4
	Small	27	44.3	4.59	5
13.5 l					
	Large	4	19.1	5.50	5
	Medium	5	23.8	4.80	4
	Small	12	57.1	4.58	4

[a] Visual score of size of swarm in opened cavity; [b] week 4 ended 15 April 1993 and week 5 ended 22 April 1993.

were classified as small, while there were 25 large and 18 medium-sizes swarms. No differences in preference for cavity size between the small and large swarms was observed ($P > 0.3$; $\chi^2 = 1.06$). Mean times of swarming for the 6 categories in table III ranged from week 4.58 to week 5.50 and median weeks of swarming were all either week 4 or week 5. The largest numbers of swarms per station were 11 and 9, and the lowest was 1 (3 stations). No trends were noted among the variables of cavity or swarm size with numbers of swarms captured at a location. Thus, no correlations were observed among the variables of swarm size, cavity preference, date of swarming, and number of swarms per station.

DISCUSSION

In the experiments with Africanized bees, all 3 cavity sizes were on the same tree. The fact that even under these ideal conditions swarms appeared to chose randomly a nest cavity indicates that Africanized honey bees exhibit no meaningful preference between cavity sizes of 13.5 and 31 l. These data are not inconsistent with the hypothesis that Africanized bees exhibit no strong preference among different sizes nest cavities within that size.

European honey bees are more selective in nest cavity sizes than Africanized bees. In choice tests, Italian *(A m ligustica)* swarms selected cavities of 13 and 24 l and rejected 5 l cavities (Jaycox and Parise, 1980). Out of 16 swarms of European black bees (*A m caucasica* and *A m carnica*) provided a choice of 5, 13, 24, 44 and 85 l cavities, none chose a 5 l cavity, 1 chose a 13 l cavity, and the remaining 15 chose larger cavities (Jaycox and Parise, 1981). Seeley (1977) reported that European swarms in New York rejected 10 l cavities when also offered 40, 70 or 100 l cavities (11 swarms), rejected 10 l cavities when offered 25 l cavities (4 swarms), and only 1 of 4 swarms accepted a 17.5 l cavity when also offered 25 l cavities. In choice test results in Arizona with European bees, 27 of 32 swarms selected 31 l cavities over 34 l cavities (Schmidt and Thoenes, 1987) and 13 of 20 swarms selected 31 l cavities over 34 l cavities ($P > 0.2$; $\chi^2 = 1.25$) (Schmidt and

Thoenes, 1992). These choice test data indicate that European bees do have distinct cavity volume preferences and they prefer nest cavity volumes of at least 20 l, but will sometimes accept cavities of 13 l, while rejecting cavities of 10 l or less volume.

The crossover experiment with European bees provides a quantitative measure of the acceptability of small cavities by swarms and reveals the strength of swarm preference for one cavity size over another. Although swarms had equal 'take-it-or-leave it' opportunities to select 31 and 13.5 l cavities, 3 times as many swarms accepted the 31 l cavities. We cannot know how many swarms would have selected a 'perfect' cavity had it been available, but we can say that of swarms that found 31 l cavities acceptable, 2 out of 3 rejected the 13.5 l cavities and chose other nest sites. Thus, 13.5 l appears to be near the lower limit of acceptable cavity size for European bees, though rare exceptions are to be expected.

The crossover experiment provides further indications of the difference between preference and acceptability of cavity size. At isolated stations, acceptability alone is measured; but at stations close together, scouts can presumably locate and compare cavities of both sizes and thereby exhibit some preference for size. This appears to be the case as only 14% of swarms chose 13.5 l cavities when 31 l cavities were in a nearby station, whereas 28% accepted 13.5 l cavities when nearby 31 l cavities were absent.

The combined data for European and Africanized bees indicate that European bees are more 'choosy' than Africanized bees and that Africanized bees more readily accept 13.5 l cavities than European bees. The conclusion that Africanized and other tropical bees will accept very small cavities (as low as '2 lb tins' to 9 l) is in agreement with literature reports (Fletcher, 1976; Winston *et al*, 1983; OR Taylor, personal communication) and the general bee industry perception (Tew, 1993). No size acceptability experiments have been conducted with Africanized bees, though preference choice experiments were conducted by Rinderer *et al* (1981, 1982). The conclusions of these authors were at variance with ours: they concluded that European bees have a minimum acceptable volume of 10 l, a maximum acceptable volume of 40 l, and no preference between these extremes, and that Africanized bees have a minimum acceptable volume of 20 l and no clear preference between volumes of 20 and 120 l (Rinderer *et al*, 1982). We have no explanation for the differences other than to note that their sample sizes were small (only 1 of 18 cavity volume options received more than 5 swarms) and statistics and conclusions based on small samples are tentative.

The large number of European honey been swarms captured enabled the analysis of some aspects of swarm behavior. One poorly understood aspect of swarm biology relates to swarm size and behavior: do small swarms behave like large swarms? In the case of the European swarms in our study area, the answer is yes. Small swarms do not prefer small cavities and large swarms large cavities. Rather, all swarms showed a preference for the large cavities. Moreover, there was no temporal differences between production of large and small swarms.

In practical terms, the differences in swarm behaviors between Africanized and European honey bees enables the design of different swarm traps for different situations. Since the 13.5 l cavity is fully attractive to Africanized honey bees, yet excludes two-thirds of the European honey bees, it can be used as a selective Africanized honey bee trap. In addition to being mostly selective for Africanized bees, smaller swarm traps are less expensive to manufacture and ship, easier to transport and deploy, less obtrusive, and more resistant to damage.

Unfortunately, because of the inherent differences in the swarm behaviour of Africanized and European honey bees, it is not likely that a swarm trap attractive to European honey bees, but not at all attractive to Africanized bees, can be designed. Nevertheless, if the goal is to capture European bees for addition to apiaries, then the larger nest cavities are preferable as they are extremely effective in attracting European honey bee swarms (Schmidt *et al*, 1989, 1993; Schmidt, 1994).

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Résumé — Sélection de cavités de nidification par les abeilles africanisées et européennes. Nous avons étudié les préférences dans la taille des cavités chez les abeilles africanisées et les abeilles européennes, en disposant des nids artificiels en bois dans l'environnement afin que des essaims sauvages puissent s'y loger. Les essaims d'abeilles africanisées ne montrent aucune préférence entre des cavités de 13,5, 24 et 31 l disposées côte à côte (tableau I). Des résultats précédents (Schmidt et Thoenes, 1987) avaient montré que dans une situation similaire les essaims européens choisissent les cavités de 31 l 5 fois plus souvent que les cavités de 24 l. Afin de déterminer de façon formelle l'acceptabilité des cavités de 13,5 l et de 31 l pour les essaims d'abeilles européennes, une expérimentation a été réalisée à Tucson, Arizona. Chaque semaine, les cavités de 31 l et de 13,5 l ont été alternées, ce qui ne donnait aux essaims que le choix d'accepter ou de rejeter une taille de cavité. Quand on leur donne un tel choix, les essaims européens choisissent 3 fois plus les cavités de 31 l que celles de 13,5 l (tableau II). Ces résultats démontrent que la taille de la cavité n'est pas importante pour les abeilles africanisées dans le climat tropical de l'Amérique centrale, et que des cavités de 31 l sont hautement préférées par les abeilles européennes en Arizona. Chez celles-ci, on a montré qu'il n'y avait pas de relation entre la taille de l'essaim et celle de la cavité et que, pendant la saison de l'essaimage, la taille de l'essaim ne dépend pas de la période (tableau III). Ces résultats démontrent i) qu'il y a des différences fondamentales dans les critères utilisés pour la sélection du nid par les essaims africanisés et européens, et ii) qu'il est possible de construire des nids de piégeage de petite taille (13,5 l) qui sont attractifs pour les essaims d'abeilles africanisées et rejetés par la plupart des essaims d'abeilles européennes.

abeille africanisée /*Apis mellifera* / essaim / abeille sauvage / cavité de nidification / phéromone

Zusammenfassung — Nisthöhlenwahl afrikanisierter und europäischer Honigbienen. Wir untersuchten, welche Nisthöhlengröße von tropischen afrikanisierten und von europäischen Honigbienen aus gemäßigten Zonen bevorzugt bezogen werden. Hierzu wurden künstliche Nisthöhlen aus einem Holz-Plastikmaterial im Freien aufgestellt, zwischen denen natürliche Schwärme wildlebender Honigbienen auswählen konnten. Die Schwärme von tropischen afrikanisierten Bienen machten keinen Unterschied zwischen Seite an Seite (Abb 1) aufgestellten Höhlen mit dem Innenvolumen von 13,5 l, 24 l oder 31 l. Frühere Ergebnisse (Schmidt und Thoenes, 1987) hatten darauf hingewiesen, daß Schwärme von europäischen Bienen in vergleichbaren Situationen Höhlen mit dem Volumen von 31 l fünfmal häufiger bezogen als Höhlen mit 24 l. Um die absolute Annahme von 13,5 und 31 l Nisthöhlen durch europäische Bie-

nen aus gemäßigtem Klima zu bestimmen, wurden die Höhlen in einer kreuzweisen Versuchsanordnung in Tucson, Arizona aufgestellt. Hierbei wurden Höhlen von 31 l oder 13,5 l an den jeweiligen Orten wöchentlich gewechselt, wodurch die Schwärme in der Umgebung diese Höhlen entweder nur annehmen oder zurückweisen konnten. Bei dieser Wahlmöglichkeit wurden drei mal so viele der 31 l-Höhlen als 13,5 l-Höhlen von Bienenschwärmen der gemäßigten Breiten bezogen (Tabelle II). Die Ergbnisse weisen darauf hin, daß im tropischen Mittelamerika die Größe der Nisthöhle für Honigbienen afrikanischer Abstammung keine Rolle spielt, während in Arizona, USA, die größere 31 l-Höhle von europäischen Honigbienen deutlich bevorzugt wird. Innerhalb der Schwärme von europäischen Honigbienen wies nichts darauf hin, daß kleine Schwärme kleine Höhlen bevorzugen und große Schwärme große Höhlen. Weiter war die Schwarmgröße nicht vom Zeitpunkt innerhalb der Schwarmsaison abhängig (Tabelle III). Diese Ergbnisse zeigen zweierlei: einmal bestehen zwischen Bienenschwärmen der tropischen und gemäßigten Klimazonen grundsätzliche Unterschiede der Kriterien für die Auswahl der Nisthöhle, zum anderen ergibt sich die Möglichkeit, unerwünschte Schwärme afrikanisierter Bienen in kleinen Schwarmkästen mit 13,5 l Volumen zu fangen, die von Bienenschwärmen der gemäßigten Breiten überwiegend zurückgewiesen werden.

afrikanisierte Honigbienen / Schwärme / wildlebende Honigbienen / Nisthöhlen / Pheromone

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