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The biology of two Exomalopsis species (Hymenoptera: Anthophoridae) with remarks on sociality in bees

by

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Abstract: Nests of the neotropical bees *Exomalopsis globosa* differ from those of *E. similis* in the presence of a second entrance, in the angle of the longitudinal axes of the cells and in the type of ground underlying them. In both species two or three females begin to build a nest and most emerging females remain associated with their natal nests. Adult females co-operate in nesting and probably not all of them lay eggs. Developmental mortality was greater in the larger nests of *E. globosa* than in the smaller ones. It is suggested that several adult females inhabit each nest because this behaviour reduces the risks the bees would encounter if they searched for new nest sites.

Exomalopsis is a mainly neotropical genus of bees. Little is known of their biology excepting that of the two North American species *E. solani* Cockerell (**Linsley, MacSwain** and **Smith,** 1954) and *E. chionura* Cockerell (**Rozen** and **MacNeill,** 1957). **Michener** (1974) considered members of the genus to be communal and possibly semisocial.

Five species have been recorded from Jamaica and the biologies of *E. globosa* (F) and *E. similis* Cresson are described here, being, apparently, the first study on tropical *Exomalopsis.* Both species have been collected in Puerto Rico (**Wolcott,** 1948) and Cuba (**Dalmau,** 1970), and the latter also in Panama (**Michener,** 1954) and Florida (**Mitchell,** 1962). They are among the commonest species of bees in Jamaica and adults of both are active throughout the year. The first nest discovered in the study area was located by observing a *Nomada cubensis* Cresson female flying low over the ground.

STUDY AREA AND METHODS

Both species nested in a little-used earth road on a hill near Temple Hall in the parish of St. Andrew. The locality is 300 m above sea level and 13.4 km

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inland. The ground was level and comprised red clay with underlying grit in some places at a depth of 0.5 m or more. Some 34 nests of *E. globosa* were discovered during the year in an area of about 55 m^2, with 0.4 to 2.5 m between neighbouring nests. About 30 nests of *E. similis* were discovered during the same period in an area next to them of about 40 m^2 and 0.5 to 3.4 m separated neighbouring nests.

The nearest nests of the two species were 17.7 m apart. Two additional villages of *E. globosa* were located several km away. One comprised ten nests at a site 790 m above sea level and the other comprised seven nests at a site 30 m above sea level.

Eight nests of each species were excavated at Temple Hall. The nest architecture was recorded and the cell contents and all of the adults associated with each nest were collected. For an hour before excavation, the entrance to each nest was covered with a wire mesh cage. A note was made on whether the bees were entering or leaving their nests when they were collected and whether or not they carried pollen loads. Bees within the nest were caught while it was being excavated.

On each bee the upper inter-ocular distance, the number of hamuli (suggested by **Richards,** 1949) and the length of the marginal cell in the fore wing were recorded to assess size, of which the last proved to be the most useful measurement. Age was assessed by the amount of mandibular wear, and ovarian development by the lengths of the longest oöcytes.

RESULTS

The nests: Each nest bore a circular tumulus of loose earth in the centre of which was the nest entrance. Often the tumulus was washed away by rain and rebuilt with fresh earth from within the nest.

A distinctive feature of *E. globosa* nests, not found in those of *E. similis,* was the presence of a second entrance. This was a lateral tunnel 33 to 80 mm long that reached the surface just outside the periphery of the tumulus. It was closed at the surface and the bees used it only if the main entrance were blocked.

In most other respects nests of the two species were similar (Fig. 1 and Table 1) and so are described together. In each species it is thought (see below) that a few founding females excavated a vertical main tunnel 30 to 45 cm long and from it two or more lateral tunnels at a depth of 10 cm or more. The laterals often had branches and a cell was constructed at the end of each. Presumably the bees that emerged from these cells continued the work because, as more females became associated with a nest, the main tunnel was extended downward (Table 1) and more cells were built.

All but the deepest *E. similis* nest were underlain with grit into which the bees did not dig. Grit was not seen under *E. globosa* nests. Sometimes *E. similis* tunnelled along cracks in the ground up to 3 mm wide and 40 cm deep.

New laterals were excavated and cells built at their extremities. Some of the earth from lower excavations was deposited in the upper, obsolete laterals while the remainder was carried to the surface and added to the tumulus. The bees did not use cells a second time. Nests are known to have been occupied by adults for up to six months.

The walls of the tunnels were lined only with smoothed earth. The laterals were horizontal or directed slightly downward, but parts of some approached the vertical. In *E. globosa* nests, whatever the angle of the proximal portion, the distal 2 to 10 mm of each lateral tunnel and the longitudinal axis of the cell following it

TABLE 1

Data on the live stages in nests of two Jamaican Exomalopsis *species*

	E. globosa								*E. similis*							
Nest number	1*	2	3	4	5	6	7	8	1	2	3*	4	5	6	7	8
Maximum depth of nest (mm)	689	904	680	729	412	456	278	227	770	568	600	334	422	594	517	425
Number of active adult females	19	16	13	11	6	5	3	2	12	9	9	7	6	5	4	3
Number of new empty cells	8	7	7	5	3	2	1	1	1			2			2	
Number of cells being provisioned	2	3	2	1	1	1			3	3	1	1	1	1	1	1
Number of cells containing live eggs	9	5	2	2	1				2	2	1	2	1	2	2	
Number of cells containing live first instar larvae	7	3	2			1			1				1			
Number of cells containing live older larvae	10	13	8	4	1	2			3	4	1	3	2	4	3	
Number of cells containing live pupae		3	2		1						1					
Number of cells containing live adults	5	3	1						1		1			1		
Total number of cells per nest	41	37	24	12	7	6	1	1	11	9	5	8	5	8	8	1

* Nests illustrated in figure 1

sloped downward at an angle of about 40° whereas the longitudinal axes of *E. similis* cells were nearly horizontal.

Cells of similar age were usually close together (Fig. 1). The minimum distance between *E. globosa* cells was about 6 mm, but at least 15 mm separated those of *E. similis*. The cells of both species were nearly ovoid in shape, the maximum diameter of 8.8 (S.D. ± 0.3) mm being toward the back of the cell. In cross section the cells were circular with a slight flattening on the lower side. Both the cells and their entrances were wax lined.

In provisioning a cell several loads of food were deposited towards the back and when sufficient had accumulated the food was moulded into a loaf bearing distinctive ridges on the sides and front (Fig. 2). An egg was attached by both its ends to the food. The cell, which seemed rather large for the amount of food provisioned, was sealed with a spirally structured plug and not re-opened. At least a part of the lateral tunnel was filled with loose earth. The larva remained on top of the food for a few days and made distinctively curved grooves on the surface of the loaf as it fed. Both species spun cocoons and attached faecal pellets to their outer surfaces.

Co-operation among adult females: Two or more adult females were associated with each nest. In most of the nests the number of such females exceeded the number of cells from which bees had emerged, but never by more than four. The correlation of the number of bees with such cells was $r = +0.99$ ($P < 0.001$) for *E. globosa* and $r = +0.98$ ($P < 0.001$) for *E. similis*, and the regression lines calculated to fit the data suggested 2.9 and 3.7 active females to inhabit those nests without such cells. It was, indeed, discovered that the nests from which bees had not yet emerged contained two or three active adult females (Tables 1 and 2).

In *E. globosa* 86% and in *E. similis* 91% of the females were collected as they entered or left their nests prior to excavation. The remaining bees were found inside the nests. More pollen laden females entered all except the smallest nests than there were cells being built and provisioned, but the number of adult females on such cells was correlated in *E. globosa*, r being +0.98 ($P < 0.001$), however, it was not in *E. similis* ($r = +0.61$, $P > 0.05$). All of the active females associated with excavated nests were examined in order to discover if castes of egg laying bees could be distinguished by their size, age or ovarian development. The numbers were 75 *E. globosa* females and 55 of *E. similis*. In some bees the largest oöcyte was 0.1 mm long, whereas all of the other bees dissected possessed one or more oöcytes at least 0.2 mm long; the longest being 1.3 mm. Throughout the year 47% of *E. globosa* and 49% of *E. similis* females possessed oöcytes 0.2 mm long or more. However, in June the respective proportions for the two species were 33% and 61%, and in December they were 59% and 35%. The seasonal difference in each species was significant ($P < 0.05$ in each case). The seasonal differences in the foraging activities of the two species are presented in another paper (**Raw,** 1976).

The marginal cells in both species varied from 1.0 to 1.3 mm long. This measurement was used as an assessment of size. Among the *E. globosa* that possessed oöcytes at least 0.2 mm long, the length of the marginal cell was positively correlated with that of the longest oöcyte in December ($r = +0.65$, $P < 0.01$), but was not so in June ($r = +0.55$, $P > 0.05$). However, the marginal cell length (or the inter-ocular distance or the number of hamuli) and oöcyte length were not correlated significantly in *E. similis*. In neither species was there a significant correlation between age, based on mandibular wear, and oöcyte length, nor was there between age and size. In both species the range in size of bees whose longest oöcyte was only 0.1 mm was as great as it was in those with longer oöcytes and many of the bees with oöcytes 1.3 mm long had been caught as they entered their nests with pollen loads.

Male behaviour: Males were seen leaving and entering nests of their own species and some were discovered in nests during excavation. They flew around the nest entrances presumably to gain shelter or to search for nubile females. They spent much time flying around flowers and pounced on both sexes of their own species that alighted there, but were never seen to pounce on members of other species.

Predators, mortality and fecundity: Female cuckoo bees (*Nomada cubensis* and *N. pilipes* Cresson) flew around the nesting area and entered the nests of both *Exomalopsis* species apparently indiscriminately. During the periods when wire cages covered the nest entrances *Nomada* females, like returning *Exomalopsis,* tried to dig under the edges of the cages to enter the nests. Host and cuckoo bees appeared to ignore each other even when in close proximity, but on one occasion a *N. pilipes,* trying to enter an *E. globosa* nest, was pushed away by three bees as they left the nest. The *Nomada* stood over the entrance while a fourth *Exomalopsis* stood in the entrance, with its head touching that of the *Nomada* for three seconds and then the cuckoo bee ran quickly over the other's back and into the nest. The *Exomalopsis* left the nest immediately afterwards.

Flies, *Megaselia (Aphiochaeta)* near *submarginalis* (Phoridae) flew near *Exomalopsis similis* nests and occasionally entered them. Beetles, *Macrosiagon* species (Rhipiphoridae) were discovered in seven cells of *Exomalopsis globosa* and in four of *E. similis,* but neither *Nomada* nor *Megaselia* was discovered in the cells.

Mortality up to the bees' emergence from their cells was measured and the post emergence mortality is estimated below. The excavated nests of *Exomalopsis globosa* contained 126 old cells and those of *E. similis* contained 83. Bees had emerged from these cells or they had died in them so their remains were discovered when the cells were opened. The emergences of the two species (49% and 52% respectively, Table 2) did not differ significantly at the 5% level. Most deaths, 43% and 37% of the real mortality (**Southwood,** 1966), were during the egg and larval stages and in these circumstances the food was mouldy, but it is not known if the mould causes the deaths. The mortality up to emergence was greater in larger than in smaller *E. globosa* nests ($P < 0.05$).

The largest *E. globosa* nest contained two male pupae, while the second largest contained one male pupa and one emerged male. None of the remaining nests of either species contained males.

When the *E. globosa* nests were excavated 62 bees had emerged from the cells. All but one of them are presumed to have been females. Because an average of three females founded each nest, the total number of adult females associated with the eight nests was estimated to be 85. Seventy females were collected live from the nests giving a mortality among them of 18%. If more than one male emerged from the nests then the incidence of mortality among the adult females was even less than this figure.

In order to estimate the mean number of eggs laid per female of each species the total number of cells in which eggs had been laid was divided by the total number of active females, giving 3.0 for *E. globosa* and 2.3 for *E. similis.* If it is presumed that only females with oöcytes longer than 0.2 mm laid eggs the respective mean figures are 6.4 and 4.8. However, it is likely that the bees had not finished laying their complements of eggs when collected for this study.

TABLE 2

Life tables of the developmental stages of two
Jamaican Exomalopsis *species*

	E. globosa							*E. similis*							
Nest Number	1*	2	3	4	5	6	Total	1	2	3*	4	5	6	7	Total
Total number of cells with eggs	45	34	28	12	6	1	126	34	16	14	8	6	4	1	83
Total number of cells with pupae	23	18	17	9	4	1	72	19	8	12	5	4	3	1	52
Total number of cells with adults	22	18	15	9	4	1	69	19	8	12	5	4	2	1	51
Total number of adults emerged	19	16	14	8	4	1	62	15	8	9	4	4	2	1	43
%survival	42	47	50	67	67	100	49	44	50	64	50	67	50	100	52

* Nests illustrated in Fig. 1

DISCUSSION

The two *Exomalopsis* species were biologically very similar, although differences were discovered in their foraging activities (**Raw,** 1976). The notable differences between their nests were the type of ground underlying them, the presence or absence of a second entrance, and the angle of the longitudinal axes of the cells. The shapes of the food masses of the two species were similar to each other and to those of *E. chionura* (**Rozen** and **MacNeill,** 1957), but without the supporting projection constructed on the loaf by that species. The location of tunnels of *E. similis* along cracks in the ground was reminiscent of the observation of those authors that the entrances of *E. chionura* were located in the sides of cracks up to 2 cm wide. Apparently the observations on *Nomada pilipes* and *N. cubensis* being associated with *Exomalopsis* are new.

There has been some speculation on the extent to which females in *Exomalopsis* species co-operate when nesting. The latter authors suggested that *E. chionura* females may co-operate, **Michener** (1966) thought likewise of *E. solani* and **Hicks** (1936) observed four pollen laden females of *E. torticornis* Cockerell enter one nest.

In both *E. globosa* and in *E. similis* probably a few females begin to build a nest because two or three females were discovered in small nests from which bees had not yet emerged. The degree of relationship among the foundresses is unknown, but in both species it is suspected to be high as new nests were built close to the older ones. The two species may be like *Halictus rubicundus* (Christ) in which usually an individual female establishes a nest and is joined by others before the first brood emerges (**Batra,** 1968).

The numbers of adult bees in the larger *Exomalopsis* nests were very similar to the numbers of cells in them from which bees had emerged, which suggests that most of the emerging bees were females and that they remained associated with their natal nests forming sister colonies. The females might have come from other nests, but the correlation of the data is so close that it casts doubt on this explanation. Probably the only significant movements of bees among nests were from older ones to start the building of new ones. The generations could not be distinguished by examining the amounts of mandibular wear.

The absence of males from the smaller nests suggests that *Exomalopsis* resembles several species known to be social, for example *Bombus* and some Halictidae (**Michener,** 1974) and Vespidae (**Spradbery,** 1973), in producing males only in the older nests.

The categories cited here are those of **Michener** (1974). The two *Exomalopsis* species may be quasi-social, where adult females co-operate in nesting, but are structurally similar. Females are presumed to have co-operated because more pollen gatherers inhabited every nest than there were cells being built and provisioned, a method of assessment suggested by **Michener** (1966). It is more likely that both species are semi-social, being the category in which there is a division of labour (particularly between egg-laying and non-egg-laying females) because a large proportion of bees had vestigial oöcytes (0.1 mm in the present study). **Michener** (1966) discovered a similar situation in *E. solani* foragers.

The estimated fecundity per adult female of *Exomalopsis* was very similar to that of *Augochloropsis sparsilis,* a halictid species with a similar level of sociality (**Michener,** 1964), but it was much lower than the range of 14 to 40 reported in several solitary Aculeata (**Gerber** and **Klostermeyer,** 1970; **Danks,** 1971a; **Raw** 1972; **Freeman** and **Jayasingh,** 1975). In contrast, the proportions of offspring in

Exomalopsis that died in the developmental stages were similar to those in the solitary species mentioned.

It is presumed, in the analysis of the developmental mortality, that *E. globosa* nests of different sizes illustrate the stages through which nests pass as they increase in size; the death rate being significantly greater in nests containing more cells. Despite this apparent disadvantage several bees inhabited each nest instead of building ones of their own.

The reason for this association is suspected to be to reduce the mortality of the young adult females. In several species of solitary bees and wasps it is estimated that the pre-nesting mortality of adult females is 50% or more (**Danks,** 1971a; **Raw,** 1972; **Freeman,** 1973). They do not succeed in building nests presumably because they cannot find suitable nest sites (**Danks,** 1971b) or because they are killed by predators while searching. By remaining associated with their natal nests *Exomalopsis* females avoid the types of post emergence mortality suffered by solitary species because they are not exposed to the risks involved in searching for new nest sites. (Mortality among *E. globosa* females was not more than 18%). This behaviour is likely to have been a major factor in initiating nesting associations of conspecific females in the aculeate Hymenoptera. The significance of adult female longevity in the evolution of apoid sociality will be discussed in a future publication.

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RESUMEN

Los nidos de la abeja neotropical *Exomalopsis globosa* se diferencian de los de *E. similis* por la presencia de una segunda entrada, por el ángulo de los ejes longitudinales de las celdillas, y también por el tipo de tierra debajo de ellos. En ambas especies hay dos o tres hembras que empiezan a construir un nido y la mayoría de las hembras que emergen quedan asociadas con sus nidos natales. Las hembras adultas ayudan en la hechura de los nidos y probablemente no todas producen huevos. La mortalidad durante el desarrollo fue mayor en los nidos más grandes de *E. globosa* que en los más pequeños. Se supone que varias hembras adultas habitan cada nido, reduciendo así los peligros a que estarían expuestas al salir en busca de otros sitios en donde fundar nuevas colonias.

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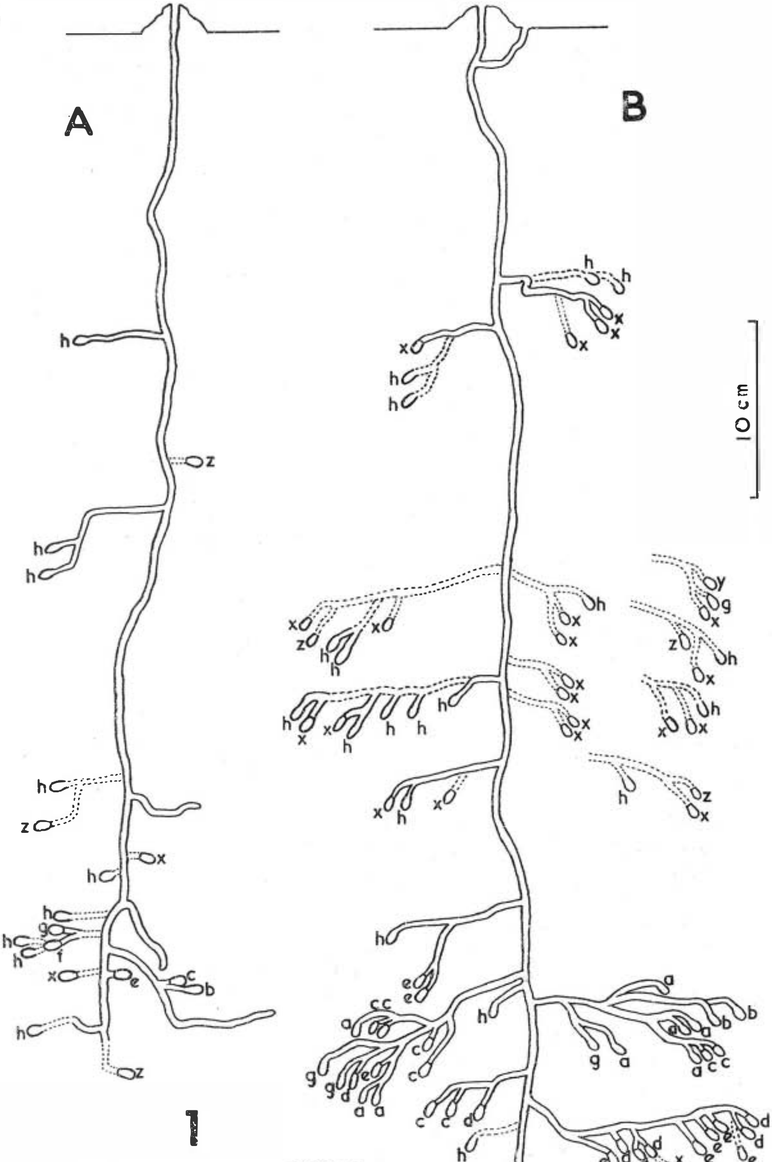
Fig. 1. Nests of *Exomalopsis similis* (A) and *E. globosa* (B).
The lettering is as follows:
a. new, empty cell
b. cell being provisioned
c. " containing live egg
d. " " " first instar larva
e. " " " older larva
f. " " " pupa
g. " " " adult
h. empty, used cell
x. cell containing dead egg or larva
y. " " " pupa
z. " " " adult

(Data on these nests are given in Tables 1 and 2)

Fig. 2. Cell of *Exomalopsis globosa* containing food and an egg, and the lateral tunnel filled with loose earth.



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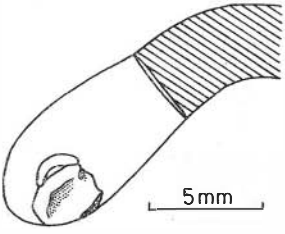

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