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OBSERVATIONS ON THE NESTING BEHAVIOR OF MONIÆCERA ASPERATA (FOX) (HYMENOPTERA, SPHECIDÆ, CRABRONINÆ) WITH COMMENTS ON COMMUNAL NESTING IN SOLITARY WASPS ⁽¹⁾

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Introduction

Moniæcera is a genus of small crabronine wasps which is confined to the southwestern United States and to Mexico. The six known species were revised by PATE (1948). Nothing is recorded concerning the nesting behavior of these wasps save for a brief account by HARTMAN (1905) on *M. abdominalis* (Fox). Hartman found two nests of this wasp in soil near Austin, Texas. The nest entrances were very small and were left open; the wasps approached their nests at a height of 10-13 cm., hovered briefly opposite the entrance, then plunged directly in with their prey. The prey was found to consist of leafhoppers, *Tylozygus bifidus* (Say).

During the last week in April, 1963, I had an opportunity to study a small aggregation of *M. asperata* (Fox) at a locality one mile west of Lajitas, Brewster Co., Texas. Although my notes are decidedly fragmentary, due to the pressure of other work and the difficulty in studying the nests of this very small wasp, they do add considerably to knowledge of the genus. *M. asperata* was found to nest communally, that is, several females share the same burrow, although presumably nesting in independent branches of the burrow. No other North American digger wasps are known to do this, but perusal of the

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literature reveals that sharing of common burrows has been observed in certain European and South American species. This information is reviewed below, and some generalizations are tendered regarding subsocial behavior in solitary wasps.

Nesting behavior of Moniæcera asperata (Fox).

Four nests of this wasps were located over a period of several days, all in bare places in powdery clay-sand among creosote bushes



FIG. 1. — Nest entrance of Moniæcera asperata, enlarged about four times, showing the complete lack of soil about the opening.

(Larrea divaricata) about 25 meters from the banks of the Rio Grande. These nests were scattered about in and around a large colony of the bembicine wasp, *Glenostictia scitula* (Fox); the *Moniæcera* nests were separated from each other by from 1.5 to 3 meters. In each case the nest entrance penetrated the hard surface crust vertically or nearly so, the entrance being more or less circular and only 1.5 mm. in diameter. In no case was there evidence of soil surrounding the nest entrance (fig. 1). The reason for this was evident when one female was observed digging. This female left the nest head-first carrying a small pellet of soil between the head and prothorax; she flew off obliquely about half a meter and dropped it on the ground, then immediately dived back into the nest. This was repeated many times, individual loads of earth being dropped in different places well removed from the nest. This manner of digging at once suggested *Anacrabro ocellatus*, a much better known crabronine wasp. *Moniæcera*

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has a less well-developed psammophore then Anacrabro, but the manner of digging appears very similar.

Females were seen many times bringing in prey to their nests. They would descend obliquely toward the entrance, hover for an instant, then plunge in without pause at the entrance, which was open at all times. The prey was always minute, 1-2 mm. long (the wasp 5-6 mm. long). It was held near the middle of the body, apparently by the middle and hind legs; without exception the abdomen of the wasp was held high, at about a 35° angle with the head and thorax (fig. 2). Several females were captured and the prey taken from them, and other prey were recovered from the



FIG. 2. — Female Moniæcera asperata approaching the nest entrance (lower left) carrying a psyllid with her middle and hind legs. The strong elevation of the abdomen is characteristic.

nests. The 42 examples of prey taken represented six species of adult insects belonging to four families and to two orders, as follows :

- А. DIPTERA :
 - Chironomidæ (determined by S. S. Roback). Procladius sp. near bellus (Loew) - 10.
- B. Hemiptera :
 - 1° Psyllidæ (determined by L. M. RUSSELL). Heteropsylla texana Crawf. - 26. Aphalaroida sp. - 1.
 - 2° Cicadellidæ (determined by J. P. KRAMER). Erythroneura sp. - 1. Sp. of Typhlocybinæ - 1.
 - 3º Miridæ.
 - A minute, undetermined sp. 2.

Observations at nest entrances indicated that more than one female brought prey into each nest. For example, the following records cover a 15 minute period on the morning of April 28 for one nest :

1150/30 : wasp left nest.	1156/25: wasp left nest.
1151/30 : wasp in with prey.	1159/30 : wasp left nest.
1153/20 : wasp in with prey.	1159/50 : wasp in with prey.
1154/10 : wasp left nest.	1200/10: wasp in with prey.
1154/40 : wasp in with prey.	1205/10 : wasp in with prey.
1154/50 : wasp in with prey.	



Evidently three females were provisioning this nest. It was relatively easy to check this by placing a flat stone somewhat loosely over the

> entrance. The wasps were able to leave the nest by pushing their way out beneath the stone, but they could not reenter when laden with prey. Thus there was a « pile-up » of provisioning females hovering over the blocked nest entrance, and in a few minutes all of them were outside hovering about with their prey. In this way it was determined that two of the nests were being worked by two females and two of them by three.

> FIG. 3. — Burrow of Moniæcera asperata terminating in four cells at a depth of 14 cm. Two additional branches of the burrow could not be traced to their terminus.

Excavation of the nests proved very difficult in the dry, finegrained soil. In each instance the burrow was found to be about 1 mm. in diameter and to be nearly vertical; in two cases it was traced to a depth of 10-11 cm. and then lost. In a third nest it was traced to a depth of 14 cm., where four cells were located in a small cluster. The cells measured about 3×5 mm, and were only 7-10 mm. apart. Each cell contained roughly 20 prey, usually well mixed as to species. No eggs were found, but one cell contained a half-grown larva. Presumably these cells were all the work of one female. There appeared to be other branches to this burrow, as shown (fig. 3), but unfortunately I could not trace these to their termini. This particular nest had been occupied by three females, and my belief is that each occupied a different branch of the burrow. Unfortunately this point remains unproved.

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Other records of communal nesting in Sphecidæ.

Although no other North American sphecid has, to my knowledge, been found nesting communally in this manner, there are several records of similar behavior from other continents. JANVIER (1928) reported that the Chilean wasp, *Euplilis longinodus* (Spinola), nests in dry, clay soil and that two or three individuals share a common nest entrance, each preparing one or more separate galleries within the nest. In this species the cells are formed in series along the branches of the burrow. The prey consists of various small muscoid and acalyptrate Diptera.

BRISTOWE (1948) has observed similar behavior in Britain for *Crossocerus (Crossocerus) elongatulus* (Linden), another species which uses various small Diptera as prey. BRISTOWE found this species nesting in the ground in crevices between paving stones. He found up to four wasps sharing a common burrow and showing no hostility to one another when two arrived with prey simultaneously. He was unable to dig out any nests because of their location, but he suggested that each wasp might occupy its own branch of the burrow.

A xylicolous wasp of the same genus, Crossocerus (Coelocrabro) leucostomoides (Richards) (= leucostomus of authors, not Linnaeus) is also known to nest communally. SAUNDERS (1896) found a nest in a cross beam over a door in England, and observed six or eight females entering the same hole. HAMM (in HAMM and RICHARDS, 1926) reports finding a nest in a fallen beech tree and another in a rotten elm; in each case « many » females were seen carrying prey into the same burrow. He states that « each of these must almost certainly have had a nest of its own, branching off from the main passage ». This species also preys upon various small Diptera.

Ectemnius (Metacrabro) quadricinctus (Fabricius), another xylicolous predator upon Diptera, is also reported by Hamm, in the same paper, as nesting communally. « Many females » were entering a burrow near the ground in a rotten, prostrate trunk of an oak; again, he believed that each female had her own branch of the burrow, although he did not dig out the nest.

Discussion.

It is worthy of note that all five of these wasps belong to the tribe Crabronini of the subfamily Crabroninæ. Just how closely related these wasps are it is difficult to say; PATE (1948) considers *Moniæcera* and *Euplilis* closely related, and many *Crossocerus* have a rather

similar facies. I have not surveyed the literature exhaustively, but I know of no other records of communal nesting in the Sphecidæ (2). It is true that some Bembicini have been reported as having nests diverging from a common entranceway, but this seems to be exceptional behavior occurring in unusually dense colonies; in my experience it usually involves a certain amount of aggression between the females. In the cases cited above, the females are not known to show aggression and appear to share not only a common entranceway but also a portion of the burrow itself. Furthermore, in *Moniæcera* at least, it appears to be a regular feature of the nesting behavior even though the nests may be widely spaced.

It is not known what selection pressures have brought about the evolution of communal nests in the Crabronini. All of the species cited above nest either in relatively hard soil or soil with a hard crust, or else in rotten wood. Whether the initial burrow is dug by one female who is later joined by others, or whether several females co-operate in digging it, is unknown. In any case each particular group of females succeeds in occupying a relatively deep nest with less time spent in digging that would otherwise be required. There is no evidence of a division of labor among these females. There were certainly no guards at the nest entrances at any time in Moniæcera asperata, and they have not been reported for the other species. The evolution of guards may be the result of pressure of parasites and predators, but it is difficult to see how communal nesting without division of labor might be influenced by parasite pressure, unless the mere fact that throughout much of the day one wasp or another is likely to be going in or out the entrance in the course of her regular activities does, in fact, reduce the opportunities for parasites to enter.

The sharing of a common burrow by several females, each of which provisions her own cells from one branch of the burrow, is a not uncommon phenomenon among solitary bees, where it has evolved in several subfamilies (MICHENER, 1958). MICHENER regards this as an important step in the evolution of social behavior in the Halictidæ. In this family, one finds certain species in which some of the females act as guard bees, although not always the same ones, and others in which there is a more marked division of labor, extending to pollen-collecting and egg laying. Finally, distinguishable castes occur in some Halictidæ. On the other hand in *Allodape* and related bees of the tribe Ceratinini, and in digger wasps of the tribe Bembicini (as well as in many vespid wasps), progressive provisioning of the brood cells occurs. Contemporary students of the Hymenoptera believe that two different courses of social evolution have been

⁽²⁾ The subgenus *Trypargilum* of the genus *Tryparylon* is unique in that each nest generally contains a pair of wasps, the male guarding the entrance while the female is away (see RICHARDS, 1934). This is, however, not communal nesting in the usual sense.

followed, one by way of communal nesting of females of the same generation and not necessarily related (many bees), the other by way of mother-daughter associations arising from progressive provisioning of the brood (some bees, social wasps, ants). Within the family Sphecidæ, one finds examples of the beginning stages of the first type in the Crabronini and of the second type in the Bembicini. There are no social Sphecidæ, but it is commonly believed that the bees arose from some now extinct stock of sphecids. It is interesting that contemporary solitary digger wasps show tendencies toward both of the courses of social evolution which occur in the bees.

Summary.

Moniæcera asperata (Fox), a species occuring in southwestern United States and provisioning its nests in the soil with small Diptera and Hemiptera, has been found to exhibit communal nesting, two or three females sharing the same burrow. Similar behavior has been reported for four other Sphecidæ, all five belonging to the tribe Crabronini. Thus both types of social evolution believed to occur in bees, by way of communal nesting and by way matrifilial associations, are exemplified, in their initial stages, in the solitary digger wasps.

Résumé.

Moniæcera asperata (Fox) est une espèce existant dans le Sud-Ouest des Etats-Unis et qui approvisionne ses nids creusés dans le sol de petits Diptères et Hémiptères. On a découvert chez cette espèce une tendance sociale qui se manifeste par le fait que plusieurs femelles (deux ou trois) partagent le même terrier. Ce comportement a déjà été observé chez quatre autres Sphecidæ, appartenant tous, comme celui-ci, à la tribu des Crabronini. Ainsi, les deux types d'évolution sociale qu'on croît s'être réalisés chez les abeilles, soit par nidification en commun, soit par association des filles avec leur mère, se retrouvent dans leurs phases initiales chez les Hyménoptères fouisseurs.

Zusammenfassung.

Moniæcera asperata (Fox), eine Art von den südwestlichen Vereinigten Staaten, versorgt ihre Erdnesten mit kleinen Diptera und Hemiptera, und hat gemeinschaftliche Nester mit 2-3 Weibchen die denselben Bau teilen. Ähnliches Verhalten ist von vier andere 6

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Sphecidæ beschrieben worden, all fünf gehören dem Tribus Crabronini an. Wir sehen also, ähnlich wie bei Bienen, den Anfang von zwei Typen von Sozialevolution der solitären Grabwespen, gesellschaftsliche Nester und Mutter-Kind-Verhältnis.

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