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OBSERVATIONS ON THE NESTING BEHAVIOR OF THREE SPECIES OF THE GENUS *CRABRO* (HYMENOPTERA, SPHECIDAE)

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Crabro is a genus of predominantly Holarctic distribution containing approximately 70 species, about half that number Nearctic. In much of the older literature, the generic name *Thyreopus* is used for these wasps. The nesting behavior of only one Nearctic species, *cingulatus* (Packard), has been described, but several of the European species have been studied. Although I have rarely found wasps of this genus nesting, in the summer of 1958 I had the unusual experience of finding three different species nesting, each in a different area. Although none of my observations are especially detailed, they do afford a better insight into the ethology of the genus as well as into the types of specific differences to be expected.

I am indebted to Karl V. Krombein for his assistance in identifying the three species of *Crabro*, to W. L. Downes for determining the dipterous parasites, and to J. G. Chillcott, R. H. Foote, F. C. Harmston, L. L. Pechuman, C. W. Sabrosky, and W. W. Wirth for determining the dipterous prey. Numbers in the text refer to field notes which, together with specimens of wasps and prey, have been placed on permanent file at Cornell University. Larvae of all three species were collected, and these have been described elsewhere (Evans, 1959).

Crabro advenus Smith

During early July, 1958, several wasps of this species nested

around my home two miles south of Ithaca, N.Y. Most of the observations were made on one individual (No. 1546) which was nesting in a bare place among tomato plants in my garden. The soil here is a rather hard clay-loam containing many stones. This individual was first seen on the evening of July first, a very hot day. She brought prey into her nest from 8:10 until 8:30 P.M., by which time the sun had set and it was getting rather dark. The nest entrance was a simple vertical hole in the ground, with no surrounding rim of soil. On the following day she was again observed bringing in prey 7:00–8:30 P.M.; on this date there was a small rim of fresh soil around the entrance, indicating fresh digging inside the nest. On July 3 there appeared to be further activity in the afternoon and evening, but the wasp was not actually seen. July 4 was a rainy day, and the nest was closed from inside all day. July 5 was also rainy, but during a period of partial clearing in the afternoon the wasp was very active, bringing prey at 3:55, 4:00, 4:08, 4:10, 4:12 P.M., and doubtless at other times before and after this. Each time she remained within the nest from 30 seconds to two minutes. On July 6 at 9:00 A.M. she was seen making a final closure of the nest. Earth was loosened with the mandibles from the nest opening, both inside and out, and scraped into the burrow. At intervals the wasp backed into the burrow and packed the soil with the tip of her abdomen. When the filling was nearly complete, the wasp was captured and the nest dug out.

When bringing prey, the wasp entered the nesting area about 20–30 cm. high, flying very swiftly, then plunged headlong into the burrow. Only by covering the nest entrance artificially was I able to observe that the fly is held venter-up against the abdomen of the wasp, grasped by the wasp's middle legs. It appeared to be held somewhat more loosely than in the bembicine wasps, and it is probable that it is held by only one of the middle legs. The burrow entrance is always left open during provisioning, but it is closed with a plug of earth during the night and periods of inclement weather. My impression is that the wasp makes this plug from the inside and spends these periods inside the nest, but I have no actual data on this point.

The nest of this individual was found to contain eight cells which varied in depth from 6 to 12 cm. (Fig. 1, No. 1546). These cells appeared to be arranged along two major branches of the

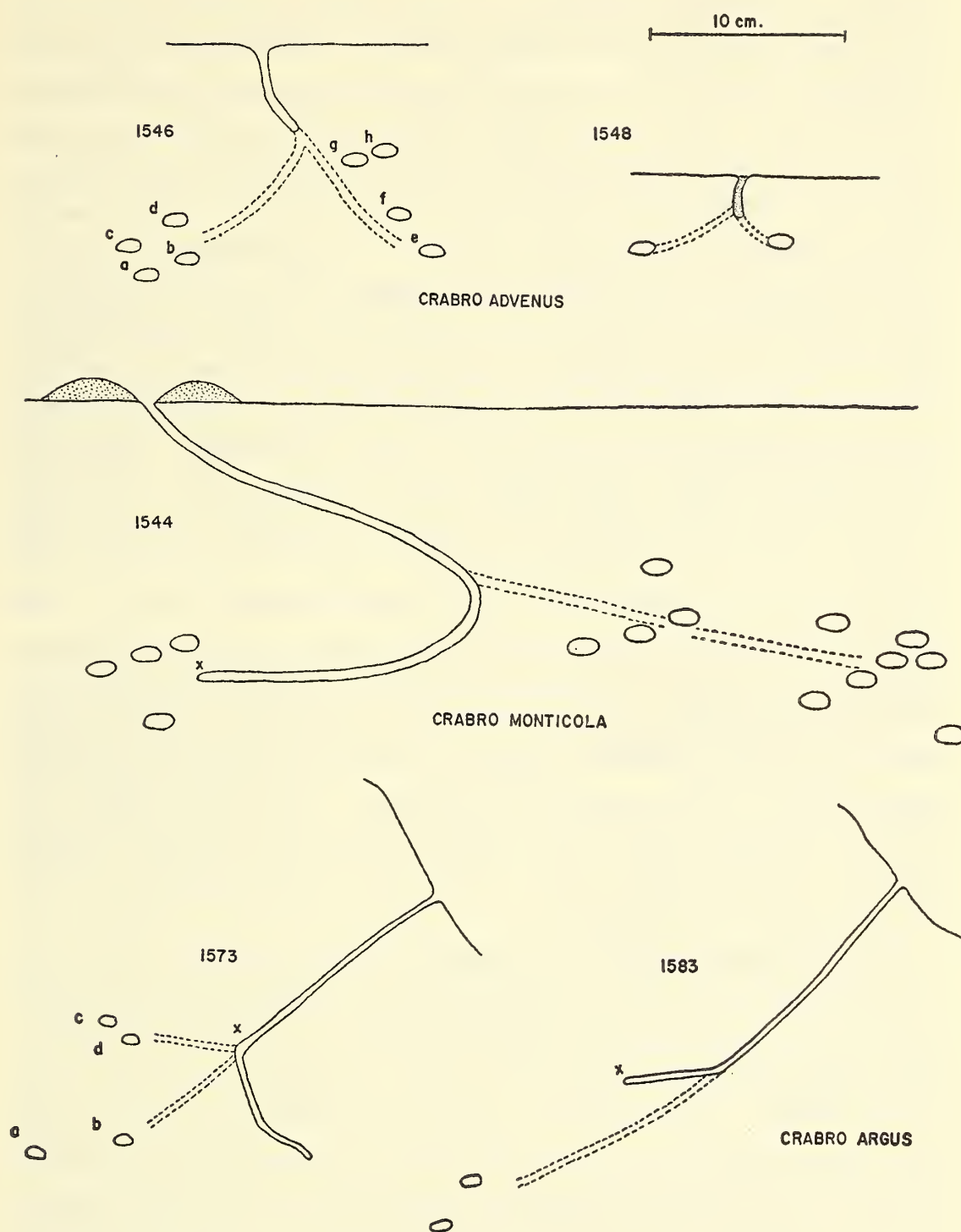


FIG. 1. Nests of three species of *Crabro*. Burrows indicated by dashed lines had been filled with soil and could not be traced exactly. The letter *x* indicates a place in the burrow where flies were found. The two branches of nest no. 1544 (*monticola*) actually formed about a 30° angle with one another; in the drawing this angle has been increased to 180° in order to avoid the need for a three-dimensional drawing.

burrow. From their contents it could be deduced that the wasp had prepared the first cell at the bottom of the burrow, then three additional cells back toward the entrance; she had then filled up this portion of the burrow and dug another branch which eventually contained four more cells, again with the first one deepest, the others progressively back toward the entrance. For example, cell *c* contained a fully grown larva, cell *d* a smaller larva, cell *f* a very small larva, and cells *g* and *h* eggs. In cells *a*, *b*, and *e* no egg or larva was found; cell *b* contained a small carabid larva, and this or another predator may have destroyed the egg or larva in these cells. The cells were broadly elliptical, nearly horizontal, measuring about 14 mm. long and 7 mm. in diameter. Each cell was packed tightly with flies, most of which were venter-up; however, the first fly placed in the cell (which bore the egg) tended to be placed obliquely against the deep end of the cell, while the last fly placed in the cell was often venter-down. The number of flies per cell varied from four to seven, and all appeared to be dead. The egg was found to be about 2 mm. long, whitish and slightly curved. One end of the egg is glued to the back of the head ventrally, while the other end extends obliquely backward over the venter of the thorax. The larva apparently begins feeding through the membranous areas about the mouth-parts or in the neck region. The larva reaches maturity after only five days of feeding.

Only one other nest in this immediate area was marked and dug out; this nest (No. 1547) contained but a single cell, at a depth of 5 cm. Another nest was found on July 6 on the edge of the lawn, about 30 meters away and again in rather hard soil (Fig. 1, No. 1548). This nest was found to contain two cells which were widely separated, one 3 and one 3.5 cm. deep; the burrow had been closed and presumably two was the full complement of cells in this nest. This individual, like the others, was most active in the evening, although at least one fly was brought in at 10:00 A.M.

The 43 flies taken from the various cells of the three nests belonged to six species of as many families. Individual cells usually contained a mixture of species, although a few contained nothing but *Fannia*. The following is a list of the flies and the numbers of each:

RHAGIONIDAE: <i>Chrysopilus proximus</i> (Wlk.)	2
TABANIDAE: <i>Chrysops univittata</i> Macq.	1
OTITIDAE: Genus and species?	1
MUSCIDAE: <i>Fannia scalaris</i> Fabr.	22
CALLIPHORIDAE: <i>Pollenia rudis</i> (Fabr.)	12
SARCOPHAGIDAE: <i>Opelousia obscura</i> Tns.	5

Patton (1897) reported briefly on the biology of this species. He found the species forming "small hillocks under the shelter of shade trees late in August, in Connecticut." He found the prey to consist of *Musca domestica* L., *Sarcophaga* sp., and *Belvosia unifasciata* Desv. The last-named fly is a tachinid which attacks the armyworm, and Patton therefore described *Crabro advenus* as "a protector of the army worm" and suggested destroying it by "pouring strong alkaline washes into the burrows."

Crabro monticola Packard

On June 28, 1958, while collecting insects in flat, open sandy country at North Haven, Conn., I discovered three nests of this larger species of *Crabro*. The nest entrances stood out very prominently, as each was surrounded by a mound of sand about 2 cm. high and 10 cm. in diameter, with the nest entrance in the center. No activity was observed at any of the nests; two of them had the entrance open, the third closed. I dug out the one with the closed entrance and found the female deep in the nest, 40 cm. from the entrance, and captured her for identification.

This nest contained a total of 15 cells which varied in depth from 7.5 to 17.5 cm., in distance from the entrance from 25 to 45 cm. (Fig. 1, No. 1544). The burrow, although long, obviously did not penetrate the soil deeply. At the end of the burrow was a single paralyzed fly; nearby was a cluster of four cells, all packed with flies, three containing eggs and one (the terminal one) a small larva. The remaining 11 cells were arranged in such a manner that they had obviously been constructed off from another major branch of the burrow which had since been filled. The five deepest cells contained cocoons, the next four large larvae, and the last two smaller larvae. Clearly this species, like *advenus*, builds its cells progressively back toward the entrance and may construct a second major branch of the burrow when the area around the first is used up.

The cells of this species were found to measure about 8 by 17 mm.; they are broadly elliptical and nearly horizontal. No cells were found in series, but some were no more than 2 cm. apart. The flies were packed in the cell venter-up, the last one sometimes venter-down. The number of flies per cell varied from 3 to 5. The egg is laid on the first fly placed in the cell; one end of the egg is glued to the middle of the back of the head, the remainder of the egg extending laterad between the eyes and the prothorax ventrally. The newly hatched larva first feeds through a hole cut through the membranous parts of the mouthparts. Only five days are required for the larva to reach maturity.

All flies taken from cells appeared to be dead. The following three species of flies were represented in the numbers stated:

TABANIDAE: <i>Tabanus lasiophthalmus</i> Macq.	25
<i>Chrysops celer</i> O.S.	1
THEREVIDAE: <i>Thereva</i> sp.	1

With the exception of one specimen of *Tabanus lasiophthalmus*, all of these flies were males. The cells containing large larvae or cocoons also contained the remains of many additional specimens of *T. lasiophthalmus*.

A second nest (No. 1545), only about two meters away, was also dug out. The entrance to this nest was open, but no adult was found in association with the nest. This nest contained 11 cells which varied in depth from 11 to 20 cm. Ten of these cells contained cocoons, the eleventh only decomposed flies. Each cocoon was surrounded by the wings of flies, and all the wings noticed appeared to be those of *Tabanus lasiophthalmus*.

The cocoons of this species are broadly elliptical and measure about 6.5 by 15 mm. They are fragile, consisting of little more than a single layer of sand grains which have been cemented together. From the outside they appear rough, since the sand grains differ in size and shape. From the inside, the wall of the cocoon is smoother and distinctly shining, as if coated with brown shellac; it is somewhat translucent as a result of light passing through the sand grains. There is little evidence of silk in the walls of the cocoon, although there may be some fibers in the matrix between the sand grains.

On July 28, 1959, Dr. and Mrs. Henry Dietrich of Cornell University found a large nesting aggregation of *Crabro monticola* at

Echo Lake, Mt. Desert Island, Maine. There were perhaps as many as 100 nests, all in flat sandy soil and most of them in a well-traveled path. Each nest entrance was surrounded by a prominent mound of sand. Although the wasps usually entered their nests very quickly with their flies, on many occasions the nest entrances were damaged or covered by persons walking along the path. Wasps which could not gain entry into their nests frequently left their flies on the ground and did not touch them again. The Dietrichs caught several of the wasps and picked up several of the flies from the ground. The flies, all males, belonged to two species:

TABANIDAE: <i>Stonemyia tranquilla</i> O.S.	2
<i>Tabanus microcephalus</i> O.S.	8

It is interesting to note that both *Tabanus microcephalus* and *T. lasiophthalmus* are hairy-eyed species (subgenus *Hybomitra*). It is also interesting that in two widely separated localities male tabanids were used almost exclusively. Presumably the hunting behavior of *Crabro monticola* is such that males of this group of tabanids are encountered more than any other flies.

Crabro argus Packard

During the period July 9–August 16, 1958, I found this species nesting in considerable numbers in a sand-bank near Six-mile Creek, Ithaca, N. Y. About 25 nests were marked during this period, and 13 of these were eventually dug out; however, the total number of nests was probably in excess of 50. Individual females appeared to make a series of successive nests, spending only a few days with each. All nests were constructed in rather fine-grained sand on the two sides of a small erosional draw in the sand-bank; the slope of the sides varied from 20 to 80 degrees, and there seemed to be no particular preference for any special degree of slope. The nests tended to be widely scattered over the available space, and in only a few cases were active nests found closer together than half a meter.

One female (No. 1569) began a nest at 11:00 A.M. on August 2. Selecting a place where the slope was about 40°, this female began loosening earth with her mandibles and pushing it out with her legs. By twisting the body first to one side and then the other, and sometimes assuming an inverted position, she succeeded in boring into the bank at about a 90° angle with the slope

of the bank. Five hours later fresh sand was still being pushed out the entrance, indicating that several hours are required to complete the burrow. The sand which is pushed out merely accumulates at the entrance or rolls down the bank; it is not leveled by the wasp. The entrance to the nest is never closed at any time by the wasp, although it sometimes becomes blocked by the slippage of sand from above, particularly following a rain.

Having completed the burrow, the female captures a number of flies which are stored in the burrow (usually at the bottom). Only after the accumulation of a number of flies is a cell constructed and the flies placed in it. For example, No. 1559 was observed bringing flies into a relatively new nest on July 25. When this nest was dug out it was found to contain five fresh flies at the bottom of the burrow, but no cells. No. 1570 was observed bringing in flies during the morning and afternoon of August 2; when this nest was dug in the evening it was found to contain one fully provisioned cell plus one additional fly in the bottom of the burrow. No. 1573 (see fig. 1) was found to have four fully provisioned cells; there were five fresh flies in the burrow which had not yet been placed in a cell.

Provisioning may occur at any time of day, occasionally as late as 7:00 P.M., but is at its peak on sunny days between 10:00 A.M. and 1:00 P.M. Females enter the nesting area only 15–30 cm. high with a flight characterized by rapid side-to-side undulations. As they approach the nest their forward flight slows down and the swerving from side to side becomes more marked; once over the entrance they plunge rapidly into it. The fly is held tightly beneath the body, probably by both middle legs. When pursued by miltogrammine flies, females laden with prey back up in flight slowly, with pronounced side-to-side movements. Sometimes they back up several meters, the miltogrammine following, face-to-face with the wasp. Eventually the wasp darts forward very quickly and regains the nesting area, only to back up again if the miltogrammine is still in pursuit. The miltogrammine flies in question all belonged, I believe, to the genus *Senotainia* (see further discussion of parasites below).

The burrow of *Crabro argus* is very small, only about 3 mm. in diameter, and is generally at about a 90° angle with the sand surface. Most burrows are nearly straight at least for a considerable distance from the nest entrance; at the bottom there

may be various kinks and side-burrows associated with the cells. Cell depth (measured from the entrance rather than from the soil directly above) varied from 18 to 35 cm. (average 27 cm.). The cells are very small, measuring about 6 by 9 mm. Most of the nests dug out contained but one cell, but three contained two and one contained four. In the nest containing four cells (No. 1573; fig. 1) the female was apparently preparing a fifth cell; there were several flies in the burrow at *x* which would presumably have been used to provision the fifth cell. No. 1583 (also figured) is a typical two-celled nest; in this nest there were also flies in the burrow at *x*, indicating that a third cell would eventually have been prepared. However, it is probable that the total number of cells per nest is never very large. Of the nests that were marked, only one was still active after as long a period as four days. Some tendency was noted for cells to be constructed progressively back toward the entrance, as in *advenus* and *monticola*. For example, in nest No. 1573 (see figure) cells *a* and *b* appeared to be older cells (each contained maggots of miltogrammine flies) while cells *c* and *d* appeared to be fresh cells (each contained a wasp egg). Within a given nest, the cells tended to be separated by from 2 to 4 cm. Since the burrow and cells are very small in relation to their depth, it was often difficult to determine the exact relationship of the cells to one another; in fact, a number of cells were undoubtedly overlooked in my excavations.

The number of flies in fully provisioned cells varied from 10 to 19 (average 15); needless to say the number of flies was related to the size of the flies, since the wasp merely packs the cell full. Most of the flies are placed in the cell venter-up, but the top few flies may be on their sides or even dorsum-up. The egg was invariably found on the fly deepest in the cell. The egg is about 2.3 mm. long, and is laid with its anterior end pressed against the ventro-posterior part of the fly's head, the remainder of the egg extending free.

Seventy-nine flies taken from cells or from wasps were found to represent 15 species belonging to three families. In some cases the flies in individual cells were well mixed, in other cases they represented one or a few species. The following is a list of flies found to be used as prey by this wasp:

DOLICHOPODIDAE

Argyra albicans Lw. 2

<i>A. calceata</i> Lw.	1
<i>Dolichopus coercens</i> Wlk.	1
<i>D. gladius</i> VanD.	1
<i>Hercostomus barbatulus</i> Lw.	3
<i>H. crassicauda</i> Lw.	6
<i>H. frequens</i> Lw.	8
<i>H. ornatus</i> VanD.	13
<i>Liancalus genualis</i> Lw.	3
<i>Plastoneurus vagans</i> Lw.	17

EPHYDRIDAE

<i>Parydra bituberculata</i> Lw.	10
<i>P. borealis</i> Cr.	1
<i>P. breviceps</i> Lw.	4

MUSCIDAE

<i>Lispe albitarsis</i> Stein	7
<i>L. nasoni</i> Stein	2

Crabro argus was attacked by two miltogrammine flies in this area. The flies which were commonly seen pursuing provisioning wasps appeared to belong to the genus *Senotainia*. One which was captured was identified as *S. sp. nr. trilineata* Wulp. There were four maggots in cell *b* of nest No. 1573 which may have represented this species, although they were not reared successfully. Cell *a* of this same nest contained a single large maggot which, in a rearing tin, actually moved about very actively and devoured a medium-sized *Crabro* larva in a neighboring cell. This maggot was successfully reared and the adult identified as *Phrosinella ?fumosa* Allen. Allen (1926) says that dissections of one species of this genus "indicate that they deposit large, active maggots. The female of this species [*fulvicornis* Coq.] has also been observed digging a pit in the sand near the burrow of fossorial Hymenoptera, for which its flattened fore tarsi are admirably adapted. Larvae were deposited in the pit. It seems probable that from this point, they burrow through the soil to the cell of their host. . . ."

Published information on *Crabro argus* consists of two host records. Hartman (1905) remarks that this species confines itself to a single species of the genus *Dolichopus*. Dow (1930) records a specimen from White Plains, N.Y., taken with the dolichopodid fly *Rhaphium vanduzeei* Curran.

DISCUSSION

Obviously there are too many unanswered questions regarding the nesting behavior of these three species to permit a detailed comparison. There are, however, several gross differences which deserve consideration (Table I). It should be pointed out that in

TABLE I

A COMPARISON OF SOME ASPECTS OF THE NESTING BEHAVIOR OF THREE SPECIES OF *Crabro*

Species	Nesting site	Type of prey	Cells per nest	Cell size	Distance of cells from entrance
<i>advenus</i>	Flat, heavy soil	Chiefly Muscoidea	Several (2-8)	7 × 14 mm.	6-12 cm.
<i>monticola</i>	Flat sand	Chiefly Tabanidae	Many (11-15)	8 × 17 mm.	25-45 cm
<i>argus</i>	Sloping sand-banks	Chiefly Dolichopodidae, Ephydridae	Few (1-5)	6 × 9 mm.	18-35 cm.

each case (if one includes published records) the generalization regarding type of prey is based on populations from more than one locality. It can hardly be doubted that these species hunt for flies in different ecological situations. They also nest in different situations, and here again (except for *argus*) there are records for more than one locality. Differences in nest depth, as is generally the case, reflect differences in soil type and in size of the wasp. The manner of flight of provisioning females of *argus* seems to be distinctive, and this species appears to grasp the prey more tightly than does *advenus*, though these points need further study.

Otherwise, one finds these wasps to be very similar in their nesting behavior. The flies are apparently killed by the sting of the wasp. They are carried to the nest beneath the body of the wasp, apparently held by one or both of the wasp's middle legs. Generalizing about the British species, Hamm and Richards (1926) state that "in flight the prey, with its ventral surface uppermost, is gripped round the neck by the right or left middle tibia; as the *Crabro* enters its burrow the prey is passed back to the hind legs and held by the spurs at the end of the tibiae."

Whether this statement is generally applicable to the American species is uncertain.

All three species leave the nest entrance open during periods of provisioning, and plunge headlong into it with their flies. Two of the species (and probably all three) store the flies in the burrow before preparing a new cell and placing them in it. The egg is always laid on the throat of the first fly placed in the cell. Iwata (1942) terms this the "*Crabro*-type" of oviposition and presents several figures (46-50) which closely approximate the manner of oviposition of the three species under consideration.

The Raus (1918) studied another North American species of *Crabro*, *cingulatus* Packard, in Missouri. This species resembles *argus* in that it makes long, slender burrows in sand-banks and preys on Ephydriidae. As in other species of the genus, the prey is killed by the sting. The nest entrance is left open during provisioning, and the flies are allowed to accumulate in the burrow before being placed in a cell. They found from two to eight cells per nest, each cell containing from 11 to 20 flies. Hamm and Richards (1926) present a review of the species occurring in Britain, *cribrarius* Fabricius, *peltarius* Schreber, and *scutellatus* Fabricius. These three species all nest in flat sand, the first two preying chiefly upon Muscoidea, the last upon Dolichopodidae; in most details they closely resemble the North American species.

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