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NESTING AND OVARIAN DEVELOPMENT IN *GEOTRUPES CAVICOLLIS* BATES (Coleoptera: Scarabaeidae)[1]

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ABSTRACT

The relation between the structure and function of the ovary and the reproductive behavior, specially nesting, is studied in *Geotrupes cavicollis* (Coleoptera: Scarabaeidae: Geotrupinae). The obtained data are compared with what is known of other species of Geotrupini. Some interesting aspects stand out: 1) A very low fecundity limited both by ethological and physiological phenomena. The ethological limitation is evident, at least under laboratory conditions, because part of the completely mature oocytes are not laid due to a slow preparation of the brood masses. The physiological limitations determine, although there are two ovaries with six ovarioles each, a definite morpho-physiological reduction of fecundity, since maturation of more than one oocyte per ovariole has never been observed. 2) Under laboratory conditions each beetle pair prepares only one nest during a prolonged period of time as a result of slow nest formation process. It is very possible that on the field pressure exerted by a rapid depletion of food may force the preparation of more than one nest. In the laboratory, with all conditions optimized, a sole nest can contain a maximum of 5 brood masses. 3) Brood masses are prepared in groups of two, with a delay of a few hours in each case. A considerable number of days will elapse before the next group is prepared. As a consequence, in the same nest, brood-masses with third stage larvae may be found together with masses containing recently laid eggs. 4) An incipient bisexual cooperation occurs and the male helps the female in provisioning the nest with dung. The formation of each of the brood masses is the exclusive task of the female.

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RESUMEN

Se estudia el comportamiento reproductor, en especial la nidificación de *Geotrupes cavicollis* asociándolo con el estado y función del ovario. Los datos obtenidos se comparan con lo conocido de otras especies de Geotrupini (Geotrupinae: Scarabaeidae: Coleoptera). Resaltan algunos aspectos interesantes como son: 1) Una muy baja fecundidad limitada, por lo menos en el Laboratorio, tanto por fenómenos etológicos como fisiológicos. La limitación etológica se pone de manifiesto porque una parte de los ovocitos que maduran totalmente no llega a ser ovipuesta dado el sistema lento de preparación de las masas-nido. Las limitaciones fisiológicas quedan de manifiesto ya que aunque existen dos ovarios, con seis ovariolas cada uno, indudablemente se presenta una marcada reducción morfo-fisiológica de la fecundidad, ya que nunca se ha visto madurar más de un ovocito por ovariola. 2) Como consecuencia del lento proceso de formación del nido y de la existencia de una masa estable y renovada de alimento, en condiciones de laboratorio cada pareja prepara un sólo nido durante un período muy prolongado. Es muy posible que en condiciones de campo la presión ejercida por la rápida desaparición del alimento obligue a preparar más de un nido. En el laboratorio aún optimizando todas las condiciones, el nido único ha tenido como máximo 5 masas-nido. 3) Las masas-nido son preparadas por conjuntos de dos, separadas entre sí por lapsos de pocas horas, y que presentan con el siguiente conjunto un intervalo de un número considerable de días. Esto trae como consecuencia que en un mismo nido puedan encontrarse masas con larvas de tercer estadío junto con masas con huevos recién puestos. 4) Se presenta una incipiente cooperación bisexual por medio de la cual el macho ayuda a la hembra al aprovisionamiento del nido. La formación de cada una de las masas-nido es tarea exclusiva de la hembra.

INTRODUCTION

Nidification in *Geotrupes* (a typical Geotrupini, the least specialized tribe of Geotrupinae) presents several features common with those of the most primitive Scarabaeinae burrowers. This, together with the presence in Geotrupini of a series of supposedly general morphological features, have led Halffter and Matthews, 1966, and Halffter and Edmonds, 1982, to suppose that Scarabaeinae derive from an ancestor of the geotrupinoid type from which they greatly differ in some characteristics closely related to coprophagous feeding and to the extraordinary nesting evolution, which allows a very pronounced reduction in the number of eggs laid. The most notable amongst these apotypic features (see discussion in Halffter and Edmonds, 1982) are the extreme ovarian reduction (Fig. 1-A) and the membranous structure of the incisive area of the mouthparts in the adult. A less specialized structure is observed in the Geotrupini: mouthparts are sclerotized and sharp; the body is that of a generalized coleopteran burrower, compact, strong legged, with few modifications. They retain still two ovaries, with six ovarioles each, (the number which we consider basic in the Scarabaeidae family), but according to species the ovarioles present different degrees of reduction (Fig. 1-B). In some species this reduction is extreme, to the point in which several ovarioles actually become residual. Also, as it is mentioned in this paper, the production of oocytes by the ovariole in minimum, apparently one for each ovariole.

The Geotrupini present a relatively complex level of nidification, with male-female cooperation. In the most simple nesting schemes, there is a great similarity between the nest and a feeding sausage. In other species there exist compound nests with brood masses in different branches, differing from the feeding sausages.

In this paper we establish the relation between the behavior during nidification and the ovarian development; we also include an analysis on reproduction in its broadest sense: nesting, sexual cooperation and larval development.

MATERIALS AND METHODS

Materials

Geotrupes cavicollis Bates comes from La Michilía Biosphere Reserve, located between 23°30' and 23°25' latitude North and 104°21' and 104°15' longitude West, in the State of Durango, México, in the Sierra Madre Occidental, with altitudes ranging between 2,250 and 2,850 m. This species and *Copris klugi sierrensis* Matthews are the largest most abundant coprophagous Scarabaeidae in the area. *G. cavicollis* prevails in pine-oak forests and in forest-prairie ecotone zones.

For Scarabaeinae and Geotrupini in La Michilía, adult activity period or activity on the surface is very short. The only time one can find adults on the surface is from late June to September (the warmest and rainy season). The rest of the time they are not found on the surface or they do not exist due to the combination of a well defined and prolonged dry season with cold winters in a dry mountain climate.

Table 1
Temperatures 1981 - 1983

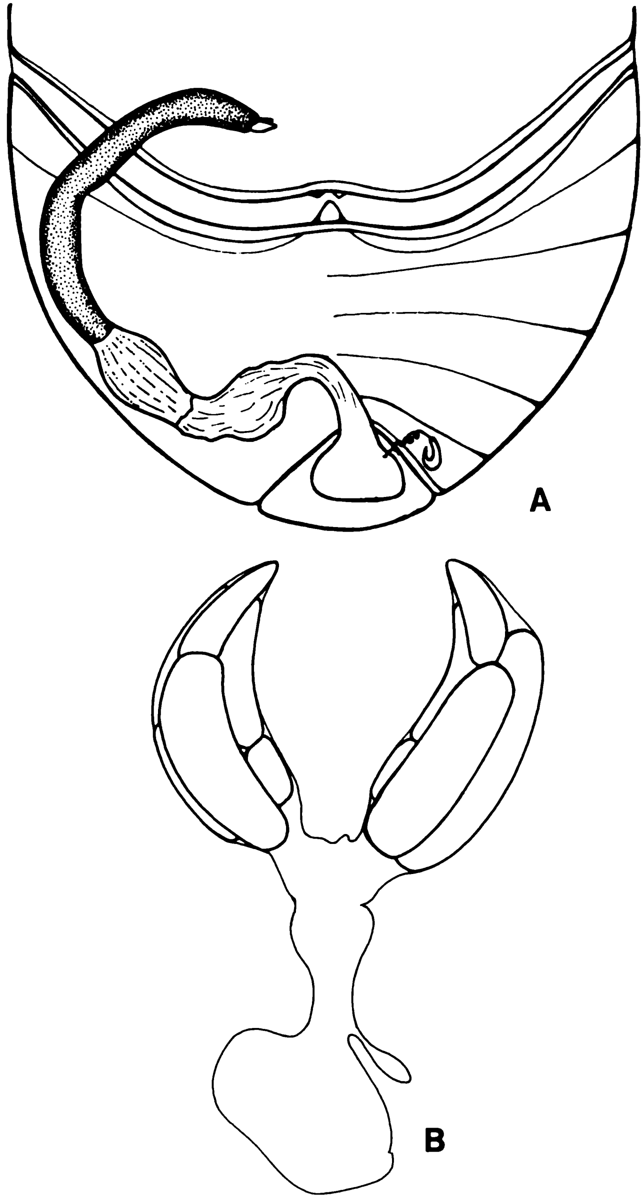
	In "La Michilía"	At The Laboratory
Mean annual temperature:	12.25°C	17.38°C
Mean temperature of coldest month:	6.37°C (January)	12.7°C (January)
Mean temperature of hottest month:	16.25°C (June)	23.97°C (July)
Mean temperature of months with greatest surface activity for *G. cavicollis:*	June: 16.25°C July: 15.45°C August: 15.70°C	June: 23.02°C July: 23.97°C August: 22.45°C

Precipitation In "La Michilía"

Mean annual precipitation (1981-1983): 581 mm (506-728 mm).

Figure 1

Female reproductive system. A- *Phanaeus daphnis* Harold (Scarabaeinae). B- *Geotrupes cavicollis* Bates. In Scarabaeinae as in Geotrupini fecundity is very low. There was only one ovary with one ovariole present in all the Scarabaeinae studied; on the contrary Geotrupini have two ovaries, with six ovarioles each, but these, at least in the case of *Geotrupes cavicollis* produce only one ovocyte each. In *G. cavicollis* the six ovarioles of each ovary are in close contact (the drawing shows only three ovarioles in each ovary). Each ovariole has one oocyte at different maturation levels and one germarium (the apical part). The pedicels of each ovariole are extremely short, actually they are not distinguished individually; they open at the common oviduct, which is also rather short.



A

B

Methods

Field observations on behavior and ecology, and the collection of material (one portion to be studied in laboratory conditions, another to be fixed at the moment of capture for a subsequent histological analysis) were carried out at La Michilía during a period of two consecutive years.

We used two kinds of terraria for laboratory work. The first, simple and unexpensive, is a plastic bucket cut in half lengthwise and joined together again with adhesive tape so that the two halves can be easily separated in each inspection.

Two thirds of the bucket are filled with soil. The cover is a screened wooden frame with a plastic semicircle placed on top of it to graduate the loss of humidity. These buckets are 48 cm high by 33 cm major diameter.

It is possible to lift and take off one of the halves without spilling the contents by carefully leaning the bucket and cutting the adhesive tapes. Afterwards the bucket is closed and joined again with adhesive tape, placing it in its original position. In this way observations on the evolution of the nest were made, without causing drastic disturbances.

The other more expensive terrarium is made of two parallel cristal walls, 1 m high by 1 m wide, placed in an aluminum frame with a separation between the two walls of 2.5 cm. On the outside, the cristal walls are covered with a thin sheet of metal foil that keeps the light off and can be easily raised to observe the underground behavior of the beetles, without disturbing them (Fig. 2).

Virgin females, male-female couples, and copulated females were placed in both kinds of terraria. Food provided every two days consisted of fresh cow-dung.

Figure 2

Terrarium consisting of an aluminum structure and two parallel sheets of glass. Each one of these is covered by an aluminum sheet in order to keep the light out. The aluminum sheet is lifted in the photograph. This type of terrariums allow the observation of underground behavior without any need of manipulation.

According to a pre-established program, every ten days two bucket terraria containing beetles of exactly the same age were inspected. One of these terraria was closed again after examination, so the nidification process would continue. In the other the couple was killed in order to study the gonads. Each year it was necessary to assemble an initial number of terraria (40, taking into account that some females could die), enough for the inspection process every ten days during five months (from July to November), gradually discarding terraria by fixation of beetles or natural death.

Gonads extracted from dissected specimens were placed in Ringer solution and later fixed in an alcoholic solution of acetic acid, formol and dimethyl sulfoxide and embedded in paraffin. Cuts of 6 and 8 microns were made and stained with Pas-hematoxylin.

ETHOGRAM

In order to feed and nest *G. cavicollis* prefers, of all excrements available at "La Michilía", cow dung and horse dung, in that order. We have never observed a nest built with carrion, but with certain frequency adult specimens are found under carcasses or carrion bait. *G. cavicollis* is a nocturnal species.

Feeding galleries

On the field as in the laboratory, *G. cavicollis* prepares between one or two feeding galleries during gonadic maturation (35 to 40 days from the time of emergence). Feeding galleries start immediately below or next to the cow-dung pad. Their average length is 11 cm by 3 cm width, and their maximum depth is 10 cm.

On the field 90% of the specimens were collected inside feeding galleries, the remaining 10% were found eating immediately below the fresh cow-dung pads, in cavities formed while burying or consuming the dung.

Both the female and the male build feeding galleries. In most cases couples are found inside the galleries, specially when the time for nesting is nearby (Fig. 3).

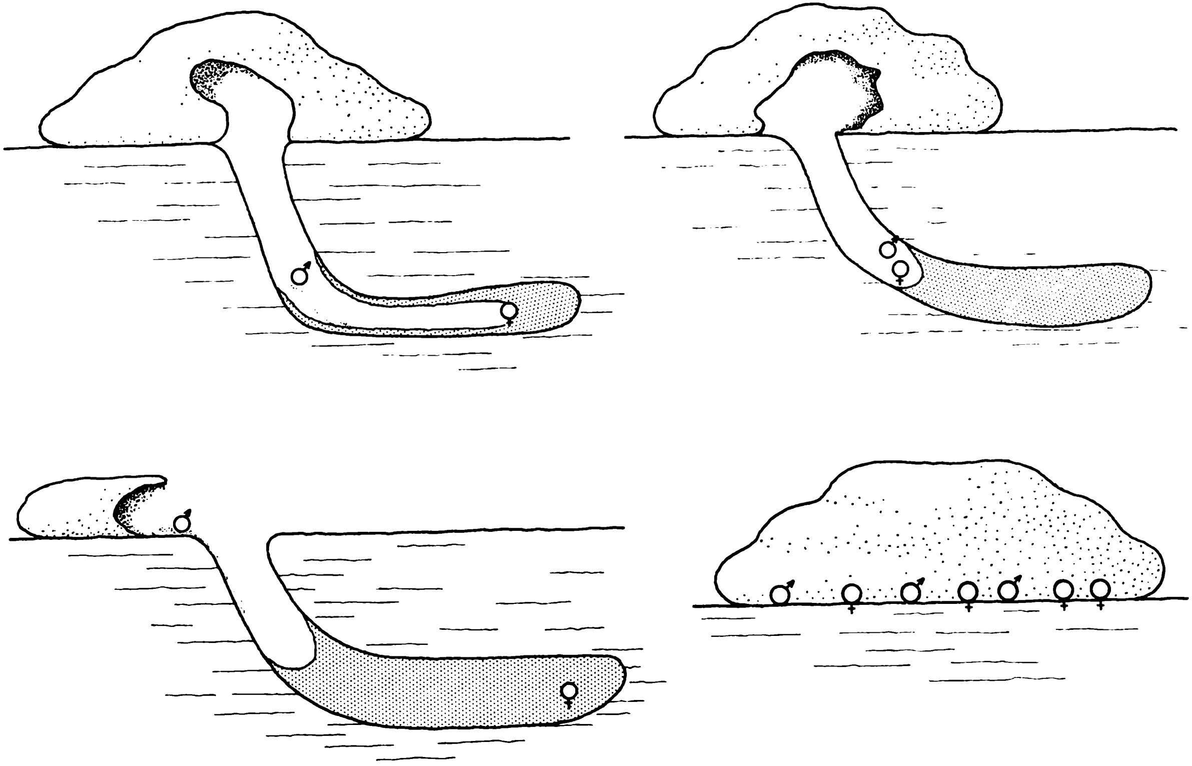


Figure 3

Three stages of a feeding gallery. Notice that before the provisioning is finished, the walls of the gallery are lined with dung to consolidate them. The feeding galleries are frequently occupied by a couple. Lower right diagram –specimen distribution under a cow dung before the gallery excavation has begun.

Feeding galleries observed on the field as in the laboratory were always simple, not branched neither racemose.

Nest burrowing

Between 35 and 40 days after eclosion (field conditions: from mid to late June) burrowing of the new gallery destined to become the nest is initiated. The female begins and later on a male joins in, although he will not participate in the burrowing. Burrowing is done by the female using her front legs. When a certain amount of loose soil has accumulated, it is pushed with the aid of head and pronotum towards the entrance of the gallery, and set aside before the beetle goes back to the inside to continue digging; in this way she will continue to enter and leave the gallery under construction until an adequate length is attained. The diameter of the gallery varies between 2.5 - 3.0 cm.

In the laboratory, while the female digs the gallery, the male remains in the cow-dung. Once the burrowing is finished, the female begins with dung provisioning. At this moment the male joins the female for preparing the nest. He begins to shred dung from the cow-dung pad, pushing it towards the entrance of the gallery and dropping it. The female is inside compacting layer by layer the dung brought in by her, she retreats through the gallery and gathers the pieces of dung dropped in by the male, going on with her refilling task (Fig. 4).

The female also leaves the nest in search of dung, meeting sometimes with the male at the entrance or in the upper part of the gallery. It is always the female the one that compacts what is to be the brood mass. To form the brood mass, she begins by placing dung on the wall and afterwards on the bottom of the branch (Fig. 4), compacting it with her head, pronotum and forelegs.

We have observed that when the female delays in reaching the surface, the male penetrates to a certain depth inside the gallery taking fragments with him and making the job easier for the female. The collaboration of the male by dropping dung and even introducing it into the gallery is an important joint task, since there is a saving of time and dung is stored fresh and rapidly.

Nest burrowing by the female and male cooperation in carrying material has been observed in European species of Geotrupini by Fabre, 1897, Ohaus, 1909, and Spaney, 1910, in *Typhoeus*

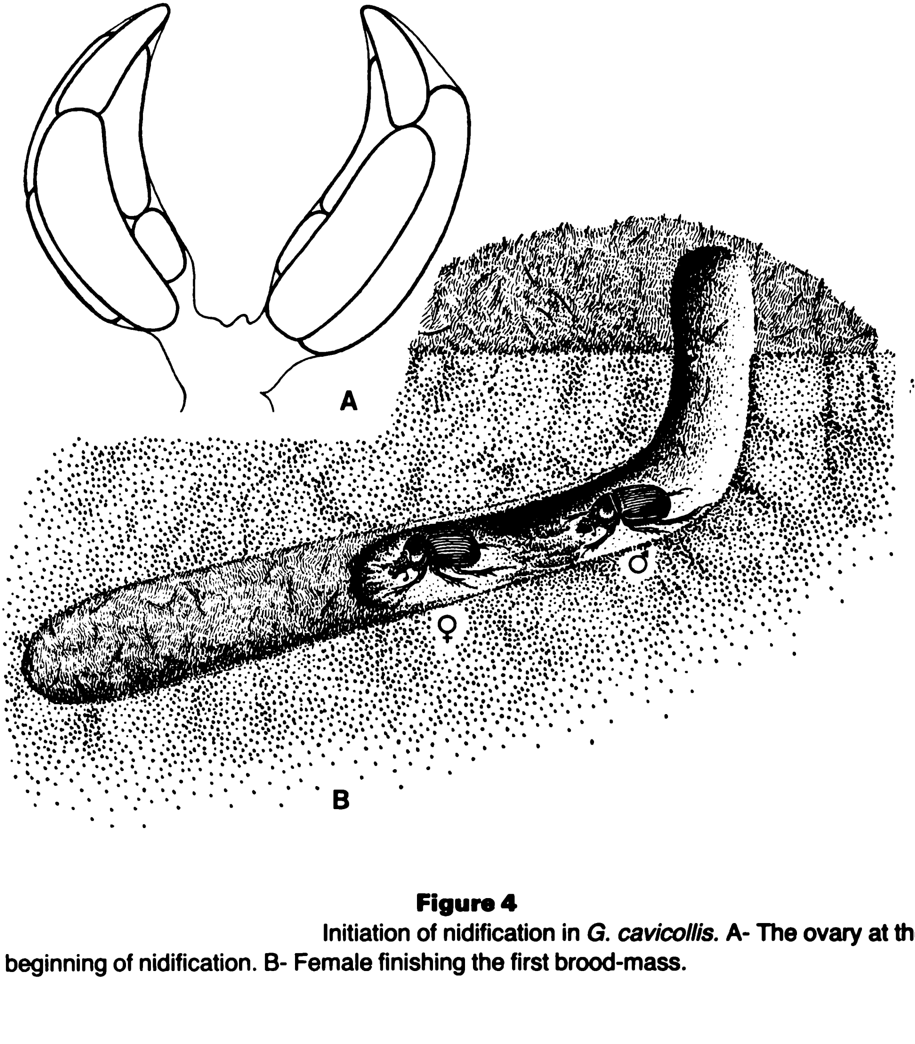


Figure 4

Initiation of nidification in *G. cavicollis.* A- The ovary at the beginning of nidification. B- Female finishing the first brood-mass.

typhoeus (Linnaeus), the male helps in digging the tunnel that can attain a depth of 150 cm; Spaney, 1910, in *Geotrupes silvaticus* Panzer; Teichert, 1955, 1956 and 1959, in *G. mutator* Marsham, *G. stercorarius* (Linnaeus), *G. vernalis* (Linnaeus) and *G. stercorosus* Scriba; Lavit and Tempère, 1965, in *Thorects sericeus* Jekel; and Klemperer, 1979, in *G. spiniger* Marsham. Lumaret, 1980, presents an excellent synthesis.

Several authors (Teichert, Klemperer and our own observations) point out the "caresses" made with the forelegs (♀) on the counterpart's elytra (♂) during the joint task, as mechanisms that maintain the bisexual pair.

Teichert, 1955, assumes that in *G. mutator* as well as in *G. stercorarius* mature ovocyctes are the stimulus that determine the initation of the nest. According to Klemperer, 1979, in *G. spiniger* nesting behavior begins a few hours after copulation has taken place.

In *G. cavicollis,* periodic dissection of females on the field as in the laboratory indicates that the end of ovaric maturation determines the initiation of burrowing by the female of the future nest. The only case of observed copula occurred when burrowing had ended and the process of provisioning was beginning. The male starts to collaborate a short time after this moment.

The Nest

The nest is compound and racemose[2]. Beginning at the vertical gallery brood masses are placed at different levels, the most superficial being located at a depth of 8 cm, and the deepest at 21 cm. They radiate in different directions, and are separated by a few centimeters and, in some cases, are practically together and parallel.

We have been able to observe many kinds of nests, from the independent gallery with only one brood mass (5% of the observed nests in the laboratory), to the more frequent vertical gallery

2 The nest of *G. hornii* Blanchard, *G. stercorarius* (Linnaeus), *G. vernalis* (Linnaeus), *G. mutator* Marsham, *G. spiniger* Marsham, *Typhoeus typhoeus* (Linnaeus) and *Mycotrupes gaigei* Olson and Hubbell (Howden, 1954), are compound and racemose. On the other hand, the nests of the *G. profundus* Howden, *G. blackburnii* (Fabricius) and *G. splendidus splendidus* (Fabricius) comprise a sole gallery, unbranched, with only one brood mass (Howden, 1952, 1955).

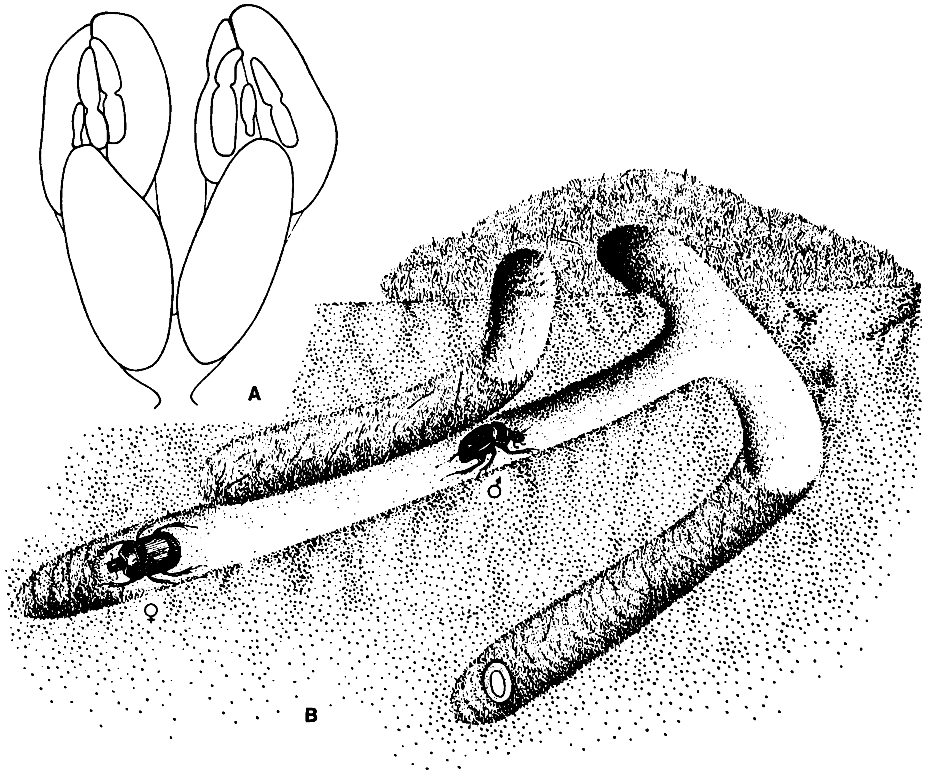


Figure 5

A more advanced stage of nidification. (50-60 days after emergence) A- The ovaries showing a totally mature ovocyte in each one of them. B- A brood-mass (with an egg) is already formed; the female working on a second brood-mass. A feeding gallery made by the same couple can be seen in the upper part.

from which two to five branches project[3], each one having a brood mass, except in rare occasions (see Fig. 6)[4]. Ther average length of the brood mass is close to 21.5 cm, with a diameter ranging from 2.5 cm to 3.5 cm, and in an exceptional case it may reach a maximun diameter of 6 cm. The average weight of a brood mass is 53.3 g; the largest found weighed 75.5 g. In *G. cavicollis,* as well as in all other known species of *Geotrupes,* each brood-mass contains only one egg.

The female prepares the egg chamber (6 x 8 mm) in the apical portion of the brood mass at 2.5 cm from the apex. In *G. cavicollis* we never find a soil cover. Teichert, 1955, always observed a sand covering in chambers of *G. mutator* and *G. stercorarius.*

In *G. cavicollis* the freshly laid egg is covered by an aqueous secretion that makes it stick somewhat to the floor of the chamber. This also occurs in other species of *Geotrupes (mutator* and *stercorarius,* according to Teichert, 1955). The position of the egg is erect and slightly oblique.

In *G. cavicollis* nests there is no upper soil cap protecting the central gallery or the brood-masses. We only found one case in which the entrance to the gallery was closed with a 3 cm cap, but made of dung.

Spaney, 1910, while studying *G. silvaticus* and *T. typhoeus* observed a soil cap in all nests. Teichert, 1955, 1957, also observed a soil cap between the upper part of the brood-mass and the vertical gallery in nests of *G. mutator, G. stercorarius* and *G. vernalis;* von Lengerken, 1954, also observed them in *G. mutator.* In these cases, in nests with several brood-masses the soil cap is located between each brood-mass and the main gallery. In nests with only one brood-mass, the soil cap lies between the brood-mass and the surface.

3 The number of brood-masses that constitute a compound nest varies from 3 to 8 for *G. stercorarius* (von Lengerken, 1954, and Spaney ,1910) to a maximum of 10 for *G. stercorarius* (Teichert, 1955); 2-8 for *G. mutator,* a species in which two broodmasses have been found in the same gallery (Teichert, 1955).

4 A nest with two brood-masses in the same gallery is exceptional. It has been observed in only two cases, from 21 nests observed in the laboratory and 4 on the field and always with a soil separation in between.

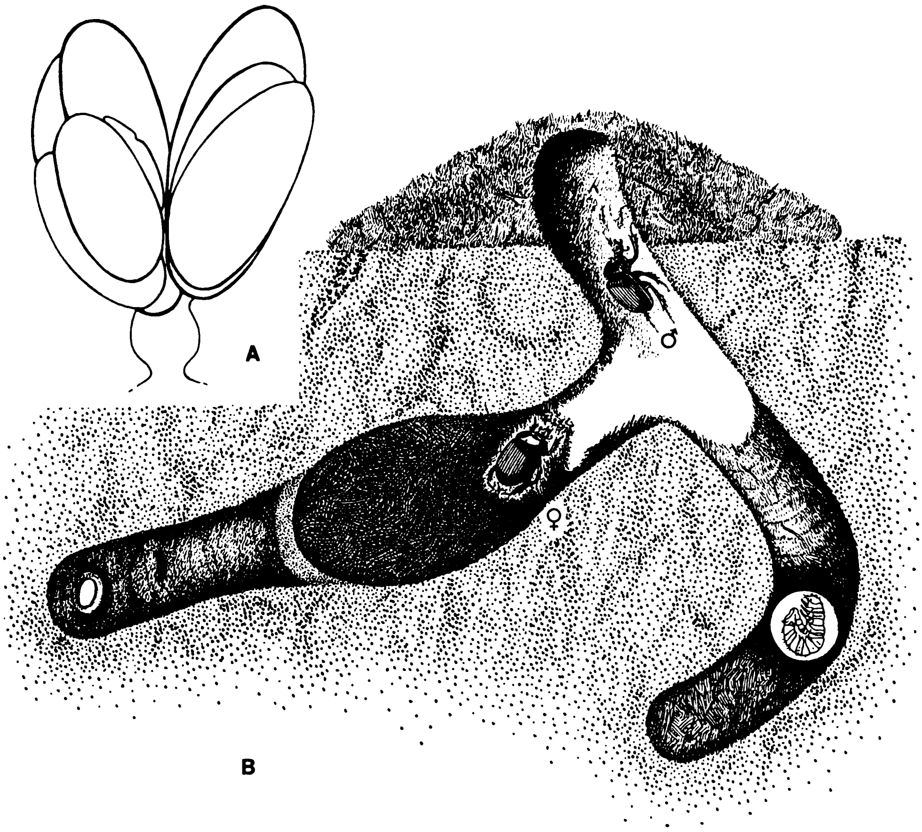


Figure 6

An exceptional case of two brood masses in the same gallery (113 days after emergence). A- Ovaries. Observe the advanced vitellogenesis present in several ovarioles. B- Nest. In the first gallery there is a third stage larvae, a brood mass with an egg exists in the upper gallery and the female is working on a second brood mass.

Nidification process

Usually, but not always, brood masses are formed two by two. Approximately 24 hours elapse between the formation of each brood-mass of one pair; and from 10 to 15 days between the end of one sequence with two brood-masses and the next one. The only nest with 5 brood-masses we have seen (Fig. 7) contained two larvae of third instar, two recently laid eggs and one mass in which an egg chamber was in preparation, all in the same nest due to the very prolonged nesting process.

Under laboratory conditions time required for provisioning the brood-mass is aproximately 12 hours.

Geotrupes is sensitive to gravity, a factor that plays an important role in the determination of gallery and brood-mass arrangement. In an experiment, Klemperer, 1979, modified the orientation of the nesting gallery of *G. spiniger,* when the female was elaborating a brood-mass, by changing the position of the terrarium by 90°. The confused female immediately regained her bearings and proceeded with her work on a plane correspondent to the new horizontal.

In *G. cavicollis* females that were with a male, which was subsequently removed, continued with the elaboration of the nesting gallery laying eggs only once or twice. This makes us assume that several copulas are necessary during nidification.

Virgin females elaborate feeding galleries and begin some sort of nest gallery but it never prospers and there is no oviposition at all.

Copula

In European species of *Geotrupes* (Teichert, 1955; Ohaus, 1904) copulation occurs under the dung pile or in the nesting gallery. We have observed it only once at the entrance of the gallery after 40 days of emergence.

We watched the male approach the female and try to hold her by softly sliding its forelegs over the elytra and pronotum. After several unsuccessful attempts, due to the smooth surface of the elytra, it managed to hold on and introduce its aedeagus, remaining still for a period of 8-10 minutes, after which the female began to move finishing

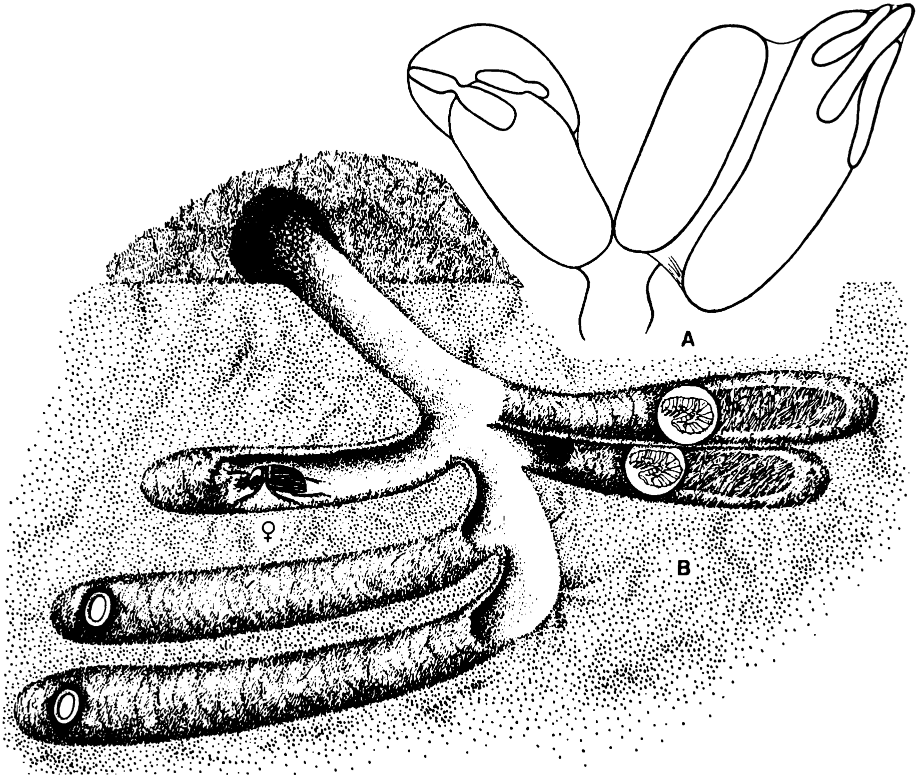


Figure 7

Nest with 5 brood masses (103 days from emergence). A- Present condition of the ovaries. In the left ovary there is a mature ovocyte, in the right one there are two, one of them about to enter the oviduct. The other ovarioles' germariums of both ovaries (not clearly visible) are very reduced. B- Brood masses of the same age are placed in pairs in a similar disposition.

the copula. At that moment the female went to the brood-mass where provisioning had begun; the chamber destined for the egg was practically finished, Twelve hours later we opened the terrarium, finding the brood-mass complete up to the union with the initial gallery and the egg in the chamber previously prepared by the female.

According to Teichert (1955) in *G. mutator,* several copulas occur up to the point when the reproduction process is almost over.

Larval development

Under laboratory conditions (16 larvae were studied) the first and second larval instars have an average duration of 10 days each. The third instar lasts an average of 190 days and the pupa 44. It takes from 30 to 40 days for the teneral adult to emerge. Estimating 10 days for the embryonic development, the complete cycle would last from 303 to 313 days.

We can compare this information to field conditions (see Table 1) where adults emerge on late June or early July. Nesting begins approximately on the fifth day of August ending from the second to the last week of September. Approximately 10 months later, next June, new adults emerge. This coincides with our observations.

With its excrement the third larval instar builds the pupal cell with a very smooth and hard surfae. The weight of a larva before pupating ranges from 2.5 to 3.0 g; after preparing the cell its weight drops to 0.5 g. This difference is due to the complete emptying of its intestine. The cell is elongated, measuring 6.0 x 3.0 cm.

In most cases, dung remains can be observed when larval development has ended; on the contrary there were some cases in which the dung accumulated by the female was not sufficient for the development and the larva perished.

Figure 8

Ovary section during the maturation period. Four ovarioles can be seen, each one of them has an ovocyte in the initial maturation stage (very initial in the third ovariole from left to right). Notice the germariums in an advanced stage of development. The germarium of the first ovariole was not in the cutting plane.

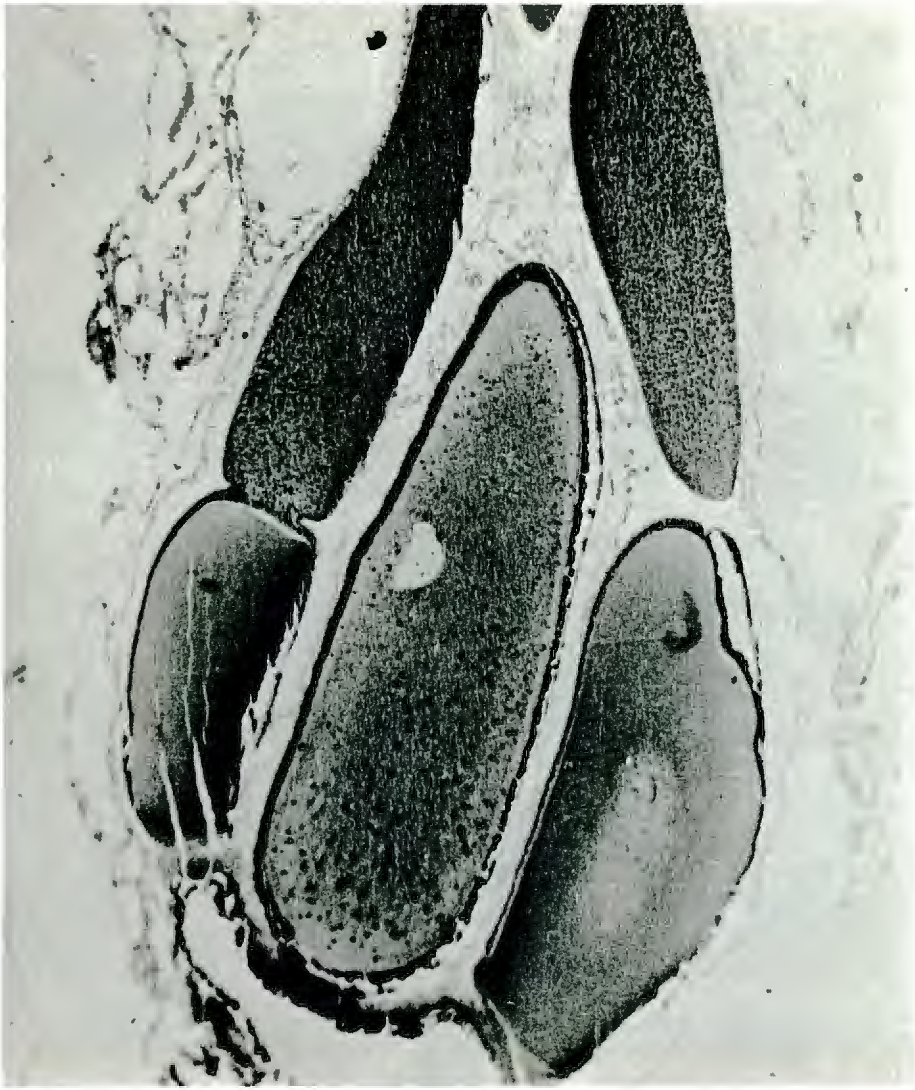


Figure 9

An ovary with ovocytes halfway through vitellogenesis. The one in the middle is more mature. The germariums are still well developed. The ovarioles missing were not in the cutting plane.

Figure 10

Mass of spermathozoids in the spermatheca (longitudinal sections of the spermatheca).

OVARY STRUCTURE AND FUNCTION

All studied *Geotrupes* species have two ovaries with six ovarioles each. There are no terminal filaments. The ovarioles of each ovary are wrapped by a thin but resistent covering (Fig. 1-B). When the oocyte is mature, the ovariole has a very short, practically unapparent pedicel. These pedicels end at the lateral oviducts, which are very short. The median oviduct is also short and profoundly pleated lengthwise. The distension of these pleats allows the passage of the egg which is several times winder than the oviduct. The intima is thin and provided with tiny thorns directed towards the vagina. The oviduct has strong circular and longitudinal muscles. The vagina also has a strong muscular structure.

In all the Geotrupini species studied by us (besides *G. cavicollis* other species of *Geotrupes* and *Ceratotrupes),* there exists a very primitive spermatheca, in comparison to that of the Scarabaeinae (see Halffter and Edmonds, 1982).

The spermatheca appears as a pear-shaped expansion of the duct. It has a thick conjunctive tissue covering. The muscles are placed longitudinally around the basal half and continue along the short duct (Fig. 11).

The chitinous intima of the spermatheca is not thick. In this way, the contraction of the muscles produces a series of transverse pleats in the basal half of the spermatheca and a reduction in its volume. This is the expulsion mechanism of spermatozoids. The expansion produces a suction effect that will move the sperm mass from the vagina to the spermatheca, a phenomenon made easier on account of the shortness of the ducts. A well developed gland ends at the contact zone of the spermatheca with the duct.

The previous description corresponds to *G. cavicollis* and to other species. Willimzik (1930) analyzes some examples that show an interesting evolution from the type described to slightly curved spermathecas, with the muscles placed on the concave side. This is an initial step towards the spermatheca of the Scarabaeinae.

Recently emerged adults are not sexually mature. The ovarioles, long and very close to each other, present a different degree of development.

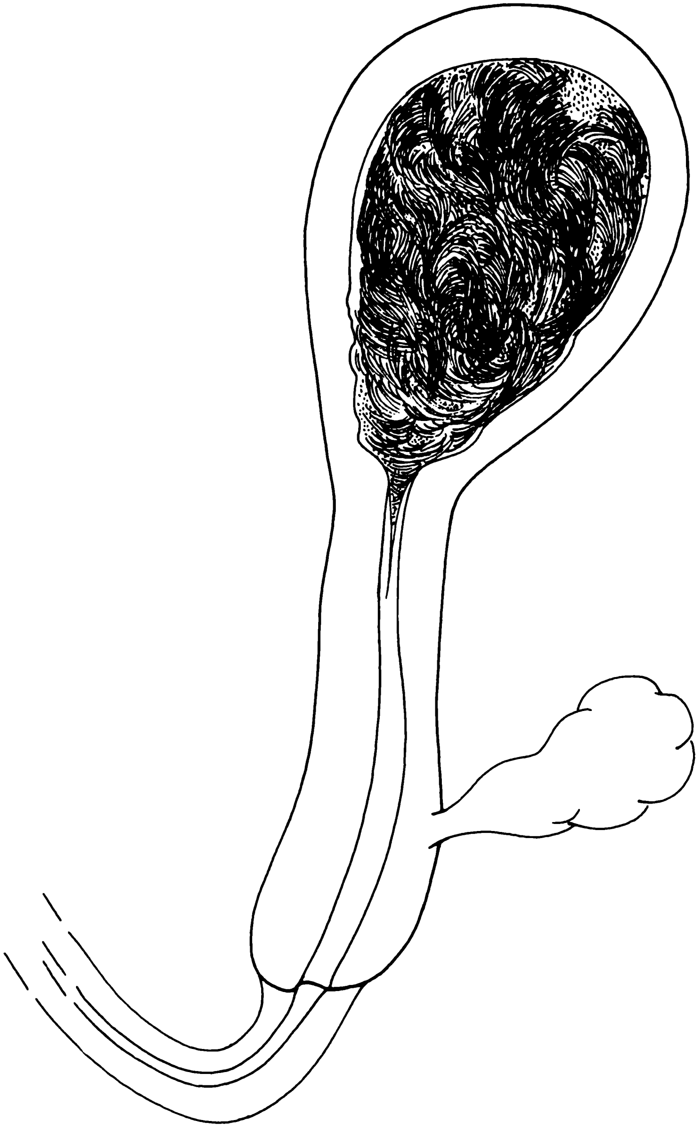


Figure 11
Complete spermatheca, the gland and the duct are visible.

We have never seen more than one oocyte per ovariole in vitellogenesis or previtellogenesis. We therefore assume that only one oocyte matures or maybe exists for each ovariole.

We have never seen trophic cords. However, Gross (1903) points out that in *G. stercorarius* and *G. silvaticus* trophic cords are evident in younger individuals, later attaining a thickness of up to 10 microns, similar to those of the Hemiptera.

As mentioned before, the maturation process in all the ovarioles is not uniform.

Under laboratory conditions, 30 days from emergence, one of the ovaries had one oocyte developing in at least two of the ovarioles (in the others there may be an incipient vitellogenesis or it may not have begun); in the other ovary there may be one developing oocyte.

When the construction of the nesting galleries is initiated (from 35 to 40 days after emergence) in five ovarioles of each ovary there is an oocyte at approximately the same stage of development; in the sixth vitellogenesis is just beginning. The germarium decreases notably in developing ovarioles (Fig. 4-A).

From the time nesting begins to the death of the female, 90 to 140 days after emergence (Figs. 5 to 7) vitellogenesis proceeds at a slow pace, at the same time the germarium undergoes an extreme reduction. The number of mature follicles that can be seen at a given time depends on the number of laid eggs. It is normal that mature oocytes compress themselves during their development. The rate of vitellogenesis is greater than the one for oviposition.

The death of the females begin between 80 and 90 days after emergence, with a maximum record of 140 days of adult life. When these specimens die their ovaries still present mature oocytes without showing any sign of absorption or degeneration. This means that death occurs before an important number of mature oocytes can be laid. This has been observed under laboratory conditions, but our field observations let us suppose that something similar is occurring to the females, since their number diminishes and they eventually disappear from the surface at the same time they are dying at the laboratory.

In relation with the great majority of Coleoptera, even with a great number of the genera of the subfamily Scarabaeinae, potential fecundity is rather low (a theoretical maximum of 12 eggs), the number of laid eggs has a maximum known value of 5. This number corresponds to laboratory conditions (we do not know how many eggs can a female lay under field conditions) with food surplus, male presence and with a similar although not so drastic temperature variation, as can be found on the field.

CONCLUSIONS

In *Geotrupes cavicollis:*

1. From the time of emergence to approximately 40 days after, there is a period of slow maturation of some oocytes (one per ovariole). During this time lapse the female feeds and builds feeding galleries, frequently in company of a male.

2. The end of this period and the beginning of nesting is determined by the complete maturation of two oocytes (one per ovary). When the female burrows a nesting gallery, a male joins in (although he does not participate in the burrowing), and copula takes place.

3. From this moment on a long nesting process takes place and brood masses are formed in lateral galleries which are generally built two by two. There is an interval of 24 hours between the construction of a pair of galleries; the interval between pairs goes from 10 to 15 days.

4. The nest is built by the female, with incipient cooperation of the male. Under laboratory conditions each female prepares only one nest.

5. The female lays far less eggs than those that mature inside her ovaries. Actually it is a very low fecundity, but it is in accordance with the nesting process which is very slow.

6. We have never observed more than one oocyte developing and maturing per ovariole.

7. The development of oocytes in different ovarioles is uneven.

8. Points 5, 6 and 7 correspond to such a drastic reduction in fecundity as can be found in more envolved nidification patterns of the Scarabaeinae (pattern III of nidification), but arrived at through a different process. There exists only one ovary with one ovariole in Scarabaeinae. In more evolved forms, this ovariole produces several oocytes, and there might even be more than one nesting wave (that is, more than one nest). In *G. cavicollis* there are two ovaries with six ovarioles each, but in each ovariole only one oocyte matures and it is even possible that one of the ovarioles per ovary may not mature an oocyte. In our work, this limited fecundity cannot be attributed to external factors: temperature, lack of adequate food, etc.

The only possible limiting factor for ovipositon which could be visualized in some terraria was the abscence of the male (he could have died before the female did). Our observations point out that once the male is taken away from the fertilized female, she finishes one and even two brood-masses (the pair of brood-masses elaborated in sequence), but nesting does not continue. It is possible that to obtain a maximum nesting effort, several copulas may be needed. This might explain some nests with few masses, but not a generalized low fecundity.

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