

## PLASTICITY IN THE NESTING BEHAVIOR OF *ONTHERUS SULCATOR* (FABRICIUS) (COLEOPTERA: SCARABAEIDAE: SCARABAEINAE)

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### ABSTRACT

*Ontherus sulcator* (Fabricius) is a species of *Dichotomiini sensu lato*, which usually constructs paracoprid nests composed only one brood ball per nesting chamber, conforming to Nesting Pattern II. The typical brood ball is spherical with a thin wall and a cylindrical, flattened T-shaped protrusion at the egg chamber pole. This study revealed that females of *O. sulcator* are capable of showing activational behavioral plasticity when, instead of constructing their stereotyped brood balls, they elaborate simpler brood balls, and even more, cylindrical brood masses. This is the first recorded case of a dung beetle having the ability to change its nesting behavior in experimental conditions, from constructing brood balls (Nesting Pattern II) to constructing brood masses (Nesting Pattern I). Cylindrical brood masses are also constructed by species of some other genera within *Dichotomiini sensu lato*, which were proposed as phylogenetically more closely related to *Ontherus*. The capability of construction of these brood masses in *O. sulcator*, shown by activational plasticity, supports these proposed relationships.

Key Words: *Dichotomiini*, dung beetle, brood ball, brood mass, activational plasticity

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Nest-building is a widespread behavior among Scarabaeinae. Usually, congeneric species of Scarabaeinae exhibit the same or similar nesting behaviors. Even more, for each species, some behavioral characters are as stable as the morphological ones (Halfpeter and Edmonds 1982). Halfpeter and Edmonds (1982) reviewed the diversity of nesting behaviors in dung beetles and recognized seven Nesting Patterns (I–VII).

Despite insects usually showing very stereotypical behaviors, many studies have shown that they may also display plasticity as an adaptive response to variable environments (Punzo 1985; Brockmann 2001; Mulrey *et al.* 2015). Snell-Rood (2013) defined two different types of behavioral plasticity, “developmental” and “activational” and outlined an explanation for the underlying mechanisms. The concept of activational plasticity proposes that different environments or conditions in a given context activate neuromuscular and hormonal mechanisms or pathways that already exist in the organism to produce changes in behavior. This kind of behavioral plasticity is an immediate and reversible response to “fine-grained” variation of the environment within the lifetime of an individual (Snell-Rood 2013).

Some previous records of changes in the nesting behavior of Scarabaeinae may be considered as

cases of activational plasticity. Some species that usually are rollers may behave occasionally as tunnelers (Sato 1998; Fávila 2001; Scholtz 2009; Halfpeter *et al.* 2013). Some species that usually display indirect provisioning may, in some cases, show direct provisioning (Klemperer 1983).

*Ontherus (Ontherus) sulcator* Fabricius, an American dichotomiine (Philips *et al.* 2004), is a coprophagous species distributed from Trinidad to southern Uruguay and central Argentina (Génier 1996). Cabrera-Walsh and Gandolfo (1996) described the nesting behavior and the brood ball of this species. More recently, Sánchez and Genise (2008) described the nest structure and provided detailed macro- and micromorphological descriptions of the brood ball. According to those records, the nest of *O. sulcator* conforms to Nesting Pattern II (Halfpeter and Edmonds 1982), being paracoprid and having only one brood ball per nesting chamber.

In this contribution, we present the first recorded case of activational plasticity in a dung beetle, *O. sulcator*, showing the capability to change its nesting pattern under experimental conditions, from constructing brood balls (Nesting Pattern II) to constructing brood masses (Nesting Pattern I). The possible causes of this significant change of behavior

and the potential phylogenetic value of activational plasticity are discussed.

### MATERIAL AND METHODS

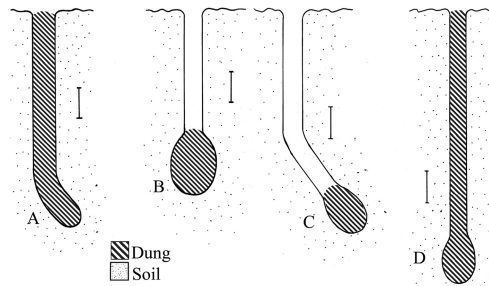
In November 2013, six adult *O. sulcator*, three females and three males, were collected at the Maldonado and Rossotti establishments (S33°51'39", W58°11'25" and S33°56'8", W58°5'56", respectively), Departamento Colonia, Uruguay. The soil at these sites was mainly covered by grasses and abundant cow dung pads. Beetles were found inside dung pads that showed excavated soil on its surface, or below them, in simple tunnels (7.5–20.0 cm deep) with dung packed into the blind end. Beetles were kept under laboratory conditions at  $25 \pm 2^\circ\text{C}$  with a 12-hour photoperiod. Three couples were placed separately inside plastic cylindrical terraria (30.0 cm in height  $\times$  20 cm in diameter) with a gauze lid and a 20 cm deep layer of soil. Fresh cow dung was placed on the soil surface and renewed twice weekly. The terraria were examined every 4–7 days to observe the storage burrows and the nests. With each examination, the terraria were emptied and subsequently refilled, and storage burrows and brood chambers were measured, photographed, and drawn.

For describing the brood chambers, the lengths of the three main orthogonal axes were measured and considered as major and minor diameters and height, respectively. A longitudinal section of each chamber was made to determine the internal structure and to measure the wall thickness and size of the egg chamber. The voucher brood chambers and the dung beetles were deposited in the Colección de Entomología, Facultad de Ciencias (Montevideo, Uruguay).

### RESULTS

Four storage burrows connected to the soil surface were found in two terraria at different examination events and not related to any of the brood balls described below. One burrow, mostly vertical and oblique near the bottom, was 1.5 cm in diameter, 14.0 cm long, and completely filled with dung (Fig. 1A). The other three burrows consisted of a cylindrical tunnel, vertical or oblique, 1.0–1.5 cm in diameter and 8–14 cm long, and ending in a spheroidal-prolate chamber that was 3–4 cm long and 2–3 cm wide. These burrows were filled with dung along their entire length or only in the distal chamber. They were constructed in no more than four days (Fig. 1B–D).

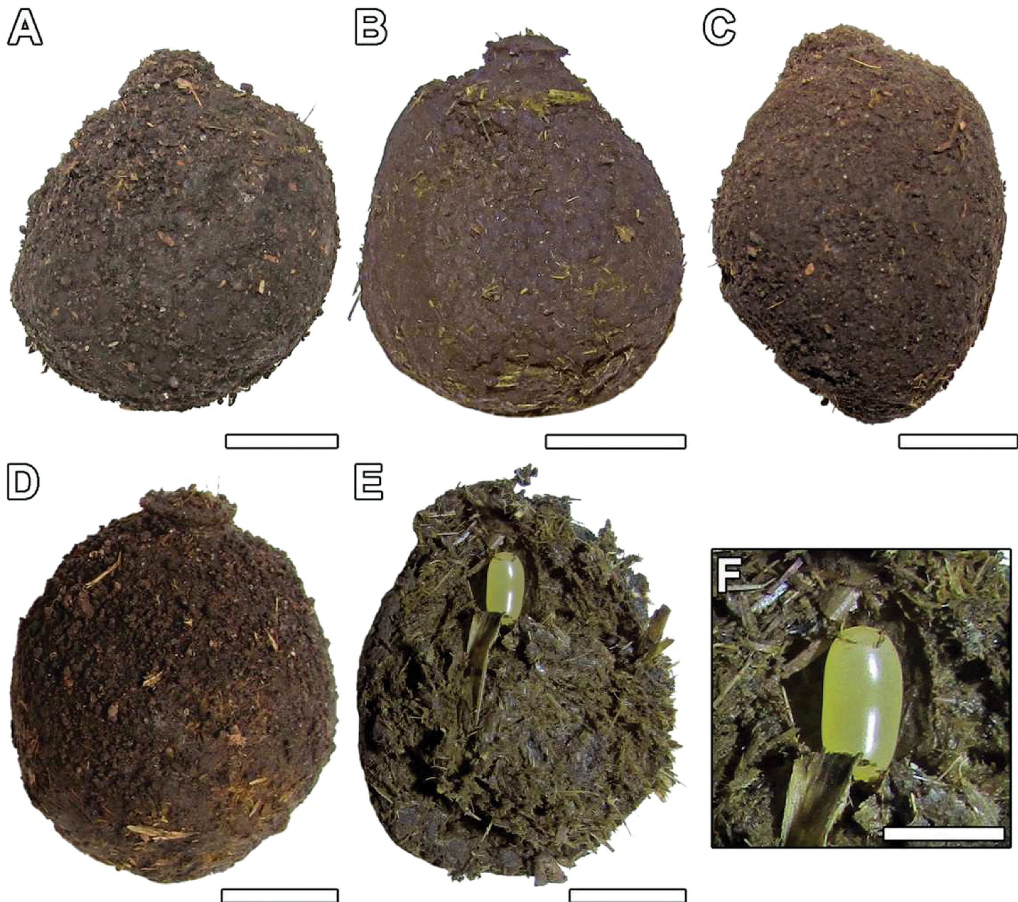
Six brood chambers (*sensu* Sanchez and Genise 2008) were obtained. One of the females made a single brood ball (Fig. 2A), another female made two brood balls (Fig. 2B–C), and a third female



**Fig. 1.** Different shapes of dung storage burrows of *Ontherus sulcator*. A) Vertical, oblique at the bottom, and completely filled with dung, B) Vertical with dung only in the distal chamber, C) Oblique at the bottom with dung only in the distal chamber, D) Vertical and filled with dung along its entire length. Scale bars = 2.0 cm.

made one brood ball (Fig. 2D) and two cylindrical brood masses. The brood balls were always found five or six days after the previous examination of the terraria. They were almost spheroidal (Fig. 2A–C), ranging in height from 2.7 to 3.0 cm, from 2.5 to 2.8 cm in maximum diameter, and from 2.0 to 2.3 cm in minimum diameter ( $n = 4$ ). Only two of these brood balls had a flattened T-shaped protrusion (Fig. 2B, D), which is typical of the morphology of the brood balls of this species. These T-shaped protrusions were 2.5–3.0 mm high and 6–7 mm in maximum diameter. The remaining two brood balls had a dome-shaped protrusion (Fig. 2A, C). Every brood ball had an external thin wall of soil material, 1–2 mm thick ( $n = 3$ ). The egg chambers, 8 mm high and 4.5–5.0 mm wide ( $n = 2$ ), were located in the upper part of the provision (Fig. 2E). They were internally coated by a thin layer of smooth, soft, dark brown material (Fig. 2F). The brood balls were housed in spherical nesting chambers, 12–14 cm deep and 3.5 cm in diameter, lacking any connection with the soil surface. In two cases, two short burrows filled with dung, 2 cm wide and 1 and 3 cm long, were found 10 cm deep and 2–4 cm above the brood balls (Fig. 3A). In another case, a curved burrow 10 cm long, filled with dung, and without connection with the surface was found near a brood ball (Fig. 3B). In all cases, there was no connection between those burrows and the nesting chambers.

The two cylindrical brood masses (Fig. 4A, B) were found simultaneously 11 days after one of the females made a typical brood ball (Fig. 2D) and seven days after the storage burrow depicted in Fig. 1D was found. The brood masses were 3.8 cm and 4.5 cm long, whereas their maximum and minimum widths were nearly equal, 1.8 cm and 1.5 cm. Both had a thin soil cover 1–2 mm thick. The egg chambers



**Fig. 2.** Brood balls of *Ontherus sulcator*. A) Brood ball with dome-shaped protrusion, B) Typical brood ball with flattened, T-shaped protrusion, C) Brood ball with dome-shaped protrusion, D) Typical brood ball with flattened, T-shaped protrusion, E) Longitudinal section of brood ball showing the egg chamber, dung provision, and external wall, F) Egg inside egg chamber. Scale bars A–E = 1.0 cm; scale bar F = 0.5 cm.

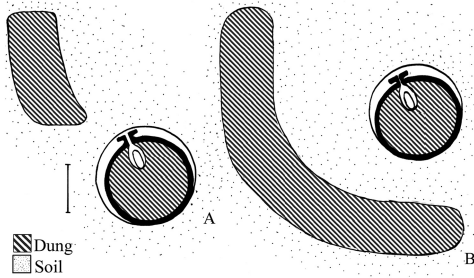
were near the upper pole and included in the dung provision. The chambers were 8 mm high and 5 mm wide and the inner covers were similar to those of the egg chambers of typical brood balls (Fig. 4C). Both brood masses were found on each side of a short, vertical, empty burrow 4 cm deep, but without connection it (Fig. 5). The shortest brood mass was 7 cm deep, whereas the other was 9.5 cm deep, both in a vertical position. They were detached from the surrounding soil and had no connection with the soil surface.

#### DISCUSSION

Our observations revealed that *O. sulcator* is capable of showing activational behavioral plasticity, as defined by Snell-Rood (2013), when, instead of constructing their stereotypical brood balls,

they elaborate brood balls with a dome-shaped protrusion, and even more, cylindrical brood masses, which are representative of Nesting Pattern I. According to Halffter and Edmonds (1982), a brood ball is an amount of provision receiving an egg, which is molded by a parent into a spheroid and may show an outer soil layer. The finished brood ball lies in a cavity and is partially surrounded by an air layer. On the other hand, a brood mass consists of an amount of provision receiving an egg, which has been packed into the blind end of a tunnel. The shape is determined by the original cavity and may be cylindrical (*i.e.*, ‘sausage-shaped’), oval, or spheroidal.

The typical brood balls constructed by *O. sulcator* females in the terraria had the same morphology as those described by Cabrera-Walsh and Gandolfo (1996) and Sánchez and Genise (2008) for the



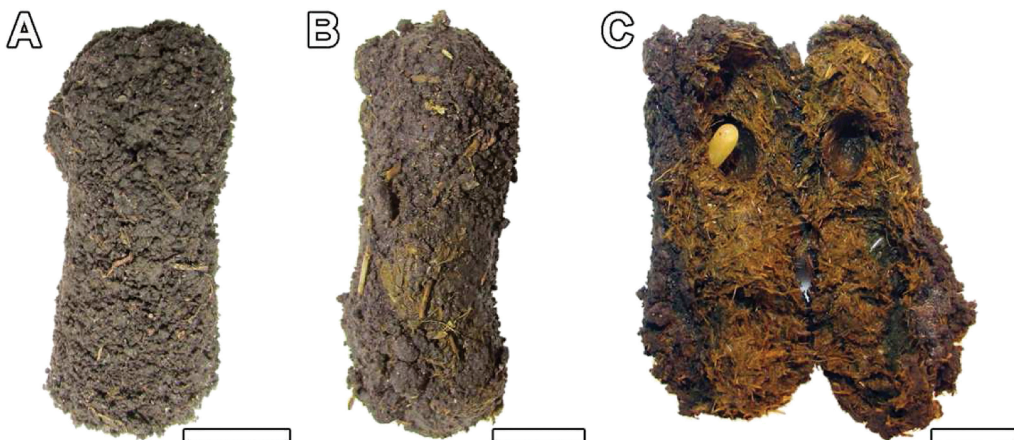
**Fig. 3.** Schematic drawings of *Ontherus sulcator* nests. A) Brood ball within a nesting chamber, 14 cm deep in the soil, and a short nearby storage burrow not connected to the soil surface or to the nesting chamber, B) Brood ball within a nesting chamber, 12 cm deep in the soil, and a long nearby storage burrow not connected to the soil surface or to the nesting chamber. Scale bars = 1.5 cm.

species. They were spherical with a thin wall, and at the egg chamber pole they had a cylindrical and flattened T-shaped protrusion that bears an aeration plug. However, one female constructed two brood balls with simplified morphology, without the complex T-shaped protrusion. On the other hand, another female constructed a typical brood ball deeper in the terrarium and two simpler and more superficial cylindrical brood masses. The outer covering observed in the brood masses of *O. sulcator* (Fig. 4) would not be a wall constructed by the adult as in brood balls but rather soil passively attached to the dung provision due to its moisture. The subsequent differential dehydration between the brood masses and the soil in the terrarium caused

the separation between them and the preservation of this soil cover on the brood mass.

The factor that induced the change in the nesting behavior of the females could have been the environmental stress caused by the periodical review of the terraria, which may have interrupted the usual nesting process. Four days after finding the first typical brood ball (Fig. 2D), a deep burrow with an ovoid chamber at the end, completely filled with dung, was found in the same terrarium (Fig. 1D). This storage burrow could have been used for the construction of a regular brood ball. The interruption of the nesting process, coupled with the probable presence of mature or almost mature oocytes in the reproductive system, could have forced this female to make two less elaborated and more superficial nests in less time. We base this hypothesis on the fact that the two brood masses were made in no more than seven days, whereas the elaboration of two brood balls took 10–12 days. Nesting by species that make brood masses is faster, which is related to greater production of eggs and offspring (Halffter and Edmonds 1982). On the contrary, tunneling species that make brood balls have rather low egg production. Delayed provisioning and more elaborate brood balls represent a greater investment of time and energy to protect each egg in particular (Halffter and Edmonds 1982). It is expected that the cylindrical brood masses constructed at a lower depth took less investment of time by the female *O. sulcator* and represented a quick solution to lay mature eggs.

The nesting behavior of *O. sulcator* typically conforms to Nesting Pattern II as defined by Halffter and Edmonds (1982). However, our study showed



**Fig. 4.** Cylindrical brood masses of *Ontherus sulcator*. A) and B) External view of the two recorded brood masses; note the external cover of soil attached to the brood mass, C) Longitudinal section of a brood mass showing the egg inside the egg chamber and the external soil cover. Scale bars = 1.0 cm.

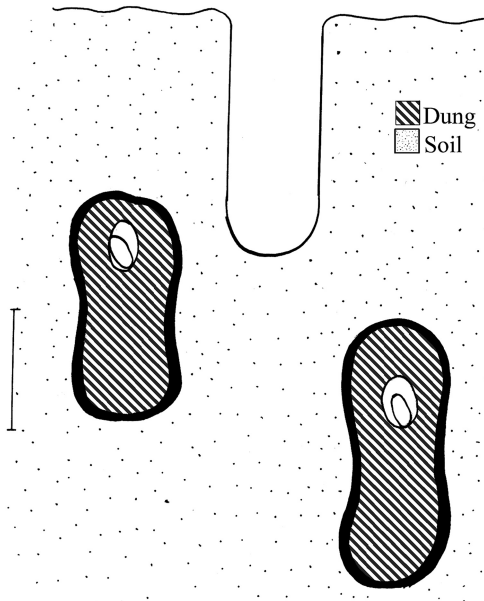


Fig. 5. Schematic drawings of two brood masses by *Ontherus sulcator*. Scale bar = 2.0 cm.

that *O. sulcator* has the capability not only to change the shape of brood balls, but also, and more importantly, to shift from constructing brood balls to brood masses and, consequently, to shift from Nesting Pattern II to I. Until now, *O. sulcator* is the only known species within Scarabaeinae that demonstrates this capability.

The alternative brood masses of *O. sulcator* were similar, to some extent, to those constructed by other species of Dichotomiini. This could provide a further element of support to the postulated phylogenetic relationships among some genera of the tribe. There are different opinions about the validity and composition of Dichotomiini *sensu lato* (according to Philips *et al.* 2004), but all phylogenetic studies support the polyphyly of this tribe (Tarasov and Genier 2015). Nevertheless, the molecular study of Ocampo and Hawks (2006) recorded strong support for relationships among *Ontherus* Erichson, *Uroxys* Westwood, *Ateuchus* Weber, and *Dichotomius* Hope within Dichotomiini. On the other hand, recent morphological and molecular phylogenetic studies (Tarasov and Genier 2015; Tarasov and Dimitrov 2016) support the more or less close relationships among *Ontherus*, *Homocopris* Burmeister, *Canthidium* Erichson, *Uroxys*, and *Ateuchus*. Significantly, the cylindrical brood masses of *O. sulcator* are similar in shape to the sausage-shaped brood masses constructed by species of the genera mentioned above, such as *Uroxys* (González-Vainer and Baruffaldi 2006), *Ateuchus* and *Canthidium* (see Halffter and Edmonds 1982), and

particularly some *Dichotomius* (see Cabrera-Walsh and Gandolfo 1996).

Faced with the unstable environment of the terrarium, the females of *O. sulcator* demonstrated the capability of changing their behavior and constructing simpler brood balls and brood masses, the latter similar in shape to those of other Dichotomiini *sensu lato*. The neuromuscular network for the construction of brood masses would be present in the closely related genera of Dichotomiini, although in the case of *Ontherus*, not as a usual behavior but as a capability to cope with environmental stress. This would be a case of activational plasticity, according to Snell-Rood (2013). It seems likely that the selection favors the subjacent retention of nesting capacities and behaviors in some species, which are usually shown by related ones. Plasticity in nesting behavior would influence the fitness of an animal in a fluctuating environment, positively affecting reproduction and assuring the stability and persistence of populations.

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