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FEEDING, REPRODUCTIVE, AND NESTING BEHAVIOR OF *CANTHON BISPINUS* GERMAR (COLEOPTERA: SCARABAEIDAE: SCARABAEINAE)

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ABSTRACT

The food relocation, reproductive, and nesting behaviors of *Canthon bispinus* Germar were studied in terraria at ambient conditions outdoors with three food resources. Individuals fed upon fish meat and dog dung but did not use cow dung. Five kinds of food manipulation behavior were observed: rolling balls, rolling dung pellets, rolling small pieces of fish, direct burial, and stationary rotation of food. To attract females, males adopt the typical headstand position for the emission of sexual pheromones beside the food source or next to a rolled ball. Males make two sizes of balls to attract females: small balls (≤ 10 mm) and large balls (≥ 11 mm). Small balls are always abandoned intact or lightly bitten after mating; they are regarded as nuptial gifts offered by males only to copulate. Most often, sexual encounters occur at the food source or, less frequently, while the male is rolling a ball without the previous emission of pheromones. Only carrion-provisioned large balls (11–21 mm maximum diameter) are used for nesting. Males assume the principal role in making and rolling the ball. Most nests are telecoprid, compound, and shallowly buried. Parental care is performed by the couple; the male remains in the nest up to 10 days, while the female usually remains for 30 to 32 days, just a few days prior to the emergence of the progeny. Survival rate was 92%. The carrion-provisioned brood balls are shaped like a figure eight or a pear. The egg chamber is separated from the provision chamber by a partition of soil material. As larval development advances, small excretions appear, increasing in number outside the ball.

Key Words: dung beetle, roller beetle, nest, brood ball, subsocial behavior, Deltochilini

The fundamental ethological display of dung beetles (Scarabaeinae) is the relocation of food for the adult's use or for nesting. Food relocation is performed, usually, by one of two methods: burrowing pieces into a tunnel dug beforehand beneath the food source (burrowers or paracoprids); or forming a ball at the food source, rolling it backwards for a certain distance, and then burying it (or not) (rollers or telecoprids) (Halffter and Edmonds 1982). There is also a small group of species of Scarabaeinae that do not relocate their food for feeding and construct the brood balls inside the food source or at soil-food interface (dwellers or endocoprids) (Halffter and Edmonds 1982; Huerta *et al.* 2003). Traditionally, tribes of Scarabaeinae have been separated into the basal dichotomy of either rollers or tunnelers, with dwellers being a subdivision of tunnelers (Scholtz 2009).

Species of the tribe Deltochilini are considered to be "rollers", although as many as 50% of the genera worldwide have not been seen to roll (Scholtz 2009). *Canthon* Hoffmannsegg is the most species-rich genus of the New World Deltochilini, with 174 currently described species distributed from southern Canada to Argentina (Medina *et al.* 2003). To date, nesting behavior has been studied in detail in only nine species: *Canthon pilularius* (L.) (Matthews 1963), *Canthon praticola* LeConte (Gordon and Cartwright 1974; Halffter and Halffter

1989), *Canthon cyanellus cyanellus* LeConte (Halffter *et al.* 1983; Bellés and Favila 1983; Favila and Díaz 1996; Favila 2001), *Canthon obliquus* Horn (Halffter and Halffter 1989), *Canthon indigaceus chevrolati* Harold (Montes de Oca *et al.* 1991), *Canthon quinque maculatus* Laporte (Halffter *et al.* 2013; Cantil *et al.* 2014a), *Canthon virens* Mannerheim (Halffter *et al.* 2013; Cantil *et al.* 2014b), and *Canthon edentulus* Harold and *Canthon mutabilis* Harold (Halffter *et al.* 2013). According to these studies, most of these species are typical rollers, the males being mainly responsible for the rolling and burial of the ball. In two species (*C. obliquus* and *C. edentulus*), females make balls but do not roll them, leaving them at the soil-excrement interface or shallowly burying them beneath the food source. On the other hand, one species (*C. mutabilis*) cuts and drags fragments under the food source, in a way similar to the behavior more frequently observed in tunnelers. Depending on the species, nests may be simple or compound. Females of *C. obliquus* and *C. mutabilis* make up to four brood balls from the initial rolled ball. Females of *C. edentulus*, a non-rolling beetle species, make several brood balls, each one from the food source (Halffter *et al.* 2013). Parental care of the offspring is provided by the female or by the couple, for a variable period of time, in all species that construct compound nests.

Judulien's (1899) pioneering observations in some Scarabaeinae of Argentina indicated that some species of *Canthon*, including *Canthon bispinus* Germar, make compound nests in subterranean chambers at variable depths under the food source and display parental care of the offspring by females. Some questions arise from the previous fact: a) Are the multiple brood balls made from a single larger ball of food previously buried under the food source or is each brood ball made directly from the food?; b) Does the male cooperate with the female in the construction of the nest?

Canthon bispinus is a common species in typical grasslands of the southern region of Rio Grande do Sul (Brazil), Uruguay, and southeastern Argentina (Pampas) (Martínez 1959; Silva 2011). It has been recorded as a preferentially necrophagous species (Silva 2011), although its nests have been reported below both excrements and dead animals (Judulien 1899). The aim of this study was to describe the feeding and nesting behavior of *C. bispinus* in outdoor terraria by offering three kinds of food resources.

MATERIAL AND METHODS

Thirty-four adults (15 males and 19 females) of *C. bispinus* were collected in January 2014 (summer) at Biarritz Beach, Canelones, Uruguay (km 70, Interbalnearia Route; S34°47'40", W55°30'30"). Individuals were found motionless on the sandy beach in the morning after a stormy and windy night, on the high-tide line along with a variety of other live and dead insects (Hemiptera, Formicidae, and Staphylinidae).

Beetles were placed in groups of 10–12 individuals in three transparent plastic cages (30.0 cm long × 23.0 cm wide × 16.0 cm high) with compacted soil 10 cm deep and kept outdoors in ambient conditions exposed to sunlight. They were fed daily with bovine dung (200 g) the first week, dog feces (80 g) the following week, and small pieces of fresh fish (about 20 g) until the end of the experiment. These resources were selected because a previous study (Silva 2011) and personal field observations (unpublished data) indicate that *C. bispinus* prefers carrion, but it is also attracted to cow dung and omnivore manure. Portions of fish that were not consumed were replaced daily by fresh ones to avoid proliferation of flies. Couples were removed and kept in similar but separate cages when they were observed rolling a ball, and food was provided daily. Four couples were fed with dog feces, while 18 couples were fed with fish. If the pair separated after a few days, the individuals were returned to their initial cages. The activity of the adults was observed directly, video recorded, and photographed daily. The soil was examined once a week to observe the nests and nesting behavior.

Air temperature was measured daily with a minimum/maximum thermometer during the rearing period. Mean air temperatures in January, February, and March 2014 were, respectively, $24.2 \pm 4^\circ \text{C}$, $21.8 \pm 4^\circ \text{C}$, and $19.3 \pm 5^\circ \text{C}$, while average monthly relative humidity values were 69%, 72%, and 73%, respectively. Mean day length was 14 h in January, 13 h 23 min in February, and 12 h 18 min in March. Daily data of relative humidity and photoperiod were provided by the Dirección Nacional de Meteorología, Uruguay.

Voucher specimens of *C. bispinus* and brood balls were deposited in the Entomological Collection of the Facultad de Ciencias, Universidad de la República (Montevideo, Uruguay).

RESULTS

Activity on the soil surface in the terraria was observed always during daylight, between 6:00 am and 8:00 pm (sunset), but it was more intense between 3:00 and 7:00 pm, when sunlight fell directly on the terraria.

Feeding Behavior. Neither food relocation nor feeding behavior were observed with bovine manure. On the contrary, five kinds of food manipulation behavior were observed with dog dung pellets and pieces of fresh fish:

a) Both males and females individually shaped balls with the two types of food and rolled them backwards with their hind legs, in the typical "pushing position" (see Halffter and Matthews 1966). The food ball is generally cut from the side of the food fragment by using the clypeus and the front legs. Simultaneously, they also moved their forelegs alternately to compress the ball and occasionally add new material to the ball during the shaping process. The balls were spherical or slightly ovoid and became coated with a loose layer of soil during rolling (Fig. 1A). These were shallowly buried (1–2 cm) by digging beneath them and completely or partially eaten. Food balls made with both resources were similar in size: dog dung food balls were 9.7 ± 1.47 mm in diameter ($n = 6$), while carrion food balls were 10.0 ± 1.1 mm ($n = 21$) ($t = 0.64$, $df = 25$, $P = 0.53$).

b) Small, ovoid dog dung pellets (19.5 ± 0.5 mm × 15.8 ± 0.2 mm, $n = 4$) were directly rolled and then buried (Fig. 1B). Smaller, irregular pieces of fish (13.0 ± 1.4 mm × 9.7 ± 0.5 mm, $n = 3$), not formed into a ball, were rolled away from the food source in the typical way and then buried (Fig. 1C).

c) Small size pieces of fish (24.0 ± 0.4 mm × 18.0 ± 0.3 mm, $n = 6$) were coated with soil by being rotated in place. The beetle positioned itself below the fragment of fish, with its back on the soil and its legs on the food source,

and rotated the food by moving its legs. The piece of food was covered with soil and became ovoid as it was rotated, and then it was rolled and buried. At other times, adults walked over and around the food, covering it with soil ($n = 3$). Then the piece of food, not rounded into a ball, was rolled slowly and with difficulty to its later burial site.

d) Frequently, both dog dung pellets ($34.0 \pm 0.9 \text{ mm} \times 18.0 \pm 0.2 \text{ mm}$, $n = 5$) and fish pieces ($30.0 \pm 0.9 \text{ mm} \times 19.0 \pm 0.4 \text{ mm}$, $n = 16$) were directly buried without transportation, 1 to 3 cm deep, by excavating the ground from beneath them. Sometimes the fish was covered with soil by the procedure described above before being buried (Fig. 2A-D).

e) Adults were observed feeding directly on the source, either on the surface or, more frequently, immediately below the portion of fish or the dog dung pellet.

Formation of Male-Female Pair: Mate pairing occurred in three ways: at the food source ($n = 18$), while the male was rolling a ball ($n = 5$), or after the ball was partially or completely buried by the male ($n = 4$). On several occasions ($n = 24$), males were observed adopting the typical position for the emission of sex pheromones: completely vertical position, standing on his fore legs, with the head down resting on the substrate, the middle legs extended sideways, alternating movements of the hind legs, and rubbing the tarsi against the abdominal sternites and then extending them. This process lasted up to an hour and a half and took place, most of the time, beside the food source or at a short distance (7–8 cm) from it ($n = 10$) (Fig. 3A). On one occasion, a male displayed the pheromone-emitting behavior for 15 minutes for the four cardinal directions around the food. Also, the male will bury the entire piece of food directly in a shallow depression by excavating the ground under it, and then emit pheromones on the soil surface ($n = 3$). Often, the males made and rolled small, spheroid balls ($8.9 \pm 1.4 \text{ mm} \times 8.0 \pm 1.2 \text{ mm}$, $n = 19$) (Fig. 3B), but they also made larger ovoid balls ($15.4 \pm 4.1 \text{ mm} \times 13.2 \pm 3.3 \text{ mm}$, $n = 12$) (Fig. 3C). Mean maximum diameters of the two ball sizes were significantly different ($t = 6.43$, $df = 29$, $P < 0.0001$).

Ball-rolling lasted up to 24 hours, with intervals in which the male rested burrowing underneath the ball. Balls of both sizes remained on soil surface or were completely or partially buried. Following this, the male began displaying the pheromone-emitting behavior either over the ball, beside it (Fig. 3B, C), or at the entrance of the shallow chamber where the ball was buried (Fig. 3D). The male can remain in the same place for up to

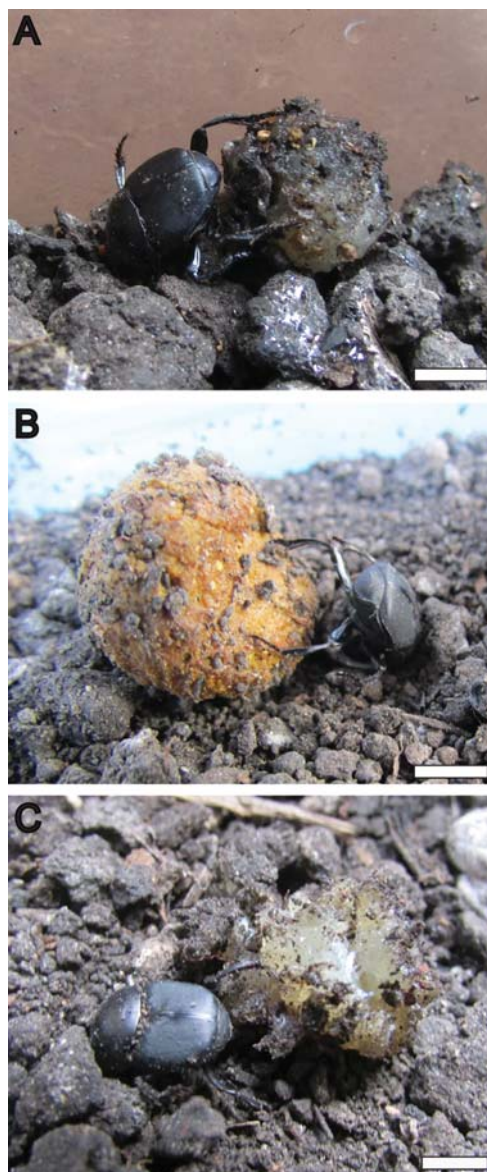


Fig. 1. Food relocation by *Canthon bispinus*. A) Individual rolling a ball made with fish meat, B) Adult rolling a small dog dung pellet, C) Adult rolling an irregular, small piece of fish. Scale bars = 5 mm.

days, buried with the ball and rising to the surface to display the pheromone-emitting behavior for up to an hour and a half. This behavior was always observed between 4 pm and 7 pm, three times with the small balls and six times with the large balls. Only on one occasion was a female attracted by a male with a small ball, whereas three females were attracted to males with large balls. When a

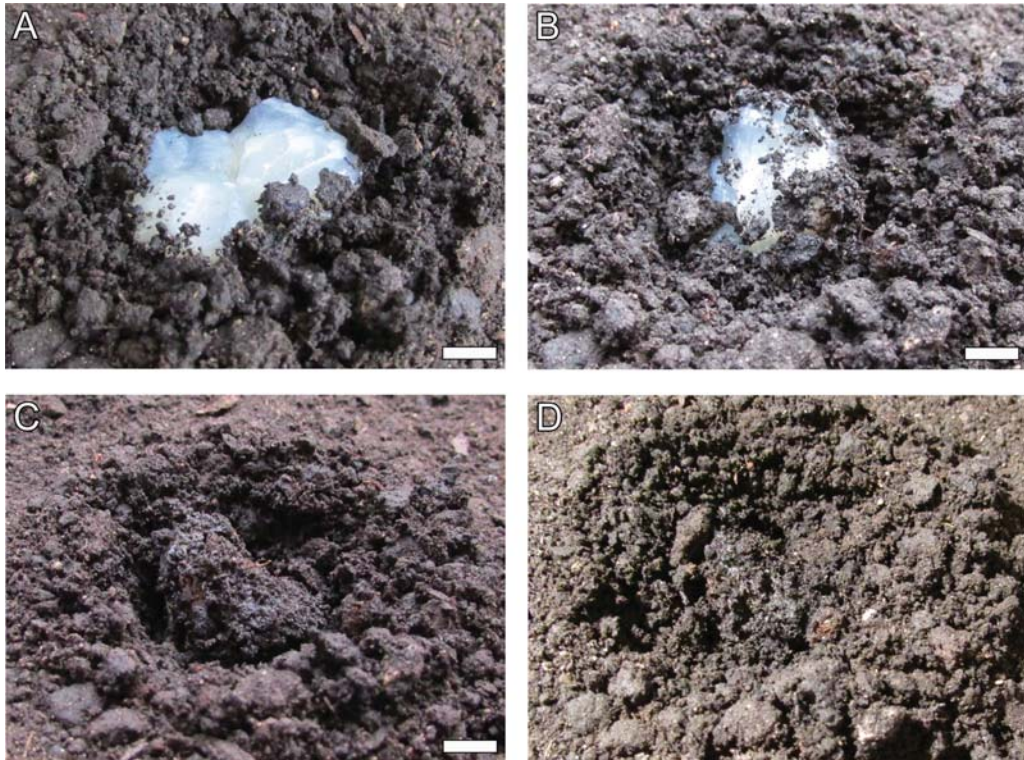


Fig. 2. Sequence showing the burial of a piece of fish *in situ* by *Canthon bispinus*. A) Piece of fish in a slight depression in the ground which was excavated by the beetle located below that, B) Piece of fish being rotated in its place, C) Food completely covered with soil and turned into an ovoid in a deeper depression, D) Food almost entirely, shallowly buried. Scale bars = 10 mm.

female approached the male, both beetles buried themselves together, or sometimes the male rolled the large ball with the female clinging to it (Fig. 4A) until the ball was buried elsewhere. During rolling, the male adopted the pushing position of head downward behind the ball, the hind legs on the ball, and the other legs applied to the ground, with the middle legs occasionally pushing the ball (Fig. 4A, B). If no female responded to the male's pheromones, the ball was eventually abandoned ($n = 21$). On two occasions, males first made and rolled large, ovoid balls (25.0×20.0 mm and 28.5×22.0 mm), emitted pheromones beside them on soil surface, and attracted a female. When females joined the males, the latter cut and shaped the balls (15.0×12.0 mm and 21.0×15.0 mm, respectively), and then these were rolled and subsequently buried.

Encounters of both sexes without previous emission of pheromones by the male occurred most often at the food source ($n = 18$) or less frequently while the male was rolling a large ball ($n = 5$). When the pair formed at the food source, the male

assumed the most active role in cutting the meat and making the ball. The female just stood on the future ball, changing its position and compressing the ball from time to time with her front legs. The process of making the ball took 30–60 minutes ($n = 18$). The male then rolled the ball in the typical way, while the female remained attached to the ball, rolling along with it (Fig. 4B). Periodically, the male stopped rolling the ball and walked around it. Rolling lasted 15–90 minutes. Finally, the ball was buried by the male by digging beneath the ball, while the female clung firmly to the top or one side of the ball, head down, and was buried with the ball. The balls made by male-female pairs measured 19.0 ± 2.1 mm \times 15.0 ± 2.4 mm ($n = 18$). The mean maximum diameter of these balls was significantly greater than that of the large balls made by single males ($n = 12$) ($t = 2.89$, $df = 28$, $P < 0.01$). Both the balls made by pairs and the large balls made by single males during the nesting period were significantly larger than the food balls ($t = 16.93$, $df = 37$, $P < 0.0001$; $t = 5.82$, $df = 31$, $P < 0.0001$, respectively).

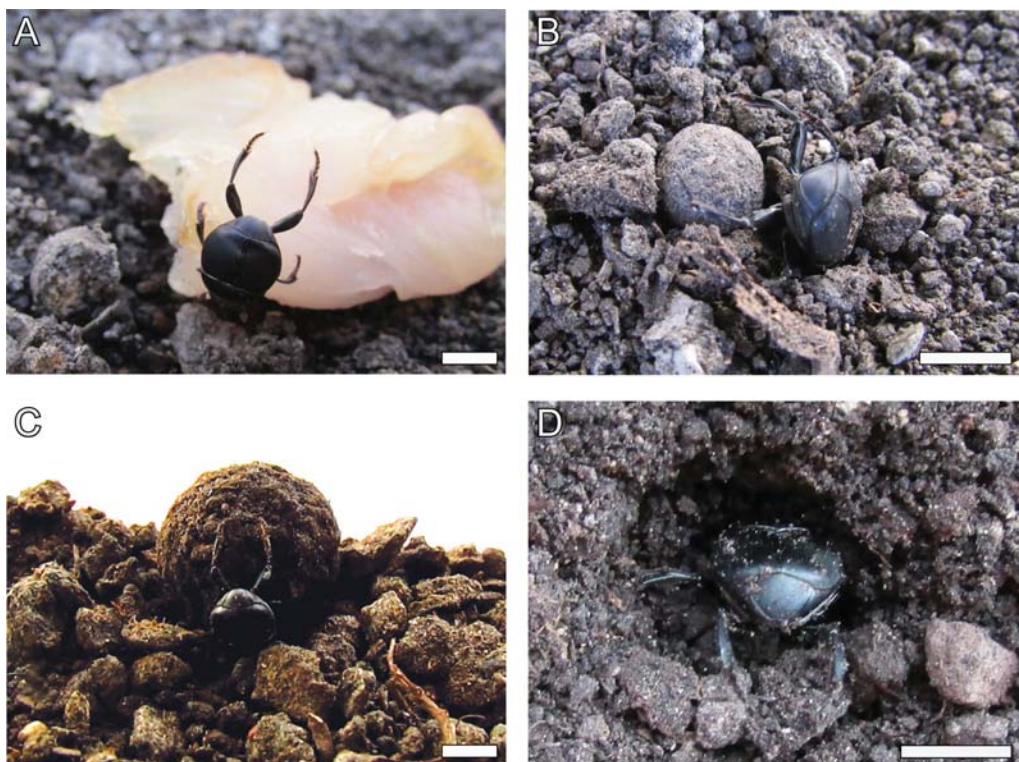


Fig. 3. Male *Canthon bispinus* in headstand position emitting pheromones. A) Beside the food, B) Beside a small food ball, C) Beside a large food ball, D) At the entrance of a gallery. Scale bars = 5 mm.

Copulation occurred underground, next to the buried ball, and lasted at least 30 minutes. Mate pairing, in all the forms described above, was not always followed by nesting. Some pairs separated 1–4 days after forming, either leaving the ball intact or departing after eating the ball completely or partially. Small balls were never used for nesting but remained most often intact or scarcely bitten. On three occasions, the males again displayed the emission of pheromones at the food source as soon as the couple separated, but no further observations were made since they returned to the general terraria.

Fights for Balls. Fights between beetles of the same sex ($n = 4$) were observed during the nesting period. On two occasions, an aggressor male attempted to appropriate the ball being rolled by a couple ($n = 2$). Each time, the aggressor tried unsuccessfully to drive off the owner of the ball and take his place rolling the ball with the female. On the other two instances, while the male was burying the ball with the clinging female, he expelled another female that tried to climb onto the ball.

Nesting Behavior. Only carrion-provisioned balls were used for nesting. From the initial ball previously

rolled and buried by the male, the female first made 1–4 spheroid, smaller balls ($n = 10$). To do this, the female opened the initial ball, removed portions of food, and molded them into smaller balls (10.0 ± 1.4 mm diameter; $n = 10$). She initially covered them with a homogenous, soft layer of soil, which later became tougher and thicker (2 mm, $n = 3$). On one pole of the ball, the female constructed the egg chamber by forming as a cup-shaped receptacle made from soil (Fig. 5). The female laid one egg and then closed the receptacle's cavity.

Thirteen nests were observed. Four of them were simple, two of which were buried at a shallow depth (2–4 cm) and the others were in depressions on the soil surface (Fig. 6). The initial ball of those on the soil surface had been partially buried. One of the shallowly buried simple nests was prepared below the food source, without rolling. The male cut a portion of meat and buried it, excavating the ground below. The following day, the food had been converted into an ovoid (18×13 mm) covered with a loose layer of soil. Two days afterwards, the female made a brood ball with it. The remaining nine nests were compound and shallowly buried, with 2–4 finished

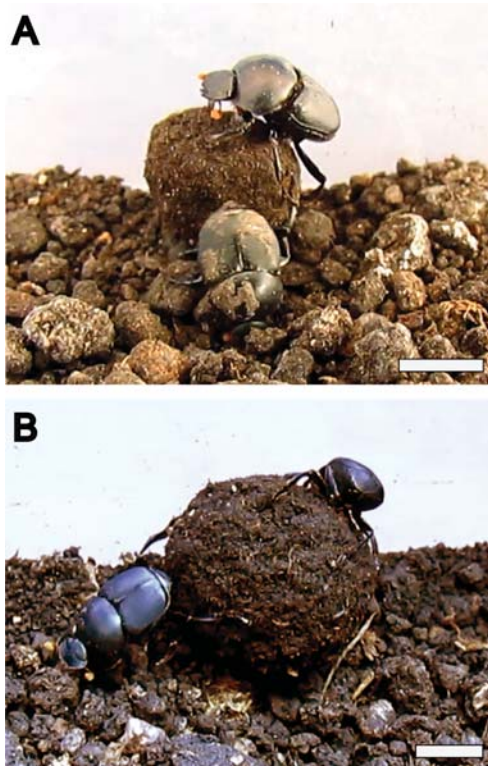
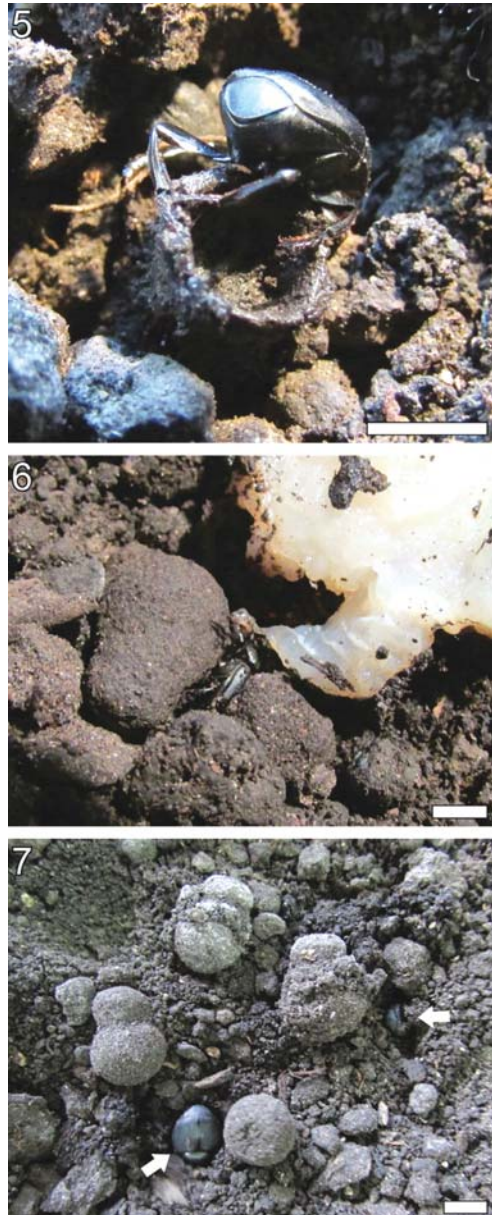


Fig. 4. Mating pair of *Canthon bispinus* rolling a food ball, male in pushing position, female on top of the food ball. A) Pair with a food ball made by the male alone, B) Ball made with the aid of female. Scale bars = 5 mm.

brood balls, and in some of them there was also a spheroid ball that had not been transformed into a brood ball yet (Fig. 7). The nest chamber was not a well-defined space. Brood balls were found immediately beneath the soil surface to a depth of 6 cm, more or less close to each other, with loose soil between them, and the mating pair or female was buried alongside or slightly below. Six males left the nest 3–13 days after burying the initial ball, when the brood balls were already completed. Females usually remained in the nest for 30–32 days until 4–9 days prior to the emergence of the progeny ($n = 6$), though occasionally a female left earlier.

Finished brood balls were shaped like a figure eight or a pear (Fig. 8A, B). Mean height was 15.0 ± 1.9 mm, with a spherical lower portion 10.0 ± 1.4 mm in diameter, and a narrower upper part 7.0 ± 0.8 mm wide and 0.6 ± 1.0 mm high ($n = 17$). The egg chamber ranged 4–5 mm in height and 3 mm wide ($n = 3$). The wall thickness of both the egg and the provision chambers was about 2–3 mm ($n = 3$), and both chambers



Figs. 5–7. Nesting behavior of *Canthon bispinus*. 5) Female building the cup-shaped egg chamber of the brood ball; 6) Female caring for a superficial brood ball; 7) Compound and subterranean nests showing the couple (arrows) caring for brood balls at different stages of development, with the larval excreta visible on both of them; one of the food balls has not been transformed into a brood ball yet. Scale bars = 5 mm.

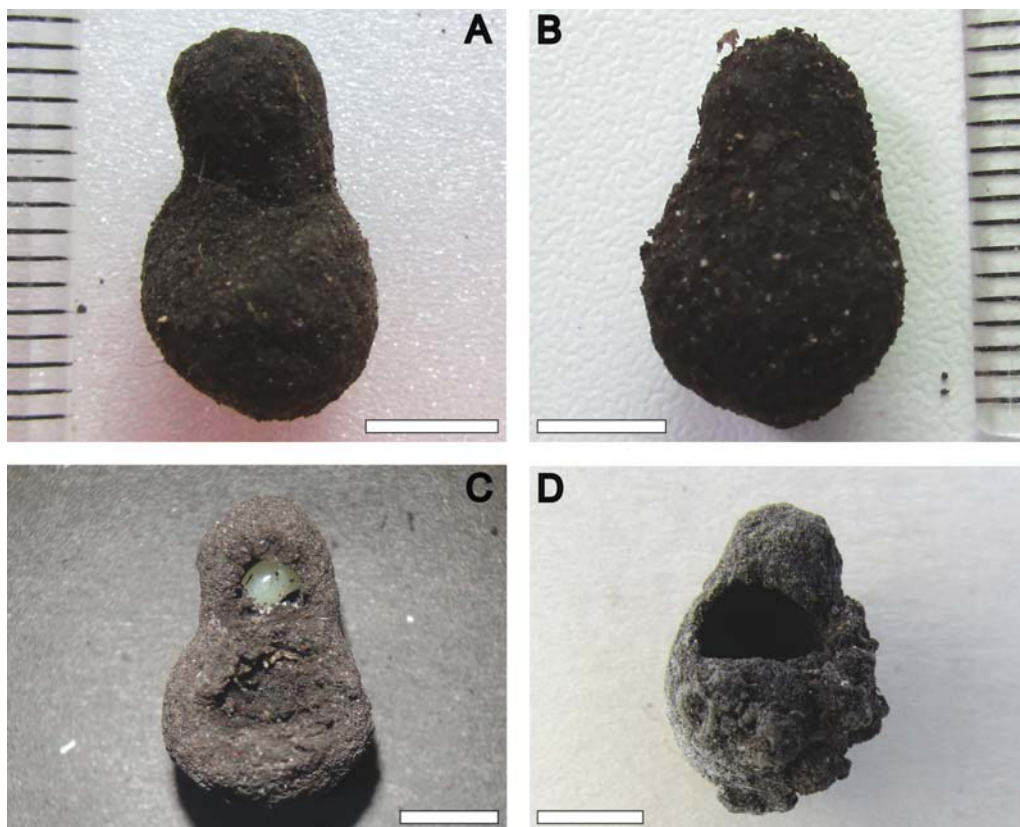


Fig. 8. Brood balls of *Canthon bispinus*. A) Shaped as a figure eight, B) Shaped as a pear, C) Internal view showing an egg in the chamber, D) Aspect after emergence of the imago emergence, showing the larval excreta outside. Scale bars = 5 mm.

were separated by a thin partition 2 mm thick (Fig. 8C). The yellow egg was 2.9–3.0 mm long \times 2.0–2.2 mm wide ($n = 3$) (Fig. 8C). Beginning with the first instar, the larva pushes lumps of excrement outwards, which solidify into pellets on the surface of the ball (Figs. 7, 8D). In some cases, when larva become pupa, the brood ball lost its initial form when the larva pupated, turning spheroid or ovoid and completely covered by the small fecal pellets (Fig. 9).

DISCUSSION

Feeding Behavior. This study, together with the observations made by Judulien (1899), reveals the plasticity in feeding and nesting behavior of *C. bispinus*, not only in relation to the resource used but also in relation to the food manipulation and relocation pattern. *Canthon bispinus* is considered a generalist, but a preferentially necrophagous species by Silva (2011) because of the observed frequencies of individuals captured with pitfalls

baited with carrion (74%) or human excrement (22%). According to personal observations (unpublished data), this species also prefers carrion (60%) over cow manure (40%) in baited pitfalls. In my study, *C. bispinus* exhibited a marked preference for fish meat and dog feces over bovine dung for feeding.

Canthon bispinus also showed a broad spectrum of food manipulation behaviors (rolling balls, rolling pellets, rolling small pieces, direct burial, and stationary rotation of food). Such behavioral plasticity has been observed in other species of Deltophilini under field and laboratory conditions (Halffter and Halffter 1989; Luzzato *et al.* 1997). Size and form of the food source, and also the level of competition, are probable factors that influence the food manipulation behavior. Further experiments should be conducted to support these hypotheses.

Attraction of the Female. The headstand position of the male and the movements of the hind legs have been observed in other species of roller dung beetles (Tribe 1975; Bellés and Favila



Fig. 9. A brood ball of *Canthon bispinus* that has lost its initial form, being covered with excreta from the larva. Scale bar = 5 mm.

1983; Sato and Imamori 1986a, 1987; Edwards and Aschenborn 1988; Favila and Díaz 1996; Sato 1998; Burger *et al.* 2002, 2008; Halffter *et al.* 2011, 2013; Favila *et al.* 2012; Cantil *et al.* 2014a). In most cases, this behavior has been associated with the releasing of sex pheromones from the abdominal and pygidial glands of males to attract females near the resource or after ball making and rolling, which is compatible with my observations. Females of *C. bispinus* were also attracted to males rolling a ball. It is possible that this ball is impregnated with chemical attractants produced in the male's its sternal glands and that these compounds serve to attract and keep the female close as was demonstrated for *C. cyanellus cyanellus* (Favila 1988).

Not always did the rolling and burial of a ball by a pair end with nesting. The male and female often separated one or two days after having eaten the ball completely or partially, or leaving it abandoned. This behavior was frequent when males shaped and rolled a small ball alone and then emitted pheromones to attract the female. When no female came to meet the male, he left the ball intact. It could be interpreted that these balls represent prenuptial gifts offered by males as a way of persuading females to copulate, as it was stated by Brown *et al.* (1997). Nuptial food gifts given by males to females at mating are widespread among insects (Sakaluk 2000). One of the hypotheses that has been raised to explain the function of prenuptial gifts is known as mating

effort, which proposes that males invest in the gift for greater quantity and quality of copulations (Thornhill 1976; Sakaluk 1984). In this regard, it has been shown in cricket species that females provisioned with food gifts were 'fooled' into accepting more sperm than they otherwise would in the absence of a gift (Sakaluk 2000). In Scarabaeinae, prenuptial offerings given by males have been recorded only in species of *Scarabaeus* L. that live in arid regions where dung is scarce (Halffter *et al.* 2011). These authors proposed that, in those ecological conditions, the contribution of the male in the form of the prenuptial offering ensures that the highest number of females reach gonadal maturity and survive until nesting. However, they also proposed that the insemination by the males of as many females as possible during the feeding maturation period could later give their sperm the opportunity to fertilize the females during the nesting stage.

In the case of *C. bispinus*, it is likely that the prenuptial gift allows the male to copulate with more than one female prior to nesting. This would represent an important advantage in the context of sperm competition where the sperm of different males compete to fertilize the ova of the female. There are quantitative data on the importance of prior copulation in *C. cyanellus cyanellus* in which 94% of the females that nest have in their spermatheca viable sperm from previous copulations with other males (Favila *et al.* 2005). Experimental studies on this species using a genetic marker have provided a quantitative estimate of the relative reproductive success of the different copulations (Favila *et al.* 2005). The paternity of a male that copulates with a female that has mated previously with another male, but that does not continue the process of nesting, is 50%, suggesting strong sperm competition. When the male does participate in nesting and copulates with the female several times before making the brood balls and participates in their preparation, paternity is high (>80%), although the large amount of variability found in paternity does not exclude the possibility of first male sperm precedence (Favila *et al.* 2005). On the other hand, larger balls made by single males, which were not used for nesting but were completely or partially eaten after mating, could also be regarded as nutritional nuptial gifts. In these cases, the female may benefit from eating the ball made by the male, which could contribute to the maturation of her oocytes. As carrion is a scarce and ephemeral resource, it would be more advantageous for the female to mate with males offering large balls. More detailed and specific experimental studies should be conducted to elucidate these subjects.

Nesting Behavior. In my study, *C. bispinus* only used fish for nesting. However, according to

Judulien (1899), this species nests using both carrion and excrements, although the author did not mention what kind of feces was used. Further studies should be performed with other types of dung to confirm the observations of Judulien (1899) and the potential nesting behavior plasticity of *C. bispinus*. Currently, the only known species that can breed normally with cow dung and carrion is *C. mutabilis* (Halffter *et al.* 2013).

Most observed nests were telecoprids (in just one case a brood ball was made below the food source). However, Judulien (1899) described compound and paracoprid nests by *C. bispinus*. Therefore, *C. bispinus* is able to display the two strategies to build their nests. In other roller species, such as the African *Scarabaeus catenatus* Gerstaecker (Sato 1998) and *Pachylomera femoralis* Kirby (Scholtz 2009), have been recorded switching from rolling to tunneling and back within their feeding and breeding behavior. Some species would have the ability to switch the nesting strategy according to environmental conditions such as the size and availability of the food source and the extent of competitive pressure. It has been proposed that rolling might have evolved to reduce interspecific and intraspecific competition by quickly transporting the ball away from the food source (Halffter and Matthews 1966; Scholtz 2009). In the temperate Pampas of South America, where large cow dung pads are abundant but dung beetle populations are not, it could be more advantageous to the mating pair of *C. bispinus*, which meet at the food source, to build the nest below the food source rather than a certain distance from it, thus investing less energy and time in rolling and avoiding predators and the potential theft of balls by conspecifics. Halffter and Halffter (1989) considered that in cases where rolling is not manifested, it is because of an adaptive and derived response due to local or regional conditions, such as the presence of an abundant and large food source or the lack of intra- or interspecific competition.

Most of the *C. bispinus* nests were compound, and simple nests were less frequently observed. These simple nests were considered finished nests because there were no additional balls to be transformed into brood balls. The number of finalized brood balls might depend on the size of the initial ball rolled. Compound nests (with 2–4 brood balls) were made from a single, large food ball. My results are consistent with those found for *C. cyanellus cyanellus* under field conditions by Favila and Díaz (1996) and those found for other species of *Canthon* under laboratory conditions by Halffter *et al.* (2013).

In spite of the plasticity of the nesting behavior of *C. bispinus*, this species should be considered exhibiting Nesting Pattern V because in most cases

the nest is subterranean to slightly shallow, telecoprid, and compound. Moreover, male and female cooperate, and parental care is conducted by the female (see Halffter and Edmonds 1982).

Brood Balls. The brood balls of *C. bispinus* have the egg chamber located in an upper protuberance, isolated from the provisions by a partition of soil material, and without an organic lining. Similar structures of brood balls have been described for the necrophagous *C. cyanellus cyanellus* (Halffter *et al.* 1983; Favila 2001; Hernández-Martínez and Martínez 2003), *C. mutabilis* and *C. virens* (Halffter *et al.* 2013), *C. quinquemaculatus* (Halffter *et al.* 2013; Cantil *et al.* 2014a), and *C. virens aff. paraguayanus* (Cantil *et al.* 2014b). The complete isolation of the egg chamber from the provision chamber by a partition of soil material is also present in necrophagous species of *Coprophanaeus* Olsoufieff (Barattini and Sáenz 1953; Cantil *et al.* 2012) This isolation was proposed as a mechanism to avoid contact between the egg and possible kleptoparasites, parasitoids, and fungi brought with the provisions (Laza 2006; Sánchez 2009). This character, together with the lack of an organic lining and the ejection of larval fecal pellets outside the ball, were proposed as adaptive responses of necrophagous species to their food (Cantil *et al.* 2014a, b).

Post-Oviposition Care. The male of *C. bispinus* does not cooperate with the female in nest care, but he remains in the nest with the female until at least oviposition is finished. The male's presence in the nest during the first week could be interpreted as guarding behavior to prevent other males mating with the female, according to Favila *et al.* (2005). Also, additional matings could occur in this period to reduce sperm competition, as was observed in *C. cyanellus cyanellus* (Favila *et al.* 2005). On the other hand, the female stays in the nest for 30 days, providing post-oviposition care to the brood balls. Female care of the offspring has been observed for several species of Scarabaeinae, not only in roller species but also in burrower and dweller species (Cambefort and Lumaret 1983; Halffter *et al.* 1983, 1996, 2011, 2013; Klemperer 1983; Sato and Imamori 1986a, b, 1987, 1988; Edwards and Aschenborn 1989; Halffter, 1997; Hunt *et al.* 2002; Huerta and Bang 2004; Huerta *et al.* 2003, 2005; Cantil *et al.* 2014a). As demonstrated in several experiments and observations, survivorship of the progeny of the subsocial species is higher when there is parental care (Halffter and Matthews 1966; Tyndale-Biscoe 1984; Favila 1993; Halffter *et al.* 1996; Huerta and Halffter 2000; Hunt *et al.* 2002). In my study, survival rate was 92%, which is consistent with the earlier studies. The role of post-oviposition care

in subsocial species appears to be different among dwellers, burrowers, and rollers (Halffter 1997). In the last group, it is likely that females provide chemical protection to the brood balls, covering them with mandibular and abdominal secretions, which prevent the growth of fungi and bacteria on them (Favila *et al.* 2012). Halffter *et al.* (2013) proposes that evolution of parental care in roller beetles is a consequence of different factors, which include competition and limited food availability, kind of food, kleptoparasitism, food contamination by microorganisms, and the growth of entomopathogenic fungi on the brood balls.

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REFERENCES CITED

- Barattini, L. P., and A. C. Sáenz. 1953.** Nuevos aportes para el conocimiento del desarrollo de *Phanaeus milon* (Blanch.) (Col. Scarab.). Revista de la Sociedad Entomológica Argentina 16: 4–29.
- Bellés, X., and M. E. Favila. 1983.** Protection chimique du nid chez *Canthon cyanellus cyanellus* LeConte. Bulletin de la Société entomologique de France 88: 602–607.
- Brown, W. D., B. J. Crespi, and J. C. Choe. 1997.** Sexual conflict and the evolution of mating systems [pp. 352–377]. In: The Evolution of Mating Systems in Insects and Arachnids (J. C. Choe and B. J. Crespi, editors). Cambridge University Press, Cambridge, UK.
- Burger, B. V., W. G. B. Petersen, B. T. Ewig, J. Neuhaus, G. D. Tribe, H. S. C. Spies, and W. J. G. Burger. 2008.** Semiochemicals of the Scarabaeinae VIII. Identification of active constituents of the abdominal sex-attracting secretion of the male dung beetle, *Kheper bonellii*, using gas chromatography with flame ionization and electroantennographic detection in parallel. Journal of Chromatography A 1186: 245–256.
- Burger, B. V., W. G. B. Petersen, W. G. Weber, and Z. M. Munro. 2002.** Semiochemicals of the Scarabaeinae. VII: Identification and synthesis of EAD-active constituents of abdominal sex attracting secretion of the male dung beetle, *Kheper subaeneus*. Journal of Chemical Ecology 28(12): 2527–2539.
- Cambefort, Y., and J. P. Lumaret. 1983.** Nidification et larves des Oniticellini afro-tropicaux. Bulletin de la Société Entomologique de France 88: 542–569.
- Cantil, L. F., M. V. Sánchez, P. A. Dinghi, and J. F. Genise. 2014a.** Food relocation behavior, nests, and brood balls of *Canthon quinquemaculatus* Laporte de Castelnau (Coleoptera: Scarabaeidae: Scarabaeinae). The Coleopterists Bulletin 68(2): 199–208.
- Cantil, L. F., M. V. Sánchez, and J. F. Genise. 2014b.** The nest and brood balls of *Canthon (Canthon) virens aff. paraguayanus* Balthasar (Coleoptera: Scarabaeidae: Scarabaeinae). The Coleopterists Bulletin 68(3): 384–386.
- Cantil, L. F., L. Sarzetti, A. Molina, and M. V. Sánchez. 2012.** Nidos y bolas de cría de *Coprophanaeus (C.) cyanescens* (Olsoufieff, 1924) en la provincia de Salta, Argentina. IX Reunión Latinoamericana de Scarabaeoidología, Buenos Aires, Argentina.
- Edwards, P. B., and H. H. Aschenborn. 1988.** Male reproductive behaviour of the African ball-rolling dung beetle, *Kheper nigroaeneus* (Coleoptera: Scarabaeidae). The Coleopterists Bulletin 42(1): 17–27.
- Edwards, P. B., and H. H. Aschenborn. 1989.** Maternal care of a single offspring in the dung beetle *Kheper nigroaeneus*: the consequences of extreme parental investment. Journal of Natural History 23: 17–27.
- Favila, M. E. 1988.** Chemical labelling of the food ball during rolling by males of the subsocial coleopteran *Canthon cyanellus cyanellus* LeConte (Scarabaeidae). Insectes Sociaux 35: 125–129.
- Favila, M. E. 1993.** Some ecological factors affecting the life-style of *Canthon cyanellus cyanellus* (Coleoptera Scarabaeidae): an experimental approach. Ethology, Ecology & Evolution 5: 319–328.
- Favila, M. E. 2001.** Historia de vida y comportamiento de un escarabajo necrófago: *Canthon cyanellus cyanellus* LeConte (Coleoptera: Scarabaeinae). Folia Entomológica Mexicana 40(2): 245–278.
- Favila, M. E., and A. Díaz. 1996.** *Canthon cyanellus cyanellus* LeConte (Coleoptera: Scarabaeidae) makes a nest in the field with several brood balls. The Coleopterists Bulletin 50(1): 52–60.
- Favila, M. E., J. Nolasco, I. Chamorro Florescano, and M. Equihua. 2005.** Sperm competition and evidence of sperm fertilization patterns in the carrion ball-roller beetle *Canthon cyanellus cyanellus* LeConte (Scarabaeidae: Scarabaeinae). Behavioral Ecology and Sociobiology 59: 38–43.
- Favila, M. E., M. Ortiz-Domínguez, I. Chamorro-Florescano, and V. Cortez-Gallardo. 2012.** Comunicación química y comportamiento reproductor de los escarabajos rodadores del estiércol (Scarabaeinae: Scarabaeini): aspectos ecológicos y evolutivos, y sus posibles aplicaciones [pp. 141–164]. In: Temas Selectos en Ecología Química de Insectos (J. C. Rojas and E. A. Malo, editors). El Colegio de la Frontera Sur, Tapachula, Mexico.
- Gordon, R. D., and O. L. Cartwright. 1974.** Survey of food preferences of some North American *Canthonini* (Coleoptera: Scarabaeidae). Entomological News 85 (5–6): 181–185.

- Halffter, G. 1997.** Subsocial behavior in Scarabaeinae beetles [pp. 237–259]. *In*: The Evolution of Mating Systems in Insects and Arachnids (J. C. Choe and B. J. Crespi, editors). Cambridge University Press, Cambridge, UK.
- Halffter, G., V. Cortez, E. J. Gómez, C. M. Rueda, W. Ciales, and J. R. Verdú. 2013.** A review of subsocial behavior in Scarabaeinae rollers (Insecta: Coleoptera): an evolutionary approach. *Monografías Tercer Milenio*, No. 9. S.E.A. and INECOL, Zaragoza, Spain.
- Halffter, G., and W. D. Edmonds. 1982.** The Nesting Behavior of Dung Beetles (Scarabaeinae): An Ecological and Evolutionary Approach. Instituto de Ecología, México D. F., Mexico.
- Halffter, H., and V. Halffter. 1989.** Behavioral evolution of the non-rolling roller beetles (Coleoptera: Scarabaeidae, Scarabaeinae). *Acta Zoológica Mexicana* (n.s.) 32: 1–53.
- Halffter, G., V. Halffter, and M. E. Favila. 2011.** Food relocation and nesting behavior in *Scarabaeus* and *Kheper* (Coleoptera: Scarabaeinae). *Acta Zoológica Mexicana* (n.s.) 27: 305–324.
- Halffter, G., V. Halffter, and C. Huerta. 1983.** Comportement sexuel et nidification chez *Canthon cyanellus cyanellus* LeConte (Col. Scarabaeidae). *Bulletin de la Société entomologique de France* 88: 585–594.
- Halffter, G., C. Huerta, and J. López-Portillo. 1996.** Parental care and offspring survival in *Copris incertus* Say, a sub-social beetle. *Animal Behavior* 52: 135–139.
- Halffter, G., and E. G. Matthews. 1966.** The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Folia Entomológica Mexicana* 12–14: 1–312.
- Hernández-Martínez, G., and I. Martínez. 2003.** Desarrollo larval de *Canthon cyanellus cyanellus* LeConte 1859 (Coleoptera: Scarabaeidae). *Acta Zoológica Mexicana* 89: 185–200.
- Huerta, C., and H. S. Bang. 2004.** Fecundity and offspring survival of *Copris tripartitus* Waterhouse (Coleoptera, Scarabaeidae: Scarabaeinae) under laboratory rearing conditions. *The Coleopterists Bulletin* 58: 501–507.
- Huerta, C., and G. Halffter. 2000.** Factores involucrados en el comportamiento subsocial de *Copris* (Coleoptera: Scarabaeidae: Scarabaeinae). *Folia Entomológica Mexicana* 108: 95–120.
- Huerta, C., G. Halffter, and V. Halffter. 2005.** Nidification in *Eurysternus foedus* Guérin-Méneville: its relationship to other dung beetle nesting patterns (Coleoptera: Scarabaeidae, Scarabaeinae). *Folia Entomológica Mexicana* 44: 75–84.
- Huerta, C., G. Halffter, V. Halffter, and R. López. 2003.** Comparative analysis of reproductive and nesting behavior in several species of *Eurysternus* Dalman (Coleoptera: Scarabaeinae: Eurysternini). *Acta Zoológica Mexicana* (n.s.) 88: 1–41.
- Hunt, J., L. W. Simmons, and J. S. Kotiaho. 2002.** A cost of maternal care in the dung beetle *Onthophagus taurus*? *Journal of Evolutionary Biology* 15: 57–64.
- Judulien, F. 1899.** Quelques notes sur plusieurs coprophages de Buenos Aires. *Revista del Museo de la Plata* (Argentina) 9: 371–380.
- Klemperer, H. G. 1983.** Subsocial behavior in *Oniticellus cinctus* (Coleoptera: Scarabaeidae): effects of the brood on parental care and oviposition. *Physiological Entomology* 8: 393–402.
- Laza, J. H. 2006.** Dung-beetle fossil brood balls: the ichnogenera *Coprinisphaera* Sauer and *Quirogaichnus* (Coprinisphaeridae). *Ichnos* 13: 217–235.
- Luzzatto, M., E. Monteresino, and M. Zunino. 1997.** Observations on the feeding behavior of *Tetraechma tarsalis* (Balthasar 1939) (Coleoptera Scarabaeidae Canthonina). *Tropical Zoology* 10: 57–61.
- Martínez, A. 1959.** Catálogo de los Scarabaeidae argentinos (Coleoptera). *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia* 5: 1–126.
- Matthews, E. G. 1963.** Observations on the ball-rolling behavior of *Canthon pilularius* (L.) (Coleoptera, Scarabaeidae). *Psyche* 70: 75–93.
- Medina, C. A., C. H. Scholtz, and B. D. Gill. 2003.** Morphological variation and systematics of *Canthon Hoffmanssegg* 1817 and related genera of New World Canthonini dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Deutsche Entomologische Zeitschrift* 50: 23–68.
- Montes de Oca, E., I. Martínez, M. Cruz, and M. E. Favila. 1991.** Observaciones de campo sobre el comportamiento y madurez gonádica en *Canthon indigaceus chevrolati* Harold (Coleoptera: Scarabaeidae). *Folia Entomológica Mexicana* 83: 69–86.
- Sakaluk, S. K. 1984.** Male crickets feed females to ensure complete sperm transfer. *Science* 223: 609–610.
- Sakaluk, S. K. 2000.** Sensory exploitation as an evolutionary origin to nuptial food gifts in insects. *Proceedings of Royal Society of London* 267: 339–343.
- Sánchez, M. V. 2009.** Trazas fósiles coleópteros coprófagos del Cenozoico de la Patagonia Central. Significado evolutivo y paleoambiental. PhD dissertation, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina.
- Sato, H. 1998.** Male participation in nest building in the dung beetle *Scarabaeus catenatus* (Coleoptera: Scarabaeidae): Mating effort versus paternal effort. *Journal of Insect Behavior* 11(6): 833–843.
- Sato, H., and M. Imamori. 1986a.** Production of two brood pearls from one dung ball in an African ball-roller, *Scarabaeus aegyptiorum* (Coleoptera, Scarabaeidae). *Kontyû* 54(3): 381–385.
- Sato, H., and M. Imamori. 1986b.** Nidification of an African ball-rolling scarab, *Scarabaeus platynotus* Bates (Coleoptera: Scarabaeidae). *Kontyû* 54: 203–207.
- Sato, H., and M. Imamori. 1987.** Nesting behaviour of a subsocial African ball-roller *Kheper platynotus* (Coleoptera, Scarabaeidae). *Ecological Entomology* 12: 415–425.

- Sato, H., and M. Imamori. 1988.** Further observations on the nesting behavior of a subsocial ball-rolling scarab, *Kheper aegyptiorum*. *Kontyû* 56: 873–878.
- Scholtz, C. H. 2009.** Nesting and breeding patterns [pp. 69–95]. *In: Evolutionary Biology and Conservation of Dung Beetles* (C. H. Scholtz, A. L. V. Davis, and U. Kryger, editors). Pensoft Publishers, Sofia, Bulgaria.
- Silva, P. G. 2011.** Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) of two non-native habitats in Bagé, Rio Grande do Sul, Brazil. *Zoological Studies* 50(5): 546–559.
- Thornhill, R. 1976.** Sexual selection and nuptial feeding behaviour in *Bittacus apicalis* (Insecta: Mecoptera). *The American Naturalist* 110: 529–548.
- Tribe, G. D. 1975.** Pheromone release by dung beetles (Coleoptera: Scarabaeidae). *South African Journal of Science* 71: 277–278.
- Tyndale-Biscoe, M. 1984.** Adaptive significance of brood care of *Copris diversus* Waterhouse (Coleoptera: Scarabaeidae). *Bulletin of Entomological Research* 74: 453–461.

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