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Feeding and reproductive behavior of the dung beetle *Canthon rutilans cyanescens* (Coleoptera: Scarabaeinae)

Malva Isabel Medina Hernández[1]*, Mariana Mrotskoski Niero[1],
Fabiana Schumacher[1], Mariah Wuerges[1]

[1]*Universidade Federal de Santa Catarina, Centro de Ciências Biológicas, Departamento de Ecologia e Zoologia, Florianópolis, SC, Brasil.*

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ABSTRACT

Canthon rutilans cyanescens is a telecoprid and coprophagous dung beetle subspecies that builds two types of balls with feeding and nesting purposes. This paperwork describes some behavior and development time characteristics, as well as it analyses the influence of the type and amount of food on this species feeding and reproductive behavior. Adult individuals were sampled in Atlantic Forest areas in southern Brazil (between 2014 and 2016) and they were kept in laboratory conditions within 24 and 27 °C in a 12 hours photoperiod. Development time was observed on brood balls built by 40 couples fed with domestic dog feces. The weight and number of brood and food balls produced by each couple were measured and counted in an experiment with 50 couples fed with feces from distinct mammal's species as well as in another experiment with 28 couples fed with 1g and 5g of domestic dog feces, distributed into two groups: small and large body size couples. The subspecies' behavior varied according to the quality of the food resource, with omnivore feces as the best one, possibly due to the higher nutritional quality and microorganism's diversity. In addition, individuals' size influenced parental investment and the availability of food resource affected dung beetle's reproductive success, since, when less food was offered, smaller amounts of food balls and smaller brood balls were built by the adult couples. Our results demonstrated that *Canthon rutilans cyanescens* has a rapid development and a behavioral plasticity related to the quality and the amount of food.

Introduction

Within subfamily Scarabaeinae, the tribe Deltochilini Lacordaire 1856 clusters more than 22 dung beetle's genera (Tarasov and Dimitrov, 2016) which feed both on the larval and adult stages from decomposing organic matter, mainly in the form of mammal feces and dead animals carcasses, by transforming it into small balls and burying it into the ground in tunnels, thereby reallocating food to build their nests (Halffter and Matthews, 1966; Halffter and Edmonds, 1982; Scholtz, 2009a). Consequently, these insects distribute and incorporate organic matter into the soil, besides performing secondary functions, such as soil aeration and seeds dispersal (Nichols et al., 2008). As feces arrangement in nature is a consequence from mammals distribution, and since it can be rapidly removed or dehydrated (Scholtz, 2009b), the telecoprid behavior is an evolutionary strategy of resource use to avoid competition (Halffter and Edmonds, 1982; Sato, 1998).

The genera *Canthon* Hoffmansegg 1817, with 174 described species (Halffter and Martínez, 1977), contains the greatest number of species within the Deltochilini tribe within the New World, and it is distributed from southern Canada to Argentina (Medina et al., 2003). Many species within the genus have subsocial behavior patterns, presenting cooperation between male and female during nesting and parental care period, through brood balls maintenance along with the offspring development (Halffter at al., 2013). The balls within the genus can be built by one or by both parents according to two distinct purposes. One refers to the balls used as food storage for adults (food balls), and the other to the balls remodeled from a food ball, where the female lays the egg (brood ball), generally covered with a layer of soil, that will serve for the larva development, and, later, as a pupation chamber (Halffter et al., 2013). In several species of *Canthon*, the visual difference between both types of the ball is given by the egg chamber, as a protuberance in the brood ball and, as an aeration soil filter on its roof (Cantil et al., 2014a, 2014b). Thus, the larva is confined within the brood ball, and then, the amount of food available for its development remains limited to the parent's provision at the time the brood ball is built. Parental investment has a balance between the benefits of greater offspring survival and the costs related to high energy investments (Alcock, 2009). Evolutionary pressures on telecoprid behavior have favored k-strategies, involving

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* Corresponding author.
E-mail: malva.medina@ufsc.br (M.I.M. Hernández).

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greater energy investments in oviposition and a reduced number of offspring, increasing individual survival (Halffter and Edmonds, 1982; Scheffler, 2005; Scholtz, 2009c). Therefore, the larvae within the nests stay protected against competitors, predators as well as unfavorable climatic conditions (Halffter and Edmonds, 1982).

Dung beetles search for vertebrate excrements of distinct qualities, which are scarce and transitory food resources in nature. This is especially true in tropical environments, because the combination between high temperatures and intense rainfalls accelerate dung decomposition (Gill, 1991). Scarabaeinae can distinguish feces from distinct mammals, and although they generally do not specialize in specific types of food, they have clear preferences in the presence of alternative resources (Simmons and Ridsdill-Smith, 2011; Bogoni and Hernández, 2014). In addition, in tropical forests mammals tend to have a lower density and biomass than in temperate ecosystems (Halffter and Matthews, 1966). Consequently, competition for these resource is fierce, evidenced by the great number of dung beetles attracted to baited traps (Hanski and Cambefort, 1991; Bogoni and Hernández, 2014). Accordingly, evolutionary trends towards phenotypic and behavioral adaptations for efficient feces use, are observed in response to great competitive rates (Halffter and Edmonds, 1982). Since, both the competition in scarce food resource and the short period in which the excrement is available are limiting factors for building both food and brood balls, a behavior trend on minimizing the effects of the environmental variation met by these beetles is a possibility. For instance, the amount of food provided by the parents in the brood balls construction can influence the offspring size and, affecting reproductive success, considering, that larger males may have greater success in mating (Hunt and Simmons, 2001; Chamorro-Florescano and Favila, 2008; Chamorro-Florescano et al., 2011) and, larger females may have greater survival and fecundity (Hunt et al., 2002).

Hence, the contribution of a certain behavior to reproductive success can directly influence individual fitness (Krebs and Davies, 1997). Those insects with greater advantages in obtaining and maintaining the supplies may present a more successful and, or a greater offspring. In the presence of great quantities of resources and with low competition, females can build brood balls containing a higher amount of food. In contrast, when there is a limited amount of food, intense competition can reduce resources available for reproduction (Scholtz, 2009a). This scenario can result in a compensation among the total number of brood balls and the mean amount of available resources per offspring in the brood balls (Scholtz, 2009b), possibly affecting the newly emerged individual's size (Lee and Peng, 1981; Moczek, 1998; Hunt and Simmons, 2000, 2002; Kryger et al., 2006).

Canthon rutilans cyanescens Harold, 1868 is a dung beetle of about 1 cm length, mainly with coprophagous feeding habit (Hernández et al., 2019). It has a blue iridescent color associated with diurnal behavior and it is common (Batilani-Filho & Hernández, 2017) and well distributed in Atlantic Forest areas from Southern Brazil (Vaz-de-Mello et al., 2014; Hensen et al., 2018). The main purpose of this paper was to describe the reproductive behavior of *Canthon rutilans cyanescens* and to assess the developing time of different life stages, as well as to test the effect of different types and quantities of food supply on the both food and brood balls constructed, as measures of reproductive success.

Material and methods

Data sampling

To determine the development time of life stages, adults of *Canthon rutilans cyanescens* were sampled in the Unidade de Conservação Ambiental Desterro (UCAD) (27°31'S and 48°30'W), in Florianópolis, Santa Catarina (SC), in southern Brazil, in September and October 2014. To measure reproductive success per couple according to the type of resource, adults were collected between February and May 2016 at Parque Estadual Serra do Tabuleiro, in Santo Amaro da Imperatriz, SC (27º44'S and 48º48'W). In order to analyze the effect of the amount of resource and body size on the number and weight of ball built by couples, the specimens were collected at the UCAD and at the Parque Municipal da Lagoa do Peri (27°43'S and 48°30'W), municipality of Florianópolis, during September and October 2016.

Live insects were collected with baited traps, made of 8 cm high and 15 cm diameter plastic pots buried at ground level with an opening to allow insects to enter, filled with a layer of soil and 50 g of dog feces, from the Central Bioterio of the Universidade Federal de Santa Catarina (UFSC). The traps were left in the areas for 48 h, and the sampled insects were transported to the Laboratório de Ecologia Terrestre Animal (LECOTA), Departamento de Ecologia e Zoologia (ECZ) of UFSC.

Laboratory breeding

The animals were separated by sex and age using a stereoscopic magnifying glass and weighed on an analytical weighing-machine, Adventurer OHAUS, with 0.0001 g accuracy. The sexual dimorphism is observed in the tibial spur of the anterior legs: the females have a sharp apical spur, while in the males the spur is enlarged as a spatula (Halffter and Martínez, 1977). We observed two parameters to make groups of age, the opacity of the elytra and the tibial wear, classifying individuals as new (those with a shiny elytra and with the tibia spines and tarsal spur intact and pointed), mature (those with a less shiny elytra, with some tibia spines missing and with a slightly worn tarsal spur) and old (those with an opaque elytra, fewer spines on the tibia and a very worn tarsal spur), including in the experiments only new and mature individuals.

The couples were placed in transparent plastic pots filled with soil from the Parque Municipal Park da Lagoa do Peri, previously sieved and heated in the microwave for 3 min to reduce parasites contamination. The soil of the containers was moistened once a week with mineral water. The insects were kept in the laboratory with a 12 h photoperiod (7 to 19 h), with average relative humidity of 70% and 24±1 to 27±1 °C, depending on the experiment. Depending on the experiment, the beetles feeding consisted of mammalian feces. Feces of *Canis lupus familiaris* (domestic dog) were taken at the Central Bioterio of the Universidade Federal de Santa Catarina and the feces of: *Cerdocyon thous* (crab-eating fox), *Sapajus nigritus* (black capuchin), *Puma concolor* (cougar) and *Tapirus terrestris* (tapir) were brought from the Pomerode Zoo, SC and from the Complexo Ambiental Cyro Gevaerd (Balneário Camboriú Zoo, SC). Feces were frozen by zookeepers, and transported to the LECOTA breeding room at UFSC, where they were kept in a frozen.

Developing time

To describe the development period from egg to adult, 40 male-female pairs were set (males were marked in the right elytra with sandpaper for a quick visual recognition of the sex), in pots of 15 cm of diameter by 15 cm in depth and fed twice a week with domestic dog feces. The brood balls built were maintained individually in smaller pots with moist soil and then opened longitudinally at every two or three days in order to perform life stages observations. After the observation of the larval development, the incision on each brood ball was closed by rubbing the surface affected with the fingers impregnate with water, and then half buried. In the analysis we included the data resulted from those beetles which completed full development until adult stage. The observation period was from September 2014 to July 2015.

Types of food

Fifty male-female pairs were fed with different types of feces. Five feeding treatments were conducted, three with feces from omnivore mammals (*Canis lupus familiaris*, *Cerdocyon thous* and *Sapajus nigritus*), one with feces from a carnivore mammal (*Puma concolor*) and one with feces from an herbivore (*Tapirus terrestris*). Each treatment had ten replicates. The couples were kept in containers (13 cm diameter by 10 cm height), which were arranged randomly on shelves, in order to avoid bias caused by the light position or other external factors. The beetles were fed twice a week, each couple receiving 5 g of feces from the mammal corresponding to its treatment each time. The treatments were organized to avoid any bias caused by individual size and age. All beetles were weighed and organized increasingly according to their weights and then distributed, resulting in individuals of different weights within treatments, but with a similar weights distribution between separate treatments. After categorizing the ages (new and mature individuals), their distribution in the treatments was done randomly in a pre-organization in a spreadsheet, so that there were similar numbers of new and mature individuals between the separate treatments. This design was carefully arranged because young individuals require maturation time after emerging (Halffter and Edmonds, 1982).

In order to measure reproductive success per couple among the distinct treatments, we weight and counted the number of food balls and brood balls, as well as the body weight and number of eclosed beetles (F1). Measurements were performed twice a week between March and April 2016, obtaining 13 measures of each treatment.

Resource amount

In order to evaluate the effects of variation in the amount of supply on the number and weight of food balls and brood balls made by dung beetles, 28 couples were set, 14 of those of small sized individuals and 14 of those of large sized individuals, with a maximum difference of 0.02 g between the individuals of the same couple. The experiment consisted in diversifying the quantity of food offered to the couples. Domestic dog feces (from Bioterium of the Santa Catarina Federal University) was offered twice a week between October and November 2016. Half of the couples of each group size fed with 1 g of feces and the other half fed with 5 g of feces per couple, totaling four treatments with seven replicates each. The couples were placed in 10 cm high and 13 cm diameter pots and arranged randomly on the laboratory shelves.

Data analysis

To analyze the data concerning to the number of balls in relation to the treatments, Generalized Linear Models (GLM) with Poisson distribution were performed, due to the asymmetric distribution of the data; for the weight measurements data, Analysis of Variance (ANOVA) with posteriori Tukey tests were used. In order to measure the fertility rate depending on the type of resource used, it was calculated the ratio between the number of F1 and the number of brood balls produced in each replicate, and then, through a GLM, differences were tested. Subsequently, we calculated by a single mean t-test if the weight of each beetle emerged was different from the average weight of the parental population which was submitted to the treatment. The tests considered significant were those with $P < 0.05$. All analyses were performed in Program R (R Development Core Team, 2015).

Results

Reproductive behavior and development time

The reproductive behavior of *Canthon rutilans cyanescens* involves the copula next to a food ball (Fig. 1A), which lasts around 30 to 40 min, followed by the subsequent transformation of the food ball into a brood ball, when the females opens a hole with the mouth parts, building a chamber where it lays the egg (Fig. 1B). Before that, it was observed that the female defecated on the chamber walls (Fig. 1D), and the male was next to the female along this process (Fig. 1C). After placing the egg, the chamber was closed by the female, who deposits a layer of soil (of about 2 mm thickness) and the couple is often observed walking on the ball, which is half or fully buried, until the larva hatches. The brood ball has shape of a drop water and measures 17±2.5 mm length by 14±1.8 mm width (n=12) (Fig. 1E). The egg lies in a rounded chamber near the upper angular part of the nesting ball, with an air intake hole, which is not always apparent. The brood ball is completely smooth and moist externally when it house the egg, but throughout the development of the larva, the external morphology of the ball was changing, which becoming rough over time, covered by round particles adhered externally, constituted of small pellets of feces produced by the larva (Fig. 1E).

The *Canthon rutilans cyanescens* egg is cylindrical, measures 5±0.8 mm length by 2.4±0.5 mm width (n=4), is white and semi-transparent (Fig. 1F). The scarabeiform larva has the same coloration as the egg in the first days (Fig. 1G), and as it begins to feed, its digestive system becomes dark due to food consumption (Fig. 1H). Along with the increase in the larva size, the mouthparts become darker (Fig. 1I) and the brood ball begins to present externally the presence of pellets of feces. Subsequently, after the larva consumes the entire food resource from the brood ball and eliminates the feces, it acquires a white coloration, presenting a yellow head and dark brown mouth pieces, and it rarely moves after the brood ball resource is fully consumed (Fig. 1J). During the pupa stage, the white color (Fig. 1K) changes to brownish and finally the adult emerges with a brown coloration acquiring the adult typical color after one or two days, which is iridescent blue (Fig. 1L).

Along the experiment about development time of *Canthon rutilans cyanescens*, 238 eggs were observed, but the whole process, until adult stage was counted only for 48 individuals (21 males, 22 females and 5 unidentified). From those, 37 individuals were born in the F1 and 11 in F2. The development time from egg to adult last around 33 days, from which approximately four days corresponded to the egg stage, 18 days to the larval period and 10 days concern to pupa stage. The number of observations (n) for each stage was independent of each other (Table 1).

Effect of the type of resource

Over distinct types of food supply, both brood and food balls were built in all treatments except those with feces from the herbivorous *Tapirus terrestris*, in which the couples were able to feed and survive but did not produce any balls. In general, couples produced twice as much food balls as brood balls, and food balls are of smaller weight (around

Table 1.
Development time of *Canthon rutilans cyanescens* life stages in the laboratory.

Stages	***X* (days)**	**SD (days)**	***n***
Egg	4.16	0.85	16
Larvae	18.14	3.93	7
Pupa	10.17	3.08	34
Total	32.92	3.55	28

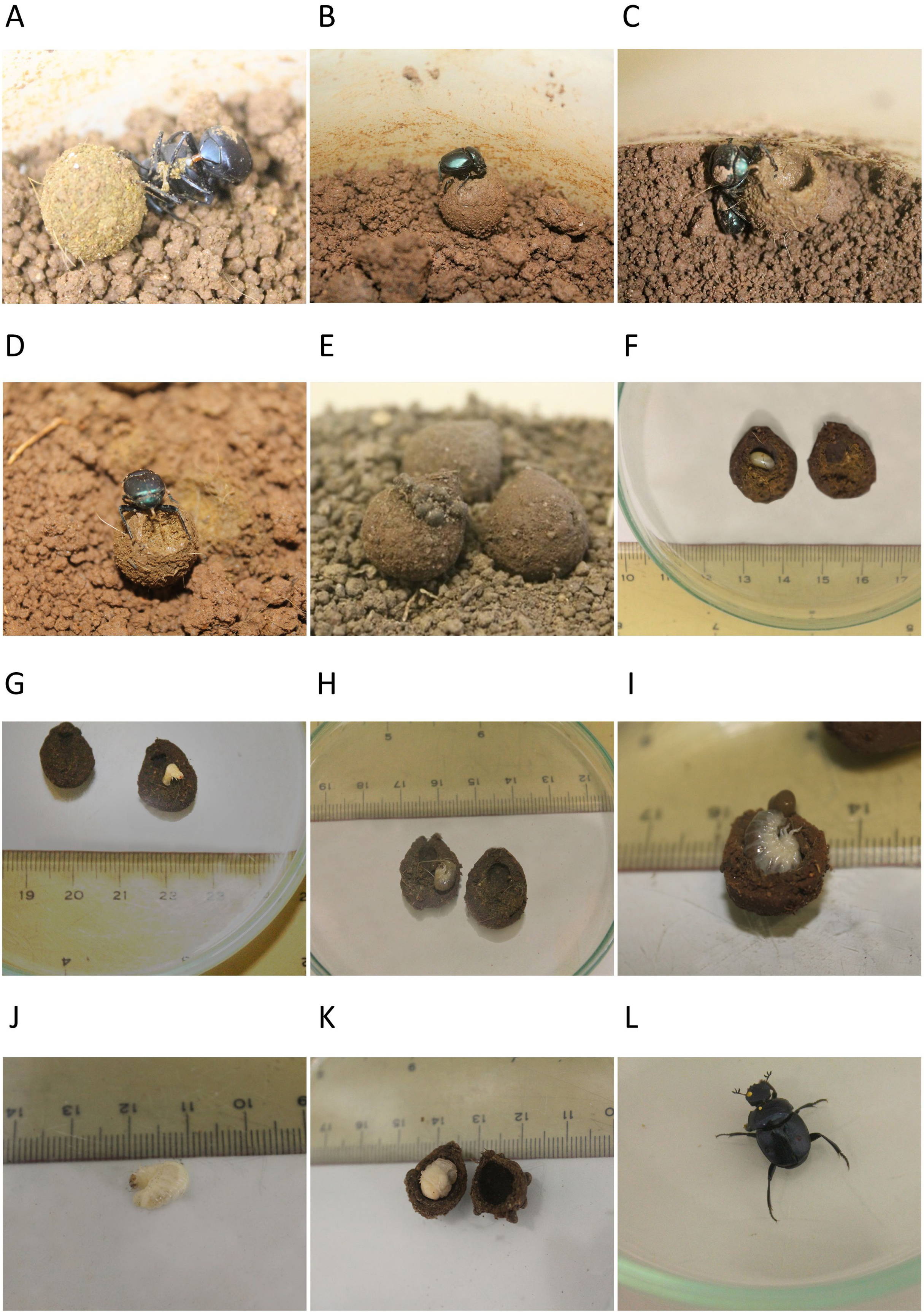

Figure 1 Reproductive behavior and development stages of *Canthon rutilans cyanescens* observed in the laboratory. A - Copula; B - Female producing the oviposition chamber inside the brood ball with its mouth parts; C - Couple next to the future brood ball; D – Female defecating inside the future brood ball chamber; E - Brood balls with external feces pellets; F - Egg; G - Newly hatched larvae; H - Larva growing as it feeds; I - Larva in its maximum size, frequently defecating; J - Last larval stage, when preparing to pupa stage, expelling all fecal contents; K - Pupa; L - Newly hatched adult with moult remains in the clypeus and pronotum.

20% smaller) than the brood balls, although it is important to take into account that the brood balls are built with a larger layer of earth.

The number of food balls produced with feces from the mammal *Canis lupus familiaris* was greater than in the other treatments, being practically twice as much as those made with feces of *Cerdocyon thous* ($Z = -8.98$, $P < 0.001$), and feces of *Sapajus nigritus* ($Z = -11.32$, $P < 0.001$), and the triple of the number produced with feces of *Puma concolor* ($Z = -14.12$, $P < 0.001$) (Fig. 2A). The weight of food balls were statistically different among treatments ($F_{3,1228} = 59.83$, $P < 0.001$). Food balls built with feces of *C. thous* ($X = 1.98$ g) were greater than balls built with feces of *S. nigritus* ($X = 1.71$ g), *C. lupus familiaris* ($X = 1.58$ g) and the smallest built with feces of *P. concolor* ($X = 1.26$ g) (Fig. 2B).

Regarding the number of brood balls made by each couple, the result of the GLM with Poisson distribution revealed that, about the intercept, *Canis lupus familiaris*, the number of brood balls produced was higher in feces from *Cerdocyon thous* ($Z = 3.14$, $P < 0.002$), and *Sapajus nigritus* feces ($Z = 1.98$, $P < 0.05$). The number of nest balls produced with *Puma concolor* feces did not differ from the *Canis lupus familiaris* treatment (Fig. 3A). Furthermore, larger brood balls were made with *C. thous* feces ($F_{3,622} = 12.27$, $P < 0.001$), with a mean weight of 2.26 g, when compared to *S. nigritus* ($X = 2.06$ g) and *C. lupus familiaris* ($X = 1.86$ g). Smaller balls were built with *P. concolor* feces ($X = 1.85$ g), when compared to all other treatments.

Eight adult individuals of the F1 generation emerged during the experiment, five of which were from the *Cerdocyon thous* treatment (two emerged in 32 days and the others 35, 39 and 49 days after the beginning of the experiment), two from *Puma concolor* treatment (which emerged 43 and 49 days after the start of the experiment) and one from *Canis lupus familiaris* (which emerged 43 days after the start of the experiment). The fertility rate was extremely low, with a mean of 0.17 for *C. thous*, 0.10 for *C. lupus familiaris* and 0.08 for *P. concolor*, with no significant difference between treatments ($F_{2,27} = 0.28$, $P = 0.76$). The mean weight of emerged individuals was of 0.12 g in the *C. thous* treatment, 0.11 g in the *C. lupus familiaris* treatment and 0.05 g in the *P. concolor* treatment. The individuals that during the larval lifespan fed on feces from the omnivorous mammals *C. thous* and *C. lupus familiaris* were about 15% smaller than the average weight of the parental individuals from their respective treatments (on a mean of 0.144 and 0.149 g respectively). However, the two individuals emerged from the carnivore *P. concolor* treatment had half the weight of their parental mean weight (0.146 g) ($P < 0.0001$).

Effect of the amount of food resource

In the experiment over the condition of different amounts of resource supply, the food balls construction behavior was presented by all couples. The number of food balls produced with 5 g was greater than those produced with 1 g of resource, for both, the small sized couples (Fig. 4A) and the big sized couples (Fig. 4B) ($Z = 8.94$, $P < 0.001$). However, the small couples produced more food balls ($Z = 1.97$, $P = 0.049$). There was no interaction between food quantity and size of the couples, evidencing that both variables do not depend on each other.

The food balls weight was greater for beetles fed with 5 g than on those fed with 1 g of resource ($F_{1,529} = 27.64$, $P < 0.001$) and they were greater for big couples than for small ones ($F_{1,529} = 52.83$, $P < 0.001$). Thus, the smallest food balls were constructed by small couples when fed with 1 g of resource ($X = 0.90$ g), however, when small couples were fed with 5 g of resource the mean weight of those was of 1.12 g (Fig. 4C), similar to the food balls made by big couples when fed with 1 g of resource ($X = 1.13$ g). The largest balls were constructed by the big couples when fed with a greater resource offer ($X = 1.43$ g) (Fig. 4D). There was also no interaction between the amount of food and the couples' size.

In small sized couples, the brood ball construction behavior was present in five of the seven couples fed with 1 g and in six of those fed with 5 g. For the big sized couples, six of them fed 1 g and all fed with 5 g built brood balls. The number of brood balls produced with 5 g of resource was greater ($Z = 4$, $P < 0.001$) for all couples, although the small couples constructed a smaller number of brood balls ($Z = -2.2$, $P = 0.024$) (Fig. 5A and 5B). There was no interaction between the amount of food and the couples' size.

The weight of the brood balls constructed from 1 g was smaller than those constructed from 5 g of resource ($F_{1,208} = 67.54$, $P < 0.001$) and the ones built by the small couples was smaller than those from the big ones ($F_{1,208} = 19.49$, $P < 0.001$). The mean weight of the brood balls constructed by the small couples was of 1.21 g from 1 g and 1.58 g from

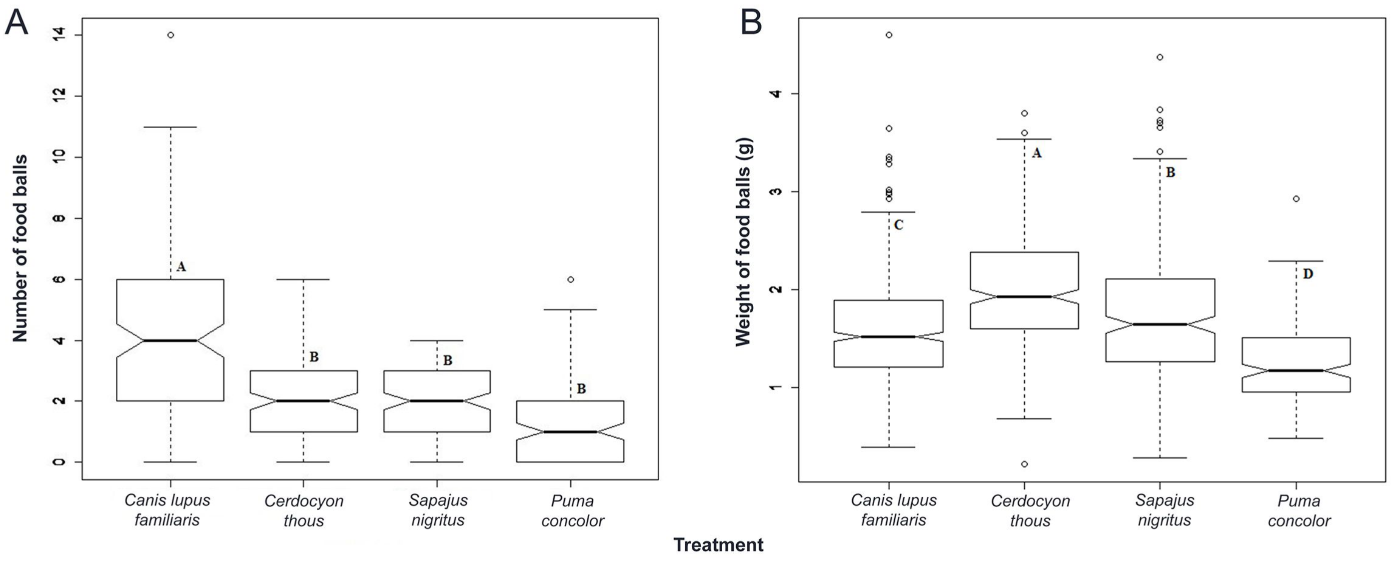

Figure 2 - Number (A) and weight (B) of *Canthon rutilans cyanescens* food balls maintained in laboratory conditions according to distinct food supplies. Treatments: feces of *Canis lupus familiaris* (domestic dog), *Cerdocyon thous* (crab-eating fox), *Sapajus nigritus* (black capuchin) and *Puma concolor* (cougar). The central line of each box corresponds to the median per couples, boxes show 75th percentile and 25th, lines are the upper and lower limits and points are outliers; different letters indicate statistical inequality.

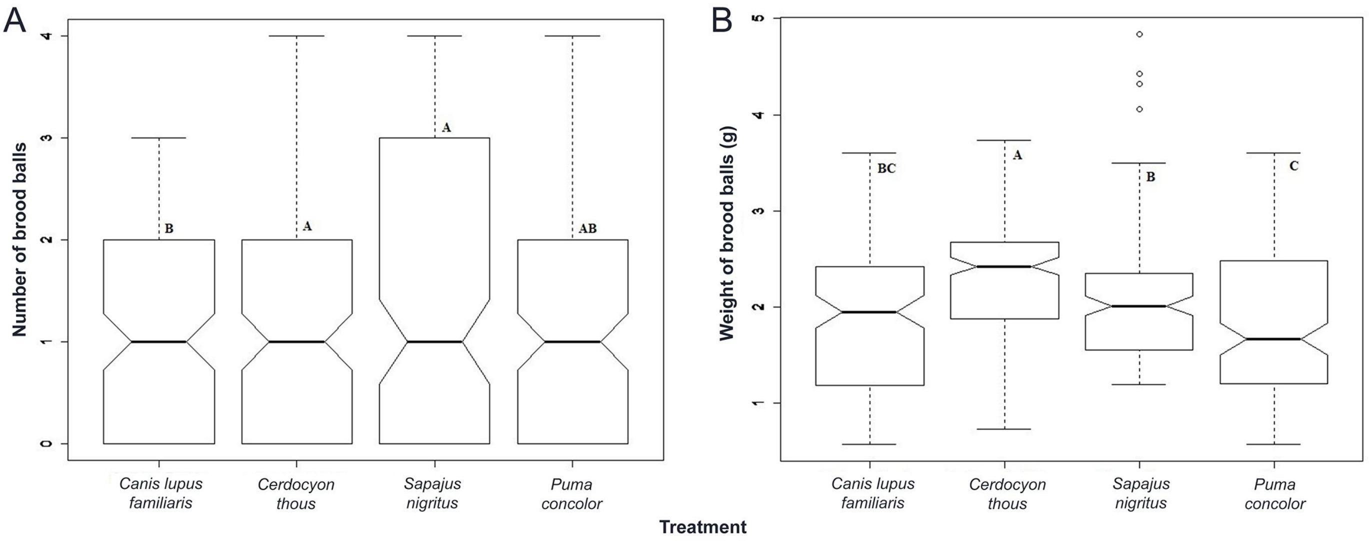

Figure 3 - Number (A) and weight (B) of *Canthon rutilans cyanescens* brood balls maintained in laboratory conditions according to distinct food supplies. Treatments: feces of *Canis lupus familiaris* (domestic dog), *Cerdocyon thous* (crab-eating fox), *Sapajus nigritus* (black capuchin) and *Puma concolor* (cougar). The central line of each box corresponds to the median per couples, boxes show 75th percentile and 25th, lines are the upper and lower limits and points are outliers; different letters indicate statistical inequality.

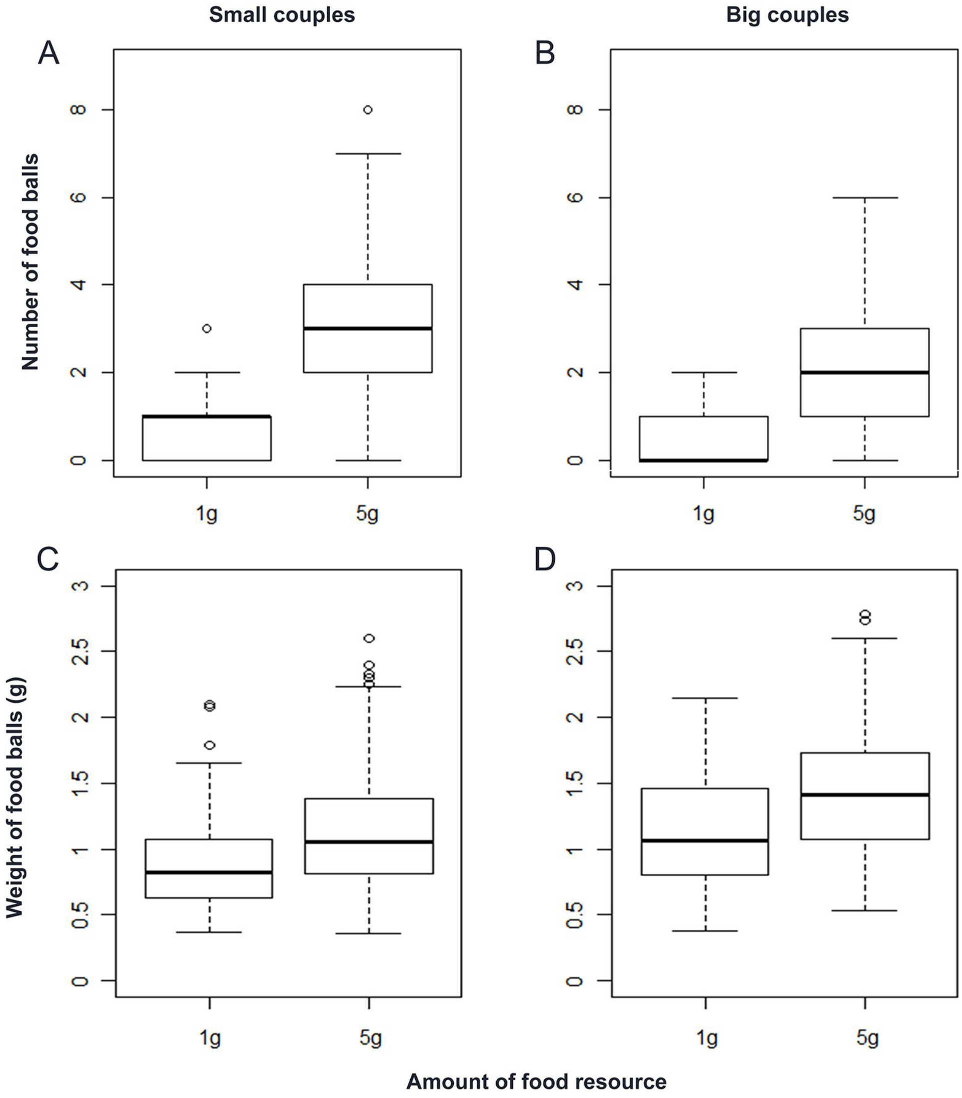

Figure 4 - Number and weight of food balls constructed by *Canthon rutilans cyanescens* couples fed with different amounts of food. A) Number of food balls, with 1 g and 5 g of food supply, built by small couples and B) by big couples. C) Food balls weight with the same amounts of food offered to small couples and D) to big ones. The central line of each box corresponds to the median per couples, boxes show 75th percentile and 25th, lines are the upper and lower limits and points are outliers.

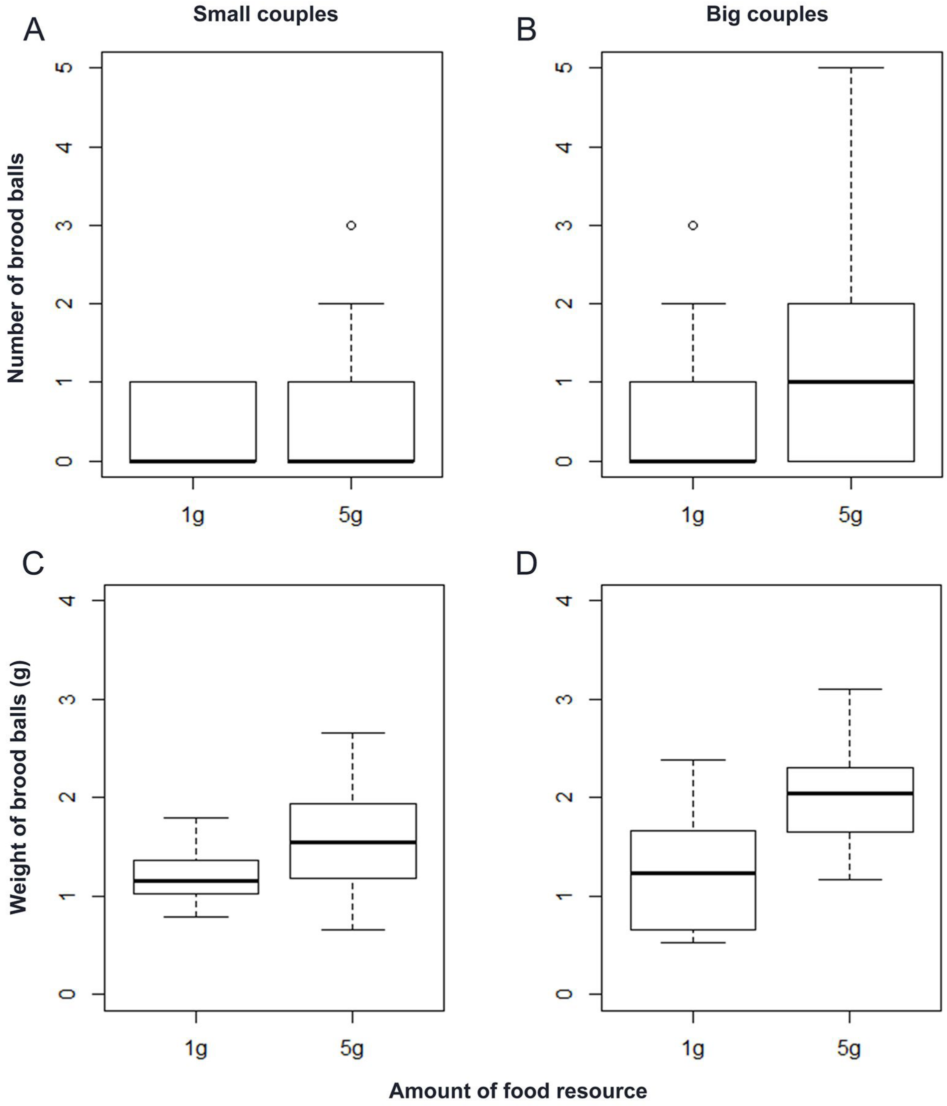

Figure 5 - Number and weight of the brood balls built by *Canthon rutilans cyanescens* couples fed with distinct amounts of food resource. A) Number of brood balls over the offer of 1 g and 5 g of supply in small and B) big couples. C) Brood balls weight constructed with the same amount of food offered to small and D) big couples. The central line of each box corresponds to the median per couples, boxes show 75th percentile and 25th, lines are the upper and lower limits and points are outliers.

5 g of resource (Fig. 5C). The balls made by the big couples weighted 1.22 g with 1 g of resource and 2.00 g with 5 g (Fig. 5D). There was an interaction between food amount and couples' size. When the beetles were fed with 1 g, they produced brood with equal weights. Although, when they were fed with 5 g, there was a difference among the brood balls weight, since heavier balls were built by the bigger couples ($F = 7.43$, $P < 0.006$).

Discussion

Our results demonstrate that *Canthon rutilans cyanescens* is an insect with a rapid larval growth, although the development time can vary according to the diet available for the larvae. The amount of food available influences this subspecies reproduction, although in general, the evolutionary pressure to generate descendants influences the couples to construct brood balls with more or less resource, depending on the offer, although big sized couples make more and heavier balls. Among the Neotropical Scarabaeinae, the genera *Canthon* has been widely used in laboratory experiments because it presents characteristics that allow reproductive behavior and sexual selection studies (i.e. *C. cyanellus cyanellus* LeConte (Bellés and Favila, 1983; Halffter et al., 1983; Favila and Díaz, 1996; Favila, 2001), *C. quinquemaculatus* Laporte (Halffter et al., 2013; Cantil et al., 2014b), *C. virens* aff. *paraguayanus* Balthasar (Cantil et al., 2014a) and *C. bispinus* (González-Vainer, 2015)). The dung beetles are classified as k-strategists, since they invest relatively little in pre-copulatory behaviors and more intensely in the construction of nests and parental care. The female can perform numerous copulas, and it has one functional ovarian and a spermatheca, where it stores the male's sperm and uses it gradually (Halffter and Edmonds, 1982). The food and brood balls construction behavior of the subspecies *C. rutilans cyanescens* is similar to the necrophagous species *C. bispinus* (González-Vainer, 2015), however, the *C. rutilans cyanescens* brood ball has a particular format when compared to the famous piriform shape, here named as "water drop". The development time from egg to adult was similar to the subspecies *C. cyanellus cyanellus* (Favila, 2001), around 30 days. Moreover, feces pellets around the brood balls, are a common characteristic and indicate a normal larval development (Favila, 1992).

The individual's reproductive performance is distinctly affected by feces type and quality (Filgueiras et al., 2009; Scholtz, 2009c). The omnivorous mammalian feces are the most attractive to *C. rutilans* *cyanescens*, which corroborates to the greater number and weight of brood balls built with *C. thous* feces. This preference also displays a strict relation to the species' reproductive success, since 60% of the first generation (F1) emerged from the brood balls built with this omnivore feces. The subspecies preference for *C. thous* feces was previously observed in a natural environment experiment. This evidence was explained by this resource nutritional quality due to balanced amounts of proteins, lipids, and carbohydrates and a lower quantity of nitrogen when compared to carnivore feces (Bogoni and Hernández, 2014). Individuals that emerged from *Puma concolor* treatment had a longer larval cycle and emerged with half the progenitors' weight. Even though this resource holds high protein content, it contains high nitrogen and low carbohydrate amounts which might have generated lower larvae nutritional balance (Bogoni and Hernández, 2014). These statements reinforce the idea that insect choice for the food resource can bear profound effects on the species' reproductive success (Favila, 2001).

The dung beetles, as their closely evolutionary relatives, the coprophagous beetles of the subfamily Aphodiinae, feed through the filtration of liquid fluids, even if their mouthparts are originally chewing structures (Holter, 2000). They evolved from detritus-eating ancestors, which depended on microorganisms for their nutritional needs. Thus, the detritus, constituted of vegetal matter fragments, is decomposed, resulting in smaller fragments which are richer in microorganisms (Cambefort, 1991). The preference for omnivorous animals' feces can be explained by a greater number of bacteria associated to these mammals' intestine, which is larger than in carnivores (Ley et al., 2008). The food resource choice behavior is known in several Scarabaeinae species: *Oniticellus egregius* produces a greater number of balls with horse feces (of better quality) than with cattle feces (Davis, 1989); *Onthophagus binodis* produces more balls with cattle feces that feed on grass in early spring than cattle that feed on grass in late summer, which has worse quality; however, in *Onitis alexis* ball production appears to be unaffected by the variation in food resource quality (Doube, 1991).

Phenotypic plasticity of dung beetles adults' size is a well-known phenomenon and results from the amount of food available to the larval development, which means, the brood ball size is usually related to the size of the individuals emerged from it (Hunt and Simmons, 2002; Scholtz, 2009b). Due to the fact that the larva supply is limited to the amount of food stored by the adults in the brood ball (Halffter and Edmonds, 1982; Edwards and Aschenborn, 1987), a greater quality food resource, or in larger quantity, should result in a shorter larval cycle and/or larger individuals. The dung beetle *Onthophagus taurus* is able to measure the quality of the food source and adjust the amount of food from the fecal mass according to its quality: adults accumulate 50% more cattle feces than horse feces in the brood ball to produce F1 individuals of the same size, that is, in this compensation, larger brood balls are produced with a lower quality supply (Moczek, 1998).

The limitation of the available resource affected *Canthon rutilans cyanescens* brood balls' weight, which might have consequences on the first generation individuals' sizes. It occurs because fewer amounts of food accessible to the larvae development produce negative effects on the adult size. Consequently, limitation in food availability might result in disadvantages toward intraspecific competition, since larger males present greater benefits in agonistic interactions for food and females (Hunt and Simmons, 2001; Chamorro-Florescano and Favila, 2008; Chamorro-Florescano et al., 2011). In addition, larger females also have greater advantages in survival and fertility (Hunt et al., 2002). We also observed that the balls constructed by larger body size couples were bigger, corroborating other studies performed with dung beetles. *Kheper nigroaeneus* shows a positive relationship between body size and the food ball diameter (Tomkins et al., 1999) and for *Onthophagus atripennis* there is a positive relation between the female size and the brood ball size built by the couple (Kishi, 2014), as well as for *Onthophagus taurus* (Hunt and Simmons, 2000). This might be a consequence from the physical limitations of the small individuals to build and roll the balls (Scholtz, 2009a; Kishi, 2014), considering that the median and hind legs are used to measure the portion of the food and to build the ball (Halffter and Matthews, 1966). However, the body size of the F1 generation in *Onthophagus gazella* does not depend on the parents' size, but on the quantity of food supply provisioned in the brood balls (Lee and Peng, 1981).

Confirming that the behavior is modified according to the environment, we observed that the smaller couples compensate the fact that their food balls are smaller by producing a greater amount of them. We also observed a smaller number of brood balls built when couples were fed with little recourse, as previously demonstrated with the species *Onthophagus taurus* (Hunt et al., 2002). Due to the unpredictability of feces as a resource, Favila (1993) demonstrated that the female's reproductive success did not vary when food was offered irregularly for *Canthon cyanellus* (15 g on a random day of the week for one group and 5 g at every three days for another group), illustrating the dung beetles adaptation to the ephemeral nature of their food resource. Excrement availability might result from consequences related to environmental conditions and species competition (Scholtz, 2009c). For the species *Kheper nigroaeneus* it was observed that the balls size decreases with higher levels of competition (Ybarrondo and Heinrich, 1996) and Beckers et al. (2015) observed divergences in several life history characteristics of two populations (one native and one introduced) of *Onthophagus taurus*, such as body size, number of brood balls and larval development time, suggesting that population divergences may also be mediated by proximal mechanisms.

Thus, *Canthon rutilans cyanescens* demonstrates behavioral plasticity in relation to different qualities and quantities of resources, showing that environmental conditions can influence feeding and reproduction processes, affecting competition relations, parental investment and the population dynamics of this subspecies. It is widely known that one of the factors that determine the presence of many species of coprophagous Scarabaeinae is the existence of abundant sources of excrement, and there is a decrease in these organisms richness associated to mammals' decline, due to the increasing of habitats loss (Nichols et al., 2009; Barlow et al., 2010; Bogoni et al., 2016). This phenomenon results in the exclusion of ecological functions and intensifies the negative density dependence on dung beetle populations. These effects might result in a decrease in the beetles' fitness since the choices made by these organisms generate consequences that may or not lead to the survival and reproductive success of the species (Goss-Custard and Sutherland, 1997). We concluded that the reproductive success of *Canthon rutilans cyanescens* depends on the food resource found in nature, with a preference for feces from omnivorous mammals, which provide a higher nutritional quality due to its higher microbial diversity. Also, it was possible to breed this subspecies under laboratory conditions as well as to investigate some behavioral characteristics. Those are significant achievements, considering this species abundance and relevance in terms of ecosystem functions in Atlantic Forest areas in southern Brazil.

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Conflicts of interest

None.

Compliance with ethical standards

Yes.

Author contribution statement

M.I.M.H. have conceived the manuscript objectives, M.M.N., F.S. and M.W. have performed the experiments in the laboratory, all authors have proceeded with data analysis and written the manuscript.

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