SOCIEDADE BRASILEIRA
DE ENTOMOLOGIA
FUNDADA EM 1937

REVISTA BRASILEIRA DE
Entomologia
A Journal on Insect Diversity and Evolution

Body size and body conditions of two dung beetles species (Coleoptera: Scarabaeidae) related to environmental temperatures

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ARTICLE INFO

Article history:
Received 22 October 2022
Accepted 24 March 2023
Available online 12 May 2023
Associate Editor: Lucas Kaminski

Keywords
Canthon rutilans cyanescens
Dichotomius sericeus
Ecophysiology
Population ecology
Scarabaeinae

ABSTRACT

Temperature affects the body size of animals, which is an important trait in natural and sexual selection. Insects do not have complex mechanisms of temperature control, thus temperature changes affect their life aspects, from enzymatic reactions to behavior. The amount of fat stored by insects is also influenced by temperature and constitutes a tissue with biosynthetic and metabolic activity, acting as an energy reservoir. We assessed the effect of environmental temperature due to elevation and seasonal temperature variations on body size and condition of two dung beetles species: *Canthon rutilans cyanescens* and *Dichotomius sericeus* (Coleoptera: Scarabaeinae). Both species are abundant in southern Brazilian forests, but they differ in habits: the first is a diurnal roller whereas the later is a nocturnal tunneler. Summer months and sites with lower elevations and higher temperatures presented larger *C. rutilans cyanescens*. A linear relationship exists between body size and soil temperatures, whereas the temperature positively influences the body length. Furthermore, *C. rutilans cyanescens* from cooler sites had more body fat. Individuals of *D. sericeus* were also larger in summer months, however, we did not find differences in the proportion of fat or a relation between body size and temperature. Thus, the body size of dung beetle species varies in relation to temporal factors, as both species are larger in summer. More interesting was to observe that the species with a diurnal habit, even though smaller in colder places, has a higher proportion of fat, which indicates an evolutionary response to environmental pressure.

Introduction

Temperature has widely been proven to influence insect distribution spatially and temporally (Wolda, 1978). Insects, in general, if exposed to lower temperatures than those considered optimal for their survival, can enter a quiescent or diapause state, when their metabolism and development are slower, and there is a chance of survival when the temperature is normalized. In extreme cases, insects may fall into a coma or die (Lee, 1991; Bale, 1993). On the other hand, when exposed to temperatures higher than optimal, insects may present accelerate development and metabolism, but very high temperatures can also lead them to death (Huey and Kingsolver, 1993; Gilbert and Raworth, 1996). Studies show that most flying insects cannot take off a flight when their thorax temperature is below 25°C and suffer thermal shock at temperatures between 45-47°C, being unable to survive in temperatures of 50–53°C (Machin et al., 1962; May, 1976, 1978; Heinrich, 1980; Christian and Morton, 1992; Wu et al., 2002; Chown et al., 2004; Verdú et al., 2006; Verdú and Lobo, 2008).

Among insects, the body surface plays a key role in the balance between the individual condition and the surrounding environment, as it is related to factors such as water exchange and thermal regulation (Le Lagadec et al., 1998; Kühsel and Blüthgen, 2015). The volume-surface ratio, mediated by insect length, predicts that larger individuals have a smaller volume-surface ratio than smaller individuals. Insects with a smaller volume-surface ratio lose less water, so they have a better heat retention capacity (Kühsel et al., 2017). Besides the volume-surface ratio, the exoskeleton thickness and color can affect the heating capacity. The thickness of the exoskeleton influences heat maintenance as thicker exoskeletons cause individuals to heat up more slowly (Amore et al., 2017). The color is also related to the period of activity in dung beetles: a variety of colors such as blue, green, and red, can be

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https://doi.org/10.1590/1806-9665-RBENT-2022-0099

found in diurnal species, while black-colored species are expected to be nocturnal (Crowson, 1981; Hernández, 2002). The thermal melanism hypothesis (TMH) proposes that dark-colored insets can acquire and preserve higher temperatures when exposed to the sun to survive in colder environments and be active in nocturnal periods (Watt, 1986; Kingsolver, 1987; Stanbrook et al., 2021). Body color also works as interspecific communication as it presents aposematic signals to predators but also favors camouflage to the nocturnal species (Otronen, 1988; Endler, 1990; Guilford and Marian, 1991; Hernández, 2002).

In addition to being a genetic factor, animal fat levels are also influenced by external temperature (Pelleymounter et al., 1995; Sun Yoo et al., 2014). For insects, body fat is a tissue with biosynthetic, and metabolic activities and acts as an energy reservoir (Law and Wells, 1989). In this sense, organisms inhabiting colder and less resourceful environments should present higher fat accumulation than individuals living in warmer and more resourceful sites for thermoregulation and energy reserve (Colinet et al., 2006; Salomão et al., 2019). Fat accumulation provides a rise in the proteins presented in the hemolymph and consequently significantly decreases the super-cooling point, defined as the temperature at which the insect freezes, of the insects so that insects can survive colder temperatures (Verdú et al., 2010; Ben-Hamo et al., 2011).

Coleoptera is the group most diverse in the number of described species, being present in all continents except the Antarctic (Rafael et al., 2012). Some species of this group were studied, and responses in color or body size were observed when they developed under different temperatures: an example is the beetle *Agasicles hygrophila* Selman & Vogt, whose adult weight changes due to the temperature at which their larvae grow (Stewart et al., 1999).

Here we investigate if there are differences in body size and body condition of different populations of two Scarabaeinae beetles related to temperature changes due to the elevation and change of temperature along the year. Dung beetles present an important role in nutrient cycling and maintenance of soil quality: through the process of burying organic matter, they contribute to the return of nutrients and water to the soil, as well as to its aeration, also, acting in the secondary dispersal of seeds (Nichols et al., 2008; Braga et al., 2013). The average air temperature is a good predictor of the dung removal rate and nutrient incorporation in the soil, whereas warmer climates positively influence ecosystems functions and can also influence reproductive behavior as well (Slade & Roslin, 2016; Amore et al., 2018; Hensen et al., 2020).

For this study, we used the dung beetle species *Canthon rutilans cyanescens* Harold, 1868 and *Dichotomius sericeus* (Harold, 1867) as models. The first one is a blue iridescent diurnal roller dung beetle, while the second one is a black nocturnal tunneler species (Hernández et al., 2020). Both species are Neotropical and widely distributed in tropical and subtropical forests in southern Brazil (Vaz-de-Mello et al., 2014; Valois et al., 2017). Differences in body size and proportion of fat of individuals inhabiting locations with different temperatures are expected, whereas larger individuals are found in warmer sites as the lower proportion of body surface to body volume minimizes evaporative water loss. In addition to the influence of temperature on body size, it is expected that insects accumulate more fat in colder sites as a reserve of energy and thermal maintenance.

Materials and methods

The study was carried out in an Atlantic Forest environment of Dense Ombrophilous Forest in Santa Catarina state, southern Brazil. This forest is characterized by complex vegetation involving lianas and epiphytes associated with woody trees, integrating an environment with heterogeneous structures and microclimates, therefore being a biodiversity hotspot for fauna and flora. All the study areas are located in a Cfa climatic region, a humid tropical location, whereas summer is considered hot with a mean temperature of 25°C, no dry season, and 1,500 mm as mean annual rainfall (Köppen, 1936; Leite and Klein, 1990; IBGE, 2012).

Body size – different locations and along the year

To verify whether the temperatures influence body size, we compared the collected individuals from two populations from distinct locations with different elevations: Santo Amaro da Imperatriz, at 200 m a.s.l. (27º44’05”S, 48º48’33”W) and Rancho Queimado, at 800 m a.s.l. (27º41’22”S, 49º00’52”W), both in Santa Catarina state and approximately 30 km apart. Populations of *C. rutilans cyanescens* and *D. sericeus* were sampled with baited pitfall traps in these localities, once a month, between June 2015 and July 2016. Previous studies in the same region presented that the expected maximum distance traveled by *Canthon rutilans cyanescens* and *Dichotomius sericeus* is much smaller than the distance between the sample sites in a period of five months (Silva & Hernández, 2015), so we believe that there is no flow of individuals or genetic flow between the studied populations.

Baited pitfall traps consist of plastic containers (15 cm diameter × 20 cm depth) buried with an opening at the ground level. Traps were covered with a plastic lid and positioned with bamboo sticks to support the bait and prevent rain flooding. The bait was about 20g of human feces wrapped in fabric and hanging below the lid. In each trap, approximately 300 ml of a solution of water with detergent was added to capture the attracted insects. Traps were left in the field for 48 hours, and the collected beetles were deposited in alcohol at Mitia Heusi Silveira Entomology Collection at the Biological Sciences Center of the Universidade Federal de Santa Catarina. These insects were measured from the clypeus to the pygidium with a digital caliper to obtain the total length. We also analyzed databases of daily temperatures of each location acquired by the installation of data loggers in the field, whereas one datalogger was installed 1 m above the soil (in a shaded location), to obtain air temperature, and another datalogger was buried in the soil (5 cm), to obtain the soil temperature.

For individuals of *D. sericeus* collected monthly throughout June 2015 and July 2016 in the locations of 200 and 800 m a.s.l., interpopulational and intrapopulational body size variation was compared by Two-way ANOVA. Due to the low number of individuals of *C. rutilans cyanescens* throughout the year in the 800 m study area (n = 8), only the populations collected in January 2016 were compared between areas using ANOVA. To understand if temperatures are crucial in defining the adult length of dung beetles, we tested the relation between the body size of both species and the mean soil temperatures of each site collection over a year by applying regression analysis. We performed tests to evaluate the normality and homoscedasticity of residuals. Pairwise tests were conducted to find differences between months when the main test was significant. All statistical analyzes were performed with R software (RStudio Team, 2020).

Body condition

To understand the difference between these physiological factors between separated populations, alive individuals of *C. rutilans cyanescens* and *D. sericeus* were collected in the two locations mentioned above during the summer of 2020 for the extraction of muscle and body fat, which requires specimens sacrificed right after capturing so they do not lose any of the features of interest and present biased results. Twelve baited pitfall traps were placed in Santo Amaro da Imperatriz and Rancho

Queimado simultaneously until at least 60 individuals of each species were acquired (about six days). To attract live insects and maintain them alive until checking each trap, the traps were left in the field for up to 24 hours; the buried containers were filled with 5 cm of local soil and 20 g of dog feces as bait, obtained from the Central Bioterium of the Universidade Federal de Santa Catarina, Brazil. We placed a lid with a triangle cutout that allows the entry of the beetles, but makes their exit difficult, in addition to an uncut lid kept just above the trap by bamboo sticks, functioning as an "umbrella".

For these individuals, we measured the total length with a digital calliper and weight, on a precision balance. Also, to quantify the muscle mass and body fat mass of each individual, we followed the methodology of González-Tokman et al. (2011). Therefore, alive insects were individually sacrificed by freezing in Eppendorf tubes and then kept in an oven at 50ºC for 48 h; after this time, they were weighed, and this measurement was recorded as the dry weight or initial weight (W1). Then 1 mL of chloroform was added to each tube, and after 48 h at room temperature, excess chloroform was drained and the beetles were placed in the oven at 50°C for 48 h then weighed to obtain the weight two (W2). The amount of body fat was calculated by subtracting W2 from W1. Afterward, 1 mL of 0.8 M KOH was added to each tube, submerging the beetles, and they were kept at room temperature for 24 h. After this period, KOH was removed and distilled water was added to each tube, followed by 24 h conditioning at room temperature. Then the distilled water was removed and 1 ml of the same liquid was added, which after 2 h of immersion was removed, and the insects were returned to the oven for 48 h at 50ºC. At the end of this period, the last weighing was carried out, recording weight three (W3). Subtracting W3 from W2, we obtained the muscle weight of each individual. The weight ratio that sets up for fat and muscle was calculated.

Finally, we verified if there were differences between the length, weight, fat mass, and muscle mass of dung beetles from the two different locations using T-tests for parametric data or Wilcoxon rank-sum test for non-parametric data after evaluating the distribution of the data (*i.e.*, normality, homoscedasticity).

RESULTS

Canthon rutilans cyanescens

Regarding the temporal variation throughout the year of *C. rutilans cyanescens*, 473 individuals were measured. The fluctuation of body length in the 200 m location showed that in December, February, and April (*i.e.*, during the summer period in the southern hemisphere), individuals were significantly larger than in other months whenever the species is present ($F_{9,473} = 8.286$, $P < 0.001$; Figure 1A). The body length was 11.17, 10.99, and 10.75 mm, respectively, compared to an average of 10.27 mm in the other months. Only eight individuals were sampled throughout the year at 800 m location, during the summer months (December and January), with no significant difference in their body length ($F_{1,481} = 0.242$, $P = 0.623$; Figure 1B).

There was a positive relationship between the average soil temperatures and *C. rutilans cyanescens* body length at the 200 m location ($R = 0.76$, $T_9 = 3.474$, $P < 0.01$; Supplementary Figure S1). Also, by linear regression, for every 1ºC of temperature, the body length of the species increases by 0.16 mm (Size = 7.3 + 0.16 * Temperature; $P < 0.01$). The 29 individuals collected during the summer of 2020 at the 200 m location and the 36 individuals from the 800 m location showed significant differences in size between both populations, with larger ones found in the lower-altitude location. Body size, measured as length and weight, was different in the insects that have developed in different places. The insects from the lowest location were 39% larger ($T_{48} = 7.755$, $P < 0.001$) and 13% heavier ($T_{54} = 7.434$, $P < 0.001$).

A significant difference in the amount of body fat between beetles sampled from the different locations was observed. Individuals collected in the highest (and coldest) location showed 56% more body fat than

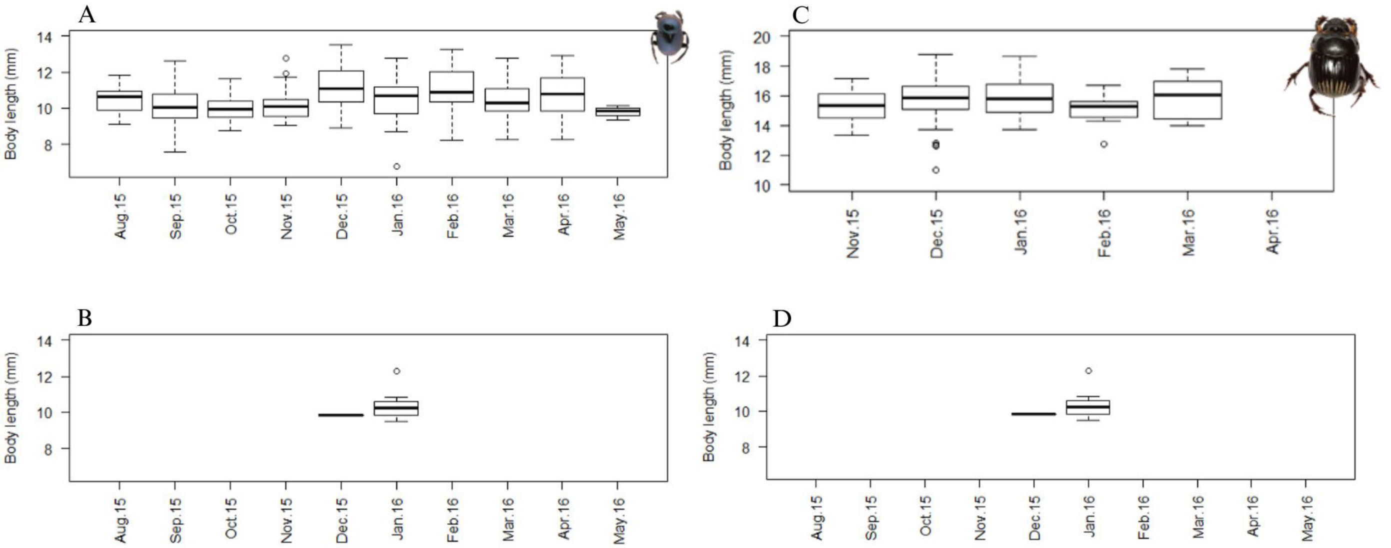

Figure 1 Measures of body length in millimeters of individuals of *Canthon rutilans cyanescens* collected between August/2015 and May/2016 in (A) Santo Amaro da Imperatriz (200 m a.s.l.), whereas Sep/2105, n= 5; Oct/2015, n= 28; Nov/2015, n=6; Dec/2015, n=18; Jan/2016, n=3; Feb/2016, n=8; Mar/2016, n=7; Apr/2016, n=0; and (B) Rancho Queimado (800 m a.s.l.) in Santa Catarina state, whereas Sep/2105, n=0; Oct/2015, n=5; Nov/2015, n=0; Dec/2015, n=25; Jan/2016, n=8; Feb/2016, n=15; Mar/2016, n=7; Apr/2016, n=5. Also, measures of body length in millimeters of individuals of *Dichotomius sericeus* collected between November/2015 and April/2016 in two locations: (C) Santo Amaro da Imperatriz (200 m a.s.l.) Nov/2015, n=10; Dec/2015, n=56; Jan/2016, n=30; Feb/2016, n=10; Mar/2016, n=10; Apr/2016, n=0; and (D) Rancho Queimado (800 m a.s.l.) in Santa Catarina state, whereas Nov/2015, n=0; Dec/2015, n=8; Jan/2016, n=30; Feb/2016, n=29; Mar/2016, n=5; Apr/2016, n=9.

those from the lowest and warmer location (W = 23, $P < 0.05$; Figure 2A). There was no difference in the amounts of muscles of individuals from different locations (W = 47, P = 0.85; Figure 2A).

Dichotomius sericeus

Comparing the populations of *D. sericeus* from the sites of 200 and 800 meters and throughout the year, the occurrence of the adults was observed between November and March at the200 m location (Figure 1C), with 116 measured individuals, and between December and April at the 800 m location (Figure 1D), with 83 measured individuals. We found that the length of *D. sericeus* varies locally ($F_{1,195} = 6.835$, $P < 0.05$), presenting a mean size of 16.33 mm in the 800 m location (Rancho Queimado) while the individuals of the 200 m location (Santo Amaro da Imperatriz) presented a mean size of 15.69 mm. Also, the body length varies monthly ($F_{5,191} = 3.145$, $P < 0.05$), with larger individuals found in January and February in Rancho Queimado, whose body length was 16.69 and 16.73 mm, respectively.

The body length of *D. sericeus* is not related to temperature, with no correlation between the body length of individuals collected at the 200 m site and the mean soil temperatures (R = 0.04, $T_3 = 0.07$, P = 0.95). Likewise, there was no correlation between the body length of individuals collected at the 800 m site and soil temperatures (R = 0.614, $T_3 = 1.32$, P = 0.27).

Furthermore, during the collection in the summer of 2020, when 60 individuals were collected, 29 in the 200 m site and 31 in the 800 m site, we found that individuals have a length 5.7% greater ($T_{51} = 3.104$, $P < 0.05$) at the 800 m site; however, there was no significant difference in relation to the weight of individuals ($T_{56} = 1.123$, P = 0.266), the fat of individuals ($T_{18} = 0.92$, P = 0.369) and the proportions of muscles ($T_{19} = 0.37$, P = 0.711) between sites (Figure 2B).

Discussion

Our results show that populations of two dung beetle species collected at sites of different temperatures present different body lenght and one of them presented differences in physiological conditions, presented as fat amount. The environmental temperature can act at an intraspecific level so that species with a complex development, such as the holometabolous, may respond differently to the temperature accordingly to the ontogenetic stage (Dahlgaard and Loeschcke, 1997; Folguera et al., 2010). The temperature affects the development rate of insects (Gillooly et al., 2002; Jarosík et al., 2002, 2004), which can result in different body sizes within the same species we have shown. This suggests distinct responses of populations when confronted with distinct environmental conditions, indicating that immature stages of insects may have influenced where to invest, in terms of physiological traits, depending on the conditions during their development (McNamara and Houston, 1996; Rombough, 2003; Folguera et al., 2010).

The body size of *C. rutilans cyanescens* varies with temperature, with larger individuals being found at periods and sites of higher temperatures. Furthermore, this species accumulates more fat when it lives in colder places. *D. sericeus* also presents differences between separated populations and is bigger in the warmer months; however, the body size is not correlated to the environment temperature, and the proportions of muscles and body fat are not different.

Our study species present different periods of activity and respond differently to environmental temperatures (Basset and Springate, 1992; Springate and Basset, 1996). Larger and dark-colored insects are predicted to be found at night (Hernández, 2002), once they are less visible to predators and the cool temperatures will not affect them due to their smaller surface area to volume ratio, maintaining the internal heat. On the other hand, small-bodied insects will be found during the daytime once they will heat up faster due to their larger surface area to volume ratio (Lima and Dill, 1990; Guevara and Avilés, 2013). These species present distinct activity patterns and body sizes: the diurnal roller species *C. rutilans cyanescens* has an iridescent blue color and an average body length of 0.9 cm long, while the nocturnal tunneler species *D. sericeus* is black and present an average body length of 1.2 cm (Silva et al., 2010; Vaz-de-Mello et al., 2014; Valois et al., 2017; Hensen et al., 2018). It is known that the composition of nocturnal and diurnal assemblages is different (Silva et al., 2019) and can be correlated to their adaptations to daily temperatures.

The smaller body sizes of *C. rutilans cyanescens* and its thinner exoskeleton exposed to sunlight during the day allow greater effectiveness

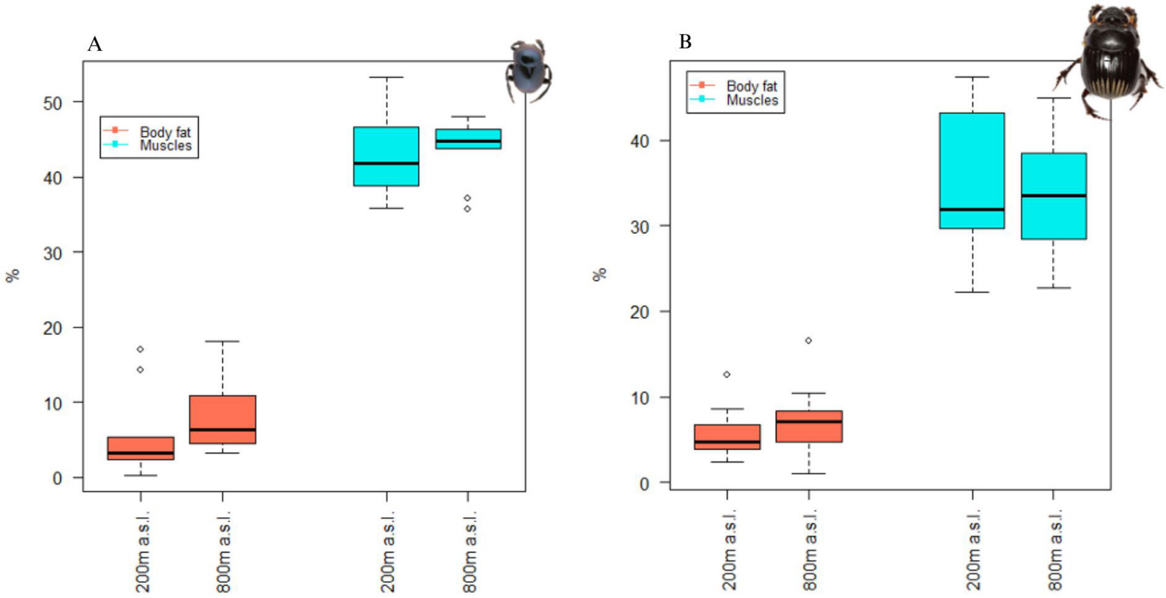

Figure 2 Body fat mass (red boxes) and muscle mass (blue boxes) of individuals of (A) *Canthon rutilans cyanescens* collected at two locations: Santo Amaro da Imperatriz (200 m a.s.l.; n=29) and Rancho Queimado (800 m a.s.l.; n=36) in Santa Catarina state; Body fat mass (red boxes) and muscle mass (blue boxes) of individuals of (B) *Dichotomius sericeus* collected at two locations: Santo Amaro da Imperatriz (200 m a.s.l.; n=29) and Rancho Queimado (800 m a.s.l.; n=31) in Santa Catarina state, south of Brazil.

in behaviors promoting heating, such as perching, in which the individuals sit in a leaf during daytime for thermoregulation. Also, an energy reservoir may be necessary so that the insect can be active on days without sun, thus, they accumulate more fat in colder sites (Young, 1984; Davis et al., 1999; Feer, 2015; Noriega and Vulinec, 2021). *D. sericeus*, being a nocturnal and bigger species, is used to be active in colder temperatures, so passive heating maintenance is expected in this species, regardless of the sites that they inhabit (Verdú and Lobo, 2008; Verdú et al., 2012; Amore et al., 2017; Gallego et al., 2018). In this sense, the results support and coincide with the thermal melanism hypothesis: under the same environmental conditions, the species with darker colors should heat faster; this can be considered advantageous for *D. sericeus* and the mechanism that allowed the species to have a larger body size, nocturnal habit and even occupy colder regions (Trullas et al., 2007; Clusella-Trullas et al., 2008; Gates, 2012; Hernández et al., 2019).

Fat levels are a direct measurement of body condition in insects, while body size is an indirect measurement, as it also depends on the environmental characteristics where the individuals are found. Insects tend to increase their fat levels when in stressful conditions, including anthropogenically disturbed scenarios (Contreras-Garduño et al., 2008; Moya-Laraño et al., 2008; González-Tokman et al., 2011; González-Tokman and Martínez-Garza, 2015; França et al., 2016). For *C. rutilans cyanescens*, we found that the populations with smaller body sizes present more fat proportion, both being indicators of stress, which shows that the allocation of resources to fat is different between populations, without affecting the allocation of resources to the muscular structure of the beetle (Salomão et al., 2018, 2019).

Here, we investigated the differences in body size and body condition of different populations of two Scarabaeinae beetles related to temperature changes due to the elevation and change of temperature along the year. Both species collected at sites of different temperatures present different body lengths: *C. rutilans cyanescens*, the diurnal roller species, presents a larger body length in the warmer site and it is positively related to the temperature. On the other hand, *D. sericeus*, the nocturnal tunneller species, is larger in summer months but its length is not correlated with the temperature; this species did not present significant differences in muscle and fat amounts in the areas with different temperatures, while *C. rutilans cyanescens* presented more fat accumulation in the colder site. We believe these different findings between the species is due to the different behaviors, as a result of an evolutionary process in which the diurnal species respond more to the environmental temperature than the nocturnal species once they have different requirements to survive in the environment that they live. We recommend future studies focusing on the resources of the natural environments with different temperatures, which can also affect the development of the insects, therefore, the size and the ratio of muscles and lipids of the insects inhabiting these sites.

Acknowledgements

We thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, Ministério da Educação, Brazil) for the scholarship awarded to COA [Finance Code 001] and for a postdoctoral grant awarded to PGdS [PNPD 88882.316025/2019-01, Finance Code 001]. We also thank CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico, Ministério da Ciência, Tecnologia e Inovação, Brazil) for a Productivity Grant awarded to MIMH [Process: 307437/2017-5].

Conflicts of interest

The authors declare no conflicts of interest.

Author contribution statement

COA contributed with conceptualization, writing, analyzing the data, measuring specimens, lab experiments, and draft preparation. PGS contributed with analyzing the data, reviewing, critical revision, and approval of the final version. MIMH contributed with the conceptualization, advising, critical revision, and approval of the final version.

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Supplementary material

The following online material is available for this article:

Figura S1 – Positive correlation between mean soil temperatures and body length of the species Canthon rutilans cyanescens collected at the site of 200 m a.s.l. in the years of 2015 and 2016.