*Oecologia Australis*
23(3):536-547, 2019
https://doi.org/10.4257/oeco.2019.2303.12

# DUNG TYPE OR INTRASPECIFIC VARIATION IN BIOMASS: WHAT IS MORE IMPORTANT IN DETERMINING DUNG BEETLE ECOLOGICAL FUNCTION?

*Paula Bernardes Braga[1], Raquel Luiza de Carvalho[2]*, Júlio Neil Cassa Louzada[1] & Lívia Dorneles Audino[1]*

[1] Universidade Federal de Lavras, Departamento de Biologia, Setor de Ecologia, Laboratório de Ecologia e Conservação de Invertebrados, CP 3037, Câmpus Universitário, CEP 37200-000, Lavras, MG, Brazil.

[2] Universidade Federal de Uberlândia, Instituto de Biologia, Laboratório de Ecologia de Insetos Sociais, Av. João Naves de Ávila, 2121, Campus Santa Mônica, CEP 38400-902, Uberlândia, MG, Brazil.

E-mails: paulabernardesb@gmail.com; raqueluly@gmail.com (*corresponding author); livia.audino@gmail.com; jlouzada@gmail.com

**Abstract:** We evaluated the relative importance of dung type and intraspecific variation in biomass on dung beetle function by quantifying the ecological functions (dung removal and soil excavation) of two dung beetle species under laboratory conditions: *Dichotomius bos*, which preferentially feeds on herbivorous dung, and *Chalcocopris hesperus*, which is a generalist coprophagous species. Two treatments were used, cattle dung and swine dung, which consisted of a container with soil, dung, and two individuals of the two species that had been weighed prior to the experiment. *Dichotomius bos* was better at dung removal and soil excavation in the treatment containing the dung of its preference, whereas for *C. hesperus*, there was no difference between the treatments. Only the quantity of ecological functions performed by *D. bos* was positively related to biomass. For *D. bos*, dung type was more important than biomass in dung removal, and biomass was more important than dung type in the amount of soil excavated. Neither biomass nor dung type explained *C. hesperus* functions. In conclusion, variables that affect ecological functions are dependent upon the species in question and the type of function evaluated, so dung beetle ecological functions are species-specific.

**Keywords:** *Chalcocopris hesperus*; *Dichotomius bos*; dung removal; Scarabaeinae; soil excavated.

## INTRODUCTION

Dung beetles (Scarabaeidae: Scarabaeinae) are detritivores that mainly use dung, carcasses, and decaying fruit for feeding and reproduction (Halffter & Matthews 1966). Most species are coprophagous, and feed on the excrement of large mammals (Halffter & Matthews 1966). Upon finding a food resource, some dung beetles dig tunnels to remove portions of dung (Hanski & Cambefort 1991), and in doing so, they perform important ecological functions such as dung burial and soil excavation (Halffter & Edmonds 1983, Nichols *et al.* 2008). These ecological functions are essential for the maintenance of natural and modified ecosystems (Ridsdill-Smith & Edwards 2011).

The ecological functions performed by dung beetles can be influenced by several factors such as biomass, body size, sex, functional guild of the beetle, and degree of habitat disturbance (Braga *et al.* 2013, Nichols & Gómez 2014, Gregory *et al.* 2015). Interspecific variation in dung beetle biomass is important in determining the magnitude of functions performed (Braga *et al.* 2013, Nichols &

Gómez 2014), and beetle communities with large total biomasses generally remove more dung and excavate more soil than those with small total biomasses (Larsen *et al.* 2005, Dangles *et al.* 2012, Braga *et al.* 2013). Previous studies have evaluated the importance of biomass at the community level, but few studies have considered the effect of intraspecific variation in biomass on the number of ecological functions performed by Scarabaeinae species (Carvalho *et al.* 2018).

Food preference can also affect dung beetles when performing their ecological functions. Most dung beetles are dietary generalists (Frank *et al.* 2018), but many species have a preference for a particular resource (Halffter & Matthews 1966, Martín-Piera & Lobo 1996, Tshikae *et al.* 2008, Whipple & Hoback 2012). Preference for a particular type of dung may occur because of biotic and abiotic conditions of the environment, and the physiological and behavioral characteristics of the species in question. Competition for, and availability of dung are among the most important factors in determining the food preference of a dung beetle species. However, this preference may depend on other environmental factors, such as the relationship between dung moisture and climate, or dung malleability and consistency (Landin 1961,Tshikae *et al.* 2008, 2013). Such a preference can also be conditioned by habitats in which mammalian dung is available; for example, pastures are a reliable source of hydrated feces (Martín-Piera & Lobo 1996). Among physiological and behavioral characteristics, food preference may depend on species, developmental stage, and feeding and reproductive behavior (Landin 1961, Rainio 1966, Dormont *et al.* 2010, Kerley *et al.* 2018).

Although a number of studies have reported the feeding preferences of dung beetles in terms of certain resource types (Tshikae *et al.* 2008, Louzada & Carvalho 2009), few studies have investigated the effects of this preference on dung beetles' performance when executing their ecological functions. There may be a relationship between food preference and ecological function performance, because carnivore, omnivore, and herbivore dung differ in their physical and chemical attributes, such as the amount of water and fiber they contain and their odor and nutritional quality (Martín-Piera & Lobo 1996). These characteristics affect dung choice by dung beetle species (Lumaret *et al.* 1993, Martín-Piera & Lobo 1996, Scholtz *et al.* 2009). Therefore, a preference for a certain type of food can result in only using a specific resource type, leading to a greater number of ecological functions performed (dung removal and soil excavation).

Little information is available on the relative importance of intraspecific variation in biomass and food preference on dung beetles' performance in conducting their ecological functions, but such information is crucial to better understand the factors that determine the ecological functions of dung beetles, and to establish a relevant theoretical basis for future studies. In addition, such information may assist in the development of conservation strategies for these beetles and their natural habitats.

The objective of this study was to investigate the relationship between dung type and beetle biomass in two species of dung beetle, and measure the amount of dung removed and soil excavated in relation to these two factors. Both species selected were coprophagous tunnelers (paracoprid), and one preferred herbivore dung (*Dichotomius bos* (Blanchard 1843)) while the other was a generalist (*Chalcocopris hesperus* (Olivier 1789)). Under laboratory conditions, we evaluated the species' performance in executing their ecological functions with or without the dung of their preference (herbivore or omnivore dung). We also weighed each individual in order to investigate the relationship between intraspecific biomass and function quantity. We tested the following hypotheses: 1) *D. bos* individuals perform their ecological functions better when using the dung of their preference, and for *C. hesperus*, the amount of dung removed and soil excavated does not differ between herbivore and omnivore dung; 2) *D. bos* and *C. hesperus* biomasses are positively related to the quantity of dung removed and soil excavated; 3) For *D. bos*, dung type is more important than intraspecific variation in biomass for dung removal and soil excavation; 4) For *C. hesperus*, intraspecific variation in biomass is more important than dung type for dung removal and soil excavation.

## MATERIAL AND METHODS

### *Selection and collection of the species studied*

The Scarabaeinae specimens were collected in areas with natural and modified vegetation in order to sample a large number of species. The collections were conducted in a fragment of the Atlantic Forest in Lavras, Minas Gerais, Brazil (21°13'22.9"S 44°59'05.7"W) and in pastures (*Brachiaria brizantha* (Hochst. ex A. Rich., 1919)) in Rio Paranaíba, Minas Gerais, Brazil (19°11'37.1"S 46°14'58.8"W). Lavras is in the transition region of two biomes, the Cerrado and the Atlantic Forest (Dalanesi *et al.* 2004).The climate of the region is classified as Cwb (Köppen 1931), with wet summers and dry winters. Rio Paranaíba is in the meso-region of Alto Paranaíba, which is an important dairy basin for Minas Gerais (Pinto & Perobelli 2016). The climate is Cwa (Köppen 1931), with wet and hot summers. Sampling was conducted in the rainy season, December 2015 to January 2016, when the beetles are more abundant (Hanski & Cambefort 1991, Andresen 2005).

Beetles were collected using 20 pitfall traps baited with cattle or swine dung. The cattle were fed grass and the swine were fed a mixture of vegetables and meat. Dung was obtained from animals raised at the Federal University of Lavras. We used both types of bait to sample a large amount of species and select generalist species. Pitfall traps were constructed by cutting the necks off 2-L plastic bottles. The tapered part was placed upside down on top of the cut bottle, forming a funnel that allowed the beetles to be trapped and prevented them from escaping. Traps were buried with their openings at ground level. We placed a small amount of soil and leaf litter inside each pitfall trap (below the funnel) in order to avoid stressing the trapped dung beetles. To attract the dung beetles, we placed a small container with 25 g of cattle or swine dung above each trap and used a plastic lid supported by bamboo sticks as a rain cover. Traps were installed at 25 m apart. After 24 h, we collected the dung beetles. Live dung beetles were transported to the Insect Ecology and Conservation Laboratory of the Federal University of Lavras for identification.

Among the specimens collected, we selected one species that exhibited a food preference for one dung type and another species that was a generalist, namely *D. bos* and *C. hesperus*, respectively. Determination of food preference was performed based on data obtained from the literature, unpublished studies, and the database of the Reference Collection in the Insect Ecology and Conservation Laboratory of the Federal University of Lavras. The two species selected had the same type of resource allocation behavior (paracoprids), because this behavior can affect the number of ecological functions performed (Andresen 2003).

*Dichotomius bos* was the most abundant species in pasture areas, and is considered an important tunnel former and burier of cattle dung (Alves & Nakano 1977). This species has a relatively long average life cycle (435 days) (Walsh *et al.* 1997), and only one population peak per year. It prefers herbivore dung. *Chalcocopris hesperus* was abundant in forested areas and is endemic to the Atlantic Forest, and is found in southern and eastern Brazilian states and in neighboring parts of Argentina and Paraguay (Rossini & Vaz-De-Mello 2015). In our study, we collected several *C. hesperus* individuals using swine dung, while Louzada & Carvalho (2009) collected this species using cattle bait. According to the database of the Reference Collection of the Insect Ecology and Conservation Laboratory, *C. hesperus* has been extensively sampled using pitfalls traps baited with cattle dung and human feces. The presence of individuals of this species in both dung types shows that *C. hesperus* is a generalist in relation to dung type.

### *Evaluation of biomass and ecological functions*

Prior to the experiment, the beetles were separated and placed in plastic containers (15 x 9.4 cm, five individuals per container) that were half-filled with a humidified mixture of soil (70%) and sand (30%). The containers were maintained under controlled conditions (relative humidity, 65±10%; temperature, 26 ± 1ºC; and photoperiod, 12/12h) for two weeks (Favila 1993). The insects were fed once a week. For the following experiment, the individuals were not fed for seven days.

To assess whether dung type or intraspecific variation in biomass affect the number of ecological functions performed by dung beetles and ascertain the relative importance of these two factors for function quantity, we evaluated the ecological functions "soil excavation" and "dung removal" under laboratory conditions using 88 individuals (44 of each species). For each species, we used two treatments: a) herbivore (cattle) dung for *D. bos* and *C. hesperus*, and b) omnivore (swine) dung for *D. bos* and *C. hesperus*.

Each treatment consisted of 11 replicates, totaling 44 sample units. Each sample unit consisted of a bucket with 5 kg of a humidified mixture of soil (70%) and sand (30%) that had been compacted to facilitate soil excavation visualization. We placed two randomly selected, adult, non-sexed individuals of the respective species and 100 g of the respective dung type in the substrate. Individuals were not sexed in order to reflect the field sex ratio. The buckets were covered with screens to prevent the beetles from escaping.

Before being placed in the buckets, the beetles' biomasses were measured using an analytical precision scale. We used 20 buckets for humidity control (10 for each dung type). For this, the average humidity loss, in grams, for each type of dung was evaluated, and the value was subtracted from the amount of dung incorporated by the individuals in each sample unit. For all treatments and humidity control, the buckets were randomly allocated to prevent site effects and allow comparisons to be made between the sample units.

The ecological functions performed by the beetles were quantified at 48 h after the experiment commenced. The dung in each bucket was weighed before and after the experiment, and using the weight difference, we calculated the amount of dung incorporated by the beetles. The soil excavation rate was estimated as the weight of soil excavated in each bucket.

### *Statistical analyses*

Initially, the relationship between the amount of dung removed and the amount of soil excavated for each species was investigated using Spearman's rank correlation coefficient in the R statistical software package (R Development Core Team 2018).

We used generalized linear models (GLMs) to compare the amounts of dung removed and soil excavated by *D. bos* and *C. hesperus* individuals for each dung type. We included dung type (cattle or swine) as a categorical, explanatory variable and the amounts of dung removed and soil excavated as response variables in the models. All of the tests were performed separately for each species, and models were run with a Gaussian distribution. The residuals obtained from the models were checked for their error distributions and model fitness (Crawley 2002).We also used GLMs to evaluate the relationship between the biomasses of each species and function quantity. The mean biomass of two individuals in each bucket was included as the explanatory variable and the amounts of dung removed and soil excavated were included as response variables. The GLM analyses were performed using the function *lmer* in the software R (Bates *et al.* 2015).

Distance-based linear modelling (DISTLM) and a permutational multivariate analysis of variance (PERMANOVA) were performed in the PRIMER V.6 statistical package (Clarke & Gorley 2006, 2009). To ascertain the relative importance of dung type and intraspecific variation in biomass for the ecological functions (dung removal and soil excavation), DISTLM modelled the relationships among the multivariate data using a similarity matrix and one or more predictor variables. This analysis evaluated how much variation was explained when the predictor variables were considered alone and together, so variations in the response variables were decomposed into independent and joint effects of the predictor variables. To perform DISTLM, dung type and intraspecific biomass variation were included as explanatory variables and the amounts of dung removed and soil excavated as response variables. The tests were performed separately for each species. The amounts of dung removed and soil excavated were transformed into a similarity matrix using Euclidean distance as a similarity index. P values were generated by 999 permutations, and the null hypothesis was that there were no significant relationships when considering the variables independent of each other as well as with each other. All of the statistical tests were conducted with a significance level set at $p < 0.05$.

## RESULTS

### *Relationship between dung removal and soil excavation*

For *D. bos,* we found a significant, positive correlation between dung removal and soil excavation ($r = 0.69$, $p < 0.01$; Figure 1), where as for *C. hesperus*, we did not find a significant correlation between dung removal and soil excavation ($r = 0.13$, $p = 0.56$; Figure 1).

### *Relationship between ecological functions and food preference*

*Dichotomius bos* individuals incorporated significantly more dung of their preference (cattle) than swine dung ($F_{1,21}$ = 17.26, p < 0.01; Figure 2), and excavated significantly more soil in treatments containing cattle dung ($F_{1,21}$ = 7.54, p < 0.01; Figure 2A). For *C. hesperus*, we found no significant differences in the amounts of dung removed ($F_{1,21}$ = 0.63 and p = 0.43; Figure 2) or soil excavated ($F_{1,21}$ = 0.14, p = 0.70; Figure 2) in relation to the type of dung used.

### *Relationship between intraspecific biomass variation and ecological functions*

For *D. bos*, individual biomass was significantly, positively related to the amounts of dung removed ($F_{1,21}$ = 12.4, p < 0.01; Figure 3A) and soil excavated ($F_{1,21}$ = 12.76, p < 0.01; Figure 3B). For *C.*

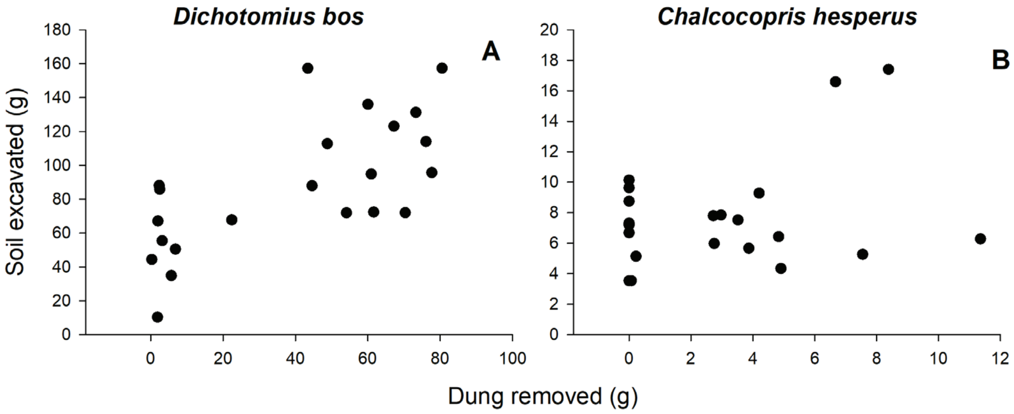


**Figure 1.** Correlation between dung removal and soil excavation performed by (A) *D. bos* and (B) *C. hesperus* individuals in the experiment.

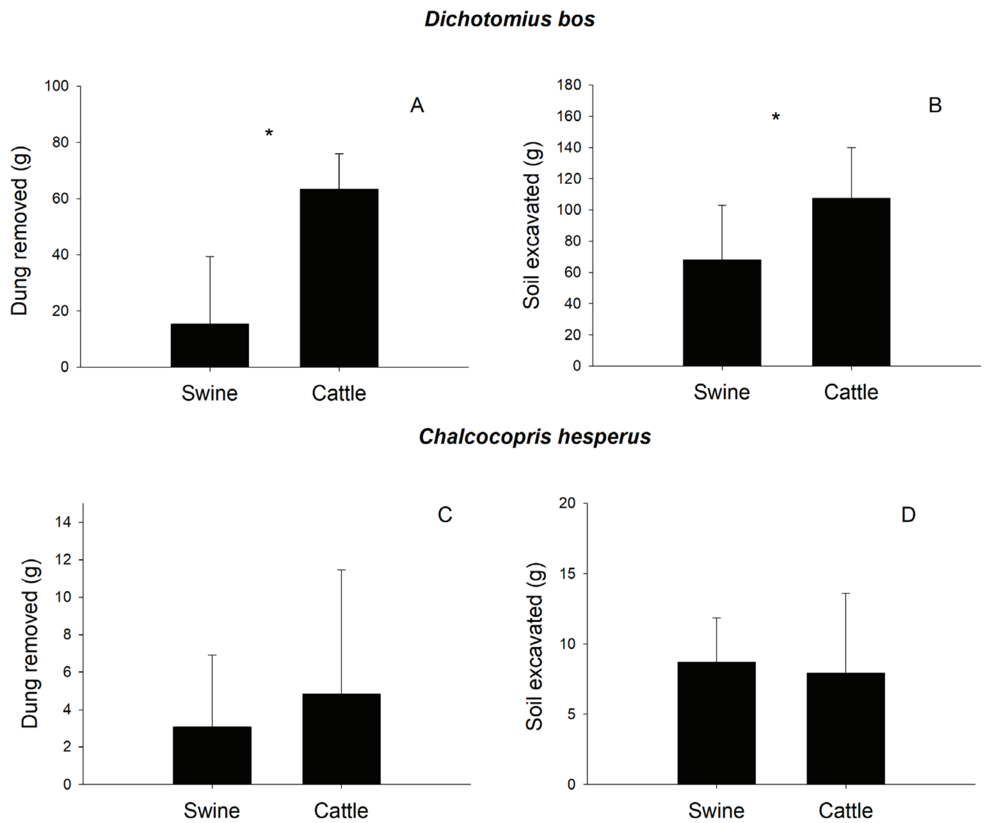


**Figure 2.** Mean and standard deviation of dung removal and soil excavation for (A - B) *D. bos* and (C - D) *C. hesperus* individuals in relation to dung type (cattle or swine). Asterisk indicates differences between treatments; NS indicates no differences between treatments at a 5% significance level.

*hesperus*, no significant relationships between individual biomass and the amounts of dung removed ($F_{1,21}$ = 1.23, p = 0.27; Figure 3C) and soil excavated ($F_{1,2}$ = 0.24, p = 0.62; Figure 3D) were found.

### *Relative importance of intraspecific biomass variation and dung type for ecological functions*

Dung type and intraspecific biomass variation explained 64 % of the variation in the amount of soil excavated by *D. bos*. Dung type accounted for more of the variation (61 %) than biomass (35 %) when considering the independent and shared effects, although both variables significantly affected dung removal. When treated independently, only dung type was significant, and accounted for 29 % of the dung removal variance; biomass alone only accounted for 2 % of the variance, which was not significant. Both variables combined accounted for 32 % of the variance (Figure 4). For soil excavation, the two variables explained 37 % of the variance, and biomass accounted for more of the variation (35 %) than dung type (23 %); however, both had a significant effect on soil excavation. Treated independently, only biomass significantly affected soil excavation (14 %), and dung type only accounted for 2 % of the variance. The two variables combined accounted for 21 % of the variance (Figure 3). For *C. hesperus*, neither dung type nor intraspecific biomass variation affected dung removal or soil excavation (Figure 4), and both accounted for 0 % of the total variation.

## DISCUSSION

Several studies have evaluated the ecological functions performed by dung beetle communities, but the individual contributions of the species and the factors responsible for these contributions remain unknown. To the best of our knowledge, this is the first study to evaluate the relative importance of intraspecific biomass variation and dung type in determining the performance of two dung beetle species in the execution of their ecological functions. Our study demonstrates that food preference and intraspecific biomass variation may be important in determining the magnitude of functions performed by the beetles.

According to our results, *D. bos* (which prefers herbivore dung), removed more dung and excavated more soil when in cattle dung than in swine dung. *Chalcocopris hesperus*, which is a dietary generalist, had the same performance in executing its ecological functions in both types of dung. This suggests that *D. bos* individuals use more of their preferred resource by using large portions of cattle dung for feeding, constructing large tunnels, and revolving a greater amount of soil. These results support our first hypothesis, and demonstrate that a species' food preference can affect ecological function performance. Species with specific food preferences spend more time manipulating the same type of resource than generalist species, so are more familiar with the physical characteristics of the food. This can result in more ecological functions performed when using preferred resources.

The dung of ruminant herbivores (e.g., cattle) has particular characteristics (cellulose, intestinal fragments, epithelium, and microbes) that differentiates it from swine dung (Hanski & Cambefort 1991). Omnivore dung (e.g., swine) contains a combination of cellulose and undigested meat with a high concentration of nitrogen, so is intermediate between herbivore and carnivore dung (Fincher *et al.* 1970, Martín-Piera & Lobo 1996, Filgueiras *et al.* 2009, Scholtz *et al.* 2009). These differences may affect the quantity of functions performed by species with food preferences. Therefore, D. *bos* individuals probably had difficulty manipulating and using swine dung.

Dung beetles that use dung from different vertebrates are considered polyphagous (Dormont *et al.* 2004), and are more efficient in locating and using resources than beetles that are specialized in one dung type, because dung is scarce and ephemeral in most ecosystems (Dormont *et al.* 2004). Food preference has been well documented in dung beetles (Estrada *et al.*1999, Vernes *et al.* 2005, Larsen *et al.* 2006, Amezquita & Favila 2010), and enables niche differentiation and species coexistence (Martín-Piera & Lobo 1996). These preferences generally refer to adaptations to dung from a group of vertebrates with similar diets, for example, herbivores, carnivores, or omnivores, and can be conditioned by factors related to beetle ecology (Dormont *et al.* 2004).

Biomass was positively related to the amount of dung removed and soil excavated for *D. bos*. Therefore, individuals of this species with high

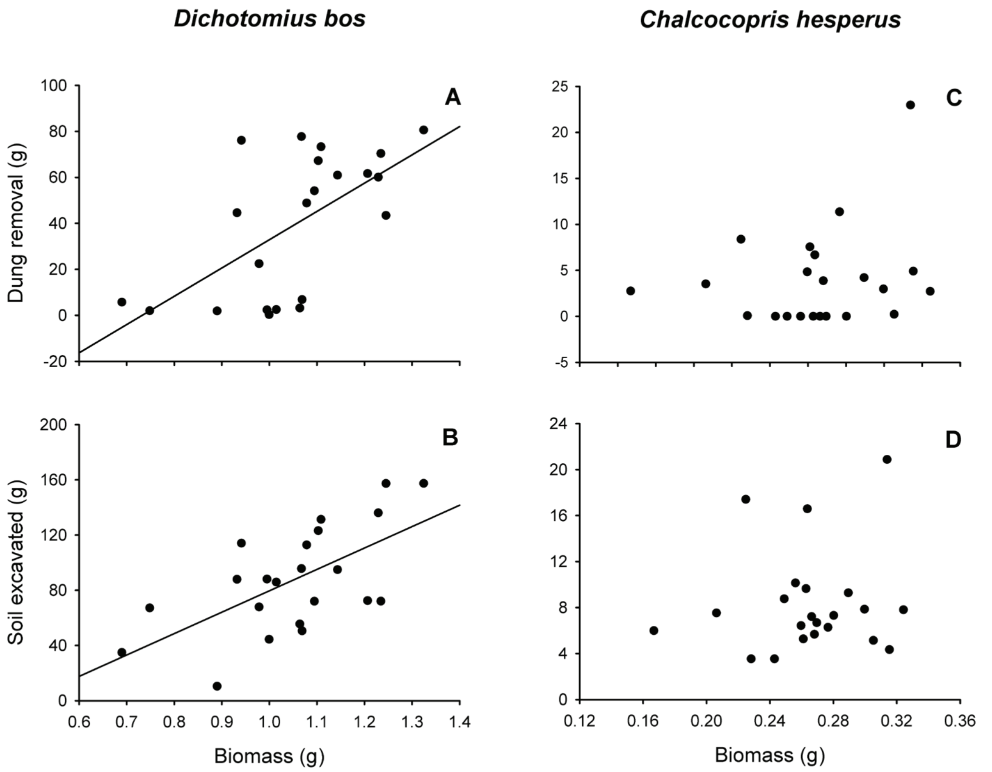


**Figure 3.** Relation between dung removal (A) and soil excavation (B) with biomass of *D. bos* individuals and relationship between dung removal (C) and soil excavation (D) with biomass of *C. hesperus* individuals.

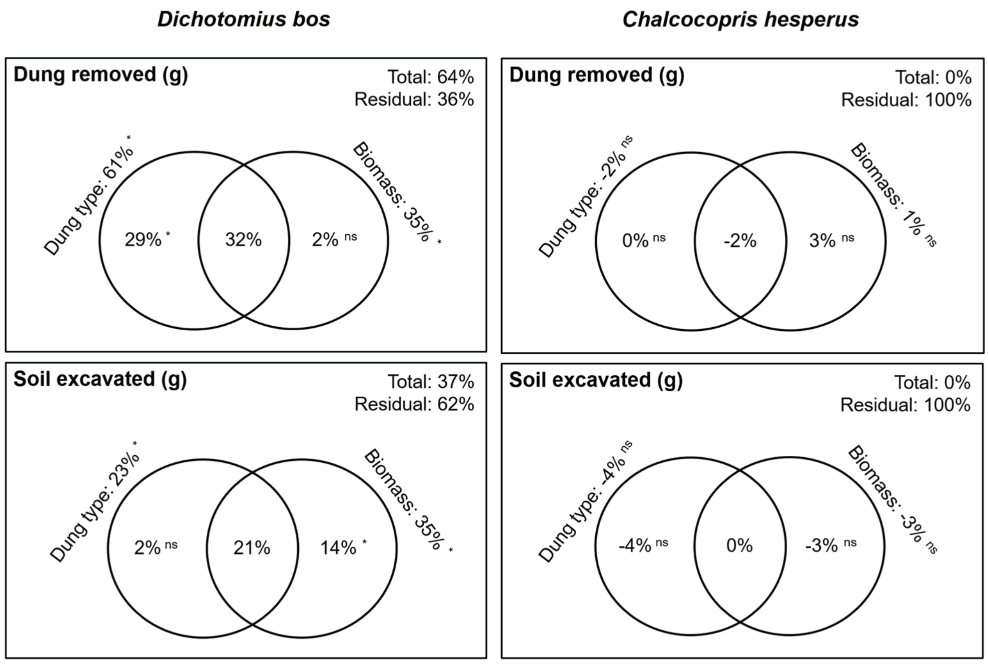


**Figure 4.** Venn Diagram showing the percentage of explanation of dung type and intraspecific biomass variation variables in dung removal and soil excavation for the species *D. bos* and the percentage of explanation of dung type and intraspecific biomass variation variables in dung removal and soil excavation for the species *C. hesperus*, according to the DISTLM analysis. Asterisk indicates that the explanation of the variable was significant; NS indicates no significant explanation. Fractions of total explanation are listed above the circles and individual fractions are indicated within the Venn diagram. Circle overlap areas indicate percentage of shared explanation between the two variables.

biomasses had a better performance in executing their ecological functions than those with low biomasses. Contrary to our expectations, we found no significant relationship between individual biomass and function performance of *C. hesperus*. This could be explained by the small intraspecific biomass variation in this species (Appendix 1). Consequently, the greater the intraspecific variation in biomass, the stronger the relationship between biomass and the number of ecological functions performed.

Species with large biomasses (in the genus *Dichotomius*) perform their ecological functions well, so beetle biomass and body size are ecologically relevant characteristics (Andresen 2003, Anduaga 2004). In general, populations of a species exhibit variations in the morphological and physiological characteristics of their individuals, and biomass can vary greatly between individuals of a dung beetle species (Carvalho *et al.* 2018). This may be related to adaptive characteristics for example, large males mate more often than small males (Moczek & Emlen 2000), and females with high biomasses have higher fecundity than those with low biomasses (Honêk 1993).

By analyzing the relative importance of food preference and intraspecific biomass variation in performing their ecological functions, we revealed that dung type was more important than biomass in determining dung removal for *D. bos*. This means that in terms of dung removal, easier resource management driven by food preference plays a more important role than individual biomass. However, biomass was more important when evaluating soil excavation. This result refuted part of our third hypothesis, because we believed that for both functions, dung type would be more important for *D. bos*. This probably occurred because soil excavation was not related to food preference, but to individual biomass. Nichols and Gómez (2014) and Gregory *et al.* (2015) found positive relationships between beetle biomass and tunnel depth.

We found a correlation between dung removal and soil excavation in dung beetles, but the processes that determine these two functions are not necessarily the same. However, the greater amount of soil excavated in dung preferred by *D. bos* was a consequence of the greater amount of dung removed with this type of resource.

Dung type and biomass variation were also important for dung removal and soil excavation in *D. bos*. Beetles with a high biomass performed more ecological functions when they could use their preferred dung. Contrary to our expectations, food preference and intraspecific biomass variation did not affect dung removal or soil excavation in *D. bos*. This result refuted our fourth hypothesis, that for both functions, biomass variation would be more important. This indicates that other variables affect the performance of these functions in *C. hesperus*. Therefore, the impact of other factors, such as functional traits, should be evaluated in future studies (Griffiths *et al.* 2015, 2016).

Studies of ecological functions have been conducted at the community level, but the individual contributions of each species to ecosystem functioning are still unknown. Our results demonstrate that biomass, which is an intrinsic morphological characteristic of the species, can influence the performance of certain functions. Habitat loss and reduced food availability are challenging problems for dung beetle species (Nichols *et al.* 2007, 2008), and for the ecological functions performed by them. Gardner (2008) demonstrated that the abundance of species with high biomasses decreases in anthropized systems, which also leads to a loss of ecological functions (Dangles *et al.* 2012). In this context, our results demonstrate that food preferences and biomass variation within the same species can affect function performance. The results of this study have increased our knowledge of beetle biology, behavior, and ecological functions, and in addition to providing information for future studies, can play an important role in developing conservation strategies not only for beetles, but also for their habitats.

## ACKNOWLEDGMENTS

RC is thankful for the receipt of scholarships from FAPEMIG and CAPES (PDSE program, process number 88881.189712/2018-01). L.D. Audino is supported by CNPq, proc. PDJ 150776/2017-9.

## REFERENCES

Alves, S. B., & Nakano, O. 1977. Influência do *Dichotomius anaglypticus (*Mannerheim, 1829) (Coleoptera, Scarabaeidae) no crescimento de plantas de Napier. Ecossistema, 2, 31–33.

Amézquita, S., & Favila, M. E. 2010. Removal rates of native and exotic dung by dung beetles (Scarabaeidae: Scarabaeinae) in a fragmented tropical rain forest. Environmental entomology, 39 (2), 328–336. DOI: 10.1603/EN09182.

Andresen, E. 2003. Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. Ecography, 26 (1), 87–97. DOI: 10.1034/j.1600-0587.2003.03362.x.

Andresen, E. 2005. Effects of season and vegetation type on community organization of dung beetles in a tropical dry forest. Biotropica, 37(2), 291–300. DOI: 10.1111/j.1744-7429.2005.00039.x.

Anduaga, S. 2004. Impact of the activity of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) inhabiting pasture land in Durango, Mexico. Environmental Entomology, 33 (5), 1306–1312. DOI: 10.1603/0046-225X-33.5.1306.

Bates, D., Mächler, M., Bolker, B., & Walker, S. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67.

Braga, R. F., Korasaki,V., Andresen, E., & Louzada. J. 2013. Dung beetle community and functions along a habitat-disturbance gradient in the Amazon: a rapid assessment of ecological functions associated to biodiversity. PLoSOne, 8, e57786. DOI: 10.1371/journal.pone.0057786.

Carvalho, R., Ferreira, R. S., Audino, L. D., Châline, N., Braga, P., &Louzada, J. 2018. Factors influencing the production of pygidial secretions in the dung roller beetle *Canthon smaragdulus* (Coleoptera: Scarabaeinae). Austral Entomology, 57 (4), 403–409. DOI:10.1111/aen.12291.

Carvalho, R., Frazão, F., Ferreira–Châline, R., Louzada, J., Cordeiro, L., & França, F. 2018. Dung burial by roller dung beetles (Coleoptera: Scarabaeinae): An individual and specific-level study. International Journal of Tropical Insect Science, 38(4), 373–380. DOI:10.1017/S1742758418000206.

Clarke, K. R., & Gorley R. N. 2006. PRIMER V6: user manual-tutorial. UK: Plymouth Marine Laboratory: p. 192.

Crawley, M. J. 2002. Statistical computing: an introduction to data analysis using S-Plus. 2nd ed.UK: Wiley–Blackwell: p: 772.

Dalanesi, P. E., Oliveira-Filho, A., & Fontes, M. A. 2004. Flora and structure of the arboreal component of the forest of the Parque Ecológico Quedas do Rio Bonito, Lavras, Minas Gerais State, and correlations between species distribution and environmental variables. Acta Botanica Brasilica, 18(4), 737–757. DOI: 10.1590/S0102-33062004000400005.

Dangles, O., Carpio, C., & Woodward, G. 2012. Size-dependent species removal impairs ecosystem functioning in a large-scale tropical field experiment. Ecology, 93(12), 2615–2625. DOI: 10.1890/12-0510.1.

Dormont, L., Epinat, G., & Lumaret, J. P. 2004. Trophic preferences mediated by olfactory cues in dung beetles colonizing cattle and horse dung. Environmental Entomology, 33(2), 370–377. DOI: 10.1603/0046-225X-33.2.370.

Dormont, L., Jay-Robert, P., Bessiere, J.M., Rapior, S., & Lumaret, J.P. 2010. Innate olfactory preferences in dung beetles. The Journal of Experimental Biology, 213, 3177–3186. DOI:10.1242/jeb.040964

Estrada, A., Anzures, A., & Coates-Estrada, R. 1999. Tropical rain forest fragmentation, Howler Monkeys (*Alouatta palliata*) and dung beetles at Los Tuxtlas, Mexico. American Journal of Primatology, 48 (4), 253–262. DOI: 10.1002/(SICI)1098-2345(1999)48:4<253::AID-AJP1>3.0.CO;2-D

Favila, M. E. 1993. Some ecological factors affecting the life-style of *Canthon cyanellus cyanellus* (Coleoptera: Scarabaeidae): an experimental approach. Ethology Ecology and Evolution, 5(3), 319–328. DOI: 10.1080/08927014.1993.9523019.

Filgueiras, B., Liberal, C., Aguiar, C., Hernandéz, M., & Iannuzzi. L. 2009. Attractivity of omnivore, carnivore and herbivore mammalian dung to Scarabaeinae (Coleoptera, Scarabaeidae) in a tropical Atlantic rainforest remnant. Revista Brasileirade Entomologia, 53(3), 422–427. DOI: 10.1590/S0085-56262009000300017.

Fincher, G., Stewart,T., & Davis, R. 1970. Attraction of coprophagous beetles to feces of various animals. Journal of Parasitology, 56(2), 378–383. DOI: 10.2307/3277680.

Frank, K., Krell, F.T., Slade, E. M., Raine, E. H., Chiew, L. Y., Schmitt, T., Vairappan, C., Walter, P., & Blüthgen, N. 2018. Global dung webs: high trophic generalism of dung beetles along the latitudinal diversity gradient. Ecology Letters, 21(8),1229–1236. DOI:10.1111/ele.13095.

Gardner, T., Hernandéz, M., Barlow, J., & Peres, C. 2008. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. Journal of Applied Ecology, 45(3), 883–893. DOI: 10.1111/j.1365-2664.2008.01454.x.

Gregory, N., Gómez, A., Oliveira, T. M., & Nichols, E. 2015. Big dung beetles dig deeper: trait-based consequences for faecal parasite transmission. International Journal for Parasitology, 45(2-3), 101–105. DOI: 10.1016/j.ijpara.2014.10.006.

Griffiths, H. M., Bardgett, R. D., Louzada, J., & Barlow, J. 2016. The value of trophic interactions for ecosystem function: dung beetle communities influence seed burial and seedling recruitment in tropical forests. Proceedings of the Royal Society B, 283,20161634. DOI: 10.1098/rspb.2016.1634.

Griffiths, H. M., Louzada, J., Bardgett, R. D., Beiroz, W., França, F., Tregidgo, D., & Barlow, J. 2015. Biodiversity and environmental context predict dung beetle-mediated seed dispersal in a tropical forest field experiment. Ecology, 96(6), 1607–1619. DOI: 10.1890/14-1211.1.

Halffter, G., & Edmonds,W. D. 1983. The nesting behavior of dung beetles (Scarabaeinae). An ecological and evolutive approach. Journal of the New York Entomological Society, 91, 512–515.

Halffter, G., & Matthews, E. G. 1966. The natural history of dung beetles of subfamily Scarabaeinae (Coleoptera:Scarabaeidae). Folia Entomológica Mexicana, 12, 1–132.

Hanski, I., & Cambefort,Y. 1991. Dung beetle ecology. United States: Princeton University Press, 481.

Hanski, I., & Krikken, J.1991. Dung beetles in tropical forests in South-East Asia. In:I. Hanski & Y. Cambefort (Eds.), Dung beetle ecology. pp. 179–197. USA: Princeton University Press.

Honěk, A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. Oikos, 66(3), 483–492. DOI: 10.2307/3544943.

Kerley, G. I. H., Landman, M., Ficetola, G. F., Boyer, F., Bonin, A., Rioux, D.,Taberlet, P., & Coissac, E. (2018). Diet shifts by adult flightless dung beetles *Circellium bacchus*, revealed using DNA metabarcoding, reflect complex life histories. Oecologia, 188(1), 107–115. DOI:10.1007/s00442-018-4203-6.

Köppen, W. 1931. Climatologia. México: Fundo de Cultura Econômica.

Landin, B. O. 1961. Ecological studies on dung-beetles: (Col. Scarabaeidae). Oposcula Entomologica, 19, 1–228.

Larsen, T. H., Lopera, A., & Forsyth. A. 2006. Extreme trophic and habitat specialization by Peruvian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). The Coleopterists Bulletin, 60(4), 315–324. DOI: 10.1649/0010-065X(2006)60[315:ETAHSB]2.0.CO;2

Larsen, T. H.,Williams, N. M., & Kremen, C. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecology Letters, 8(5), 538–547.DOI: 10.1111/j.1461-0248.2005.00749.x.

Louzada, J.,& Carvalho e Silva,P. R. 2009. Utilization of introduced Brazilian pastures ecosystems by native dung beetles: diversity patterns and resource use. Insect Conservation and Diversity, 2(1), 45–52. DOI: 10.1111/j.1752-4598.2008.00038.x.

Lumaret, J. P., Galante, E., Lumbreras, C., Mena, J., Bertrand, M., Bernal, J. L., Cooper, J. F., Kadiri, N., & Crowe, D. 1993. Field effects of Ivermectin residues on dung beetles. Journal of Applied Ecology, 30(3), 428–436. DOI: 10.2307/2404183.

Martín-Piera, F., & Lobo, J. M. 1996. A comparative discussion of trophic preferences in dung beetle communities. Miscellania Zoologica, 19, 13–31.

Moczek, A. P.,& Emlen, D. 2000. Male horn dimorphism in the scarab beetle, *Onthophagus taurus*: do alternative reproductive tactics favour alternative phenotypes? Animal Behaviour, 59(2), 459– 466. DOI:10.1006/anbe.1999.1342.

Nichols, E., & Gomez, A. 2014. Dung beetles and fecal helminth transmission: patterns, mechanisms and questions. Parasitology, 141(5), 614– 623. DOI: 10.1017/S0031182013002011.

Nichols, E., Larsen, T., Spector, S., Davis, A. L., Escobar, F., Favila, M. E., & Vulinec, K. 2007. Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. Biological Conservation, 137(1), 1– 19. DOI: 10.1016/j.biocon.2007.01.023.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., & Favila, M. E. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biological Conservation, 141(6), 1461– 1474. DOI: 10.1016/j.biocon.2008.04.011.

Pinto,D. G., & Perobelli, F. S. 2016. Determinantes do Crescimento da Pecuária de Leite em Minas Gerais: uma análise para o período de 2005 a 2014. Reflexões Econômicas, 2, 44– 67.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rainio, M. 1966. Abundance and phenology of some coprophagous beetles in different kinds of dung. Annales Zoologici Fennici, 3, 88– 98.

Ridsdill-Smith, T. J., & Edwards, P. B. 2011. Biological control: ecosystem functions provided by dung beetles. Ecology and Evolution of Dung Beetles. In: Simmons, L. W., & Ridsdill-Smith, T. J. (Eds.), Ecology and evolution of dung beetles. pp: 245–266. Wiley-Blackwel. DOI: 10.1002/9781444342000.ch12.

Rossini, M., & Vaz-de-Mello, F. 2015. A review of the genus *Chalcocopris* Burmeister, 1846 (Coleoptera: Scarabaeidae: Scarabaeinae), with description of a new species. Zootaxa 3920(2), 291– 300. DOI: 10.11646/zootaxa.3920.2.5.

Scholtz, C. H., Davis, A. L., & Kryger, U. 2009. Evolutionary biology and conservation of dung beetles. Bulgaria: Pensoft Publishers. p. 567.

Tshikae, B. P., Davis, A. L., & Scholtz, C. H. 2008. Trophicassociationsofadungbeetleassemblage (Scarabaeidae: Scarabaeinae) in a woodland savanna of Botswana. Environmental of entomology, 37(2), 431– 441. DOI: 10.1093/ee/37.2.431.

Tshikae, B.P., Davis, A., & Scholtz, C.H. 2013. Does an aridity and trophic resource gradient drive patterns of dung beetle food selection across the Botswana Kalahari? Ecological Entomology, 38(1), 83–95. DOI: 10.1111/j.1365-2311.2012.01409.x.

Vernes, K., Pope, L. C., Hill, C. J., & Bärlocher, F. 2005. Seasonality, dung specificity and competition in dung beetle assemblages in the Australian Wet Tropics, north-eastern Australia. Journal of Tropical Ecology, 21(1), 1–8. DOI: 10.1017/S026646740400224X.

Walsh, C. G., Cordo, H. A., Briano, J. A., Gandolfo, D. E., & Logarzo, G. A. 1997. Laboratory culture of beneficial dung scarabs. Journal of economic entomology, 90(1), 124–129. DOI: 10.1093/jee/90.1.124.

Whipple, S. D., & Hoback, W. W. 2012. A comparison of dung beetle (Coleoptera: Scarabaeidae) attraction to native and exotic mammal dung. Environmental Entomology, 41(2), 238– 244. DOI: 10.1603/EN11285.

*Submitted: 05 August 2018*
*Accepted: 10 March 2019*
*Published online: 14 march 2019*
*Associate Editor: Gudryan Barônio*

**Appendix 1.** Intraspecific biomass variation of the *Dichotomius bos* and *Chalcocopris hesperus* individuals used in experiment.