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RESEARCH ARTICLE

Where should I perch? The effects of body size, height, and leaf surface on the vertical perching position of dung beetles (Scarabaeidae: Scarabaeinae) in an Amazonian area

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Abstract
Among dung beetles, 'sit and wait' comprise a common strategy, in which individuals perch on leaves. The goal of this study was to assess the spatial dynamics of dung beetle perching in a region of the Amazon. We analysed the intra- and interspecific relationships between individual body size, leaf area, leaf shape, and the height at which beetles perched. When analysing intraspecifically, the larger individuals of *Canthidium bicolor* perched higher than the small ones. When considering the three most abundant species, the smallest species (*C. bicolor*) perches lower, the intermediate species (*Canthidium deyrollei*) perches higher, and the largest species (*Canthon triangularis*) perches at an intermediate height. The leaf area also explained the vertical distribution, both when considering all individuals and intraspecific for *C. bicolor*, where there is a positive relationship between leaf area and perch height. Our results suggest that intra- and interspecific perching dynamics also depend on species life history, which could be further analysed under functional group approaches.

KEYWORDS
competition, resource search, Scarabaeinae, traits

INTRODUCTION

One of the most frequently used foraging strategies among animals, particularly dung beetles (Coleoptera: Scarabaeinae), is the one known as 'sit and wait'. In this perching behaviour, beetles position themselves near potential food sources, such as areas frequented by animals, and wait for dung to be deposited (Noriega & Vulinec, 2021). Since this is a spatial segregation strategy with potential effects on competition for food resources (Hanski, 1991), it is to be expected that there are factors that strongly affect perching dynamics. The traits of the leaves used for perching, especially the height at which they are found, can play a critical role in the success of this behaviour (Noriega et al., 2020). Aspects such as leaf size, area, and height can modulate the frequency or success of perch dynamics. However, few studies have explicitly explored the potential connection between plant traits and beetle traits; more specifically, no study has analysed how perching behaviour may be determined by vertical distribution and interspecific variation of perching sites.

Dung beetles are an ecologically diverse group of insects that are notable for their pivotal role in nutrient cycling and soil health (Brown et al., 2010; Maldonado et al., 2019; Yamada et al., 2007). While their behaviours, such as dung-rolling and burrowing, have been extensively studied by researchers (Halffter & Edmonds, 1982; Tonelli, 2021), an intriguing aspect of their ethology that deserves further exploration is perching behaviour (Feer, 2015; Noriega & Vulinec, 2021). Perching entails dung beetles ascending to elevated points and maintaining stillness for prolonged periods, calling the attention of researchers for its potential implications in, for example, thermoregulation and sensory perception (Noriega & Vulinec, 2021). Perching behaviour is observed in various species (e.g. *Canthidium cupreum* Blanchard, 1846 and *Canthon luteicollis* Erichson, 1847; Noriega et al., 2020) and habitats, highlighting its ecological significance. Notably, dung beetle perching could serve to locate food sources through odour (Howden et al., 1991; Noriega & Vulinec, 2021). By ascending to higher vantage points, dung beetles might gain a better olfactory perspective to detect distant sources of dung, aiding in efficient foraging (Noriega & Vulinec, 2021). Furthermore, the act of perching might offer thermoregulatory advantages (Noriega & Vulinec, 2021). Through exposure to diverse temperature and humidity gradients, dung beetles can effectively regulate their body temperature, mitigate desiccation risks, and optimize metabolic functions in response to changing environmental conditions (Davis, 1999; Young, 1984).

Understanding intra- and interspecific spatial distribution dynamics is crucial for assessing the ecological relationships among dung beetles in tropical forests (Halffter & Halffter, 2009; Scholtz et al., 2009). Through the investigation of inter- and intraspecific perching dynamics, novel insights may be gained about community structure and ecological relationships among different dung beetle species. Perching behaviour is mostly observed in trees and plays a vital role in spatial segregation within and between dung beetle species, which may be related to resource partition and thus decreases in competition (Noriega & Vulinec, 2021). Intraspecific perching dynamics vary due to factors like individual body size, with larger individuals having been found to perch higher than smaller ones (Howden & Nealis, 1978; Noriega et al., 2020). The different spatial perching patterns within a species can impact resource competition (Feer, 2015) and consequently individual fitness. Interspecific perching dynamics, in turn, involve differences in perching behaviour among species, influenced by factors, such as functional guilds, food preferences, and body size (Noriega et al., 2020).

The aim of this study is to analyse the spatial dynamics of dung beetle perching in a region of the central Amazon. We analyse the relationships between individual body size, leaf area, leaf shape, and the height at which the beetles perched. In addition, we also explore the differences in perching distribution among beetle species. This study is performed at two biological scales: individual level and species level. Considering the fierce intra- and interspecific competition among dung beetles (Chamorro-Florescano et al., 2011; Hanski & Cambefort, 1991; Scholtz et al., 2009), we expect that perching patterns differ among species. Previous studies suggest that intraspecifically, larger dung beetle individuals often perch at higher levels (Feer, 2015; Noriega et al., 2020; Noriega & Vulinec, 2021). When it comes to interspecific relationships, literature shows contrasting vertical distribution patterns among species (Rangel-Acosta et al., 2018; Tregidgo et al., 2010). Due to the heterogeneity in behaviours among dung beetles (Halffter &

Edmonds, 1982; Halffter & Matthews, 1966; Hanski & Cambefort, 1991; Scholtz et al., 2009), when considering the whole assemblage data, we expect that there is no relationship between species body size and height at which they perch. In contrast, at the intraspecific level, fine changes in environmental preferences are expected according to individual traits (Cerqueira et al., 2023; Salomão et al., 2020, 2022). Previous studies hypothesized that larger dung beetles perch higher to seek larger resource quantities and avoid being distracted by the odour of smaller resource amounts (Hanski & Cambefort, 1991), such hypothesis having now been partially confirmed (Howden et al., 1991; Noriega et al., 2020). Based on all these statements, we expect that larger individuals perch at higher levels. Lastly, due to the physical requirements of large-bodied individuals, we predict that larger individuals and species perch at larger leaves in comparison to smaller ones.

METHODS

Study area

The study was conducted in a RAPELD study module (RAPELD is an ecological approach for rapid studies that comprises transects throughout environmental gradients within landscapes designed for long-term projects, see Magnusson et al., 2005). This RAPELD module is located in central Amazonia, within the limits of Presidente Figueiredo municipality, Amazonas state, Brazil (1°45′ S, 60°08′ W). This RAPELD module is located in a conserved Amazonian area, with low levels of anthropogenic activities limited to a few rural properties along the BR-174 highway, and trails inside the conserved forest. Presidente Figueiredo comprises the nearest urban settlement that represents an intense land transformation in the region, which is located ca. 38 km far from the study site, has a population of 38 000 inhabitants and a population density of 1 inhabitant/km^2 (IBGE, 2022). Regarding the vegetation physiognomies of the region, *terra firme* forests are the dominating ones, with smaller areas of seasonal floodplain forests (*várzea*). Fabaceae, Sapotaceae, and Caesalpinaceae comprise the dominant families in the local flora (Tello et al., 2008). The region's climate is classified as tropical monsoon, according to the Köppen classification. The mean annual temperature is 25.5°C and mean annual precipitation is 2028 mm, this comprises a rainy season from December to May (mean monthly rainfall: 345 mm) and a dry season from June to November (mean monthly rainfall: 160 mm) (Climate-Data, 2022).

Dung beetle sampling, leaf area, leaf shape, and beetles' body size

Samplings were performed on 7th and 8th June 2022, at the beginning of the dry season. To the best of our knowledge, there are no studies analysing seasonal effects on perching dynamics in dung beetle assemblages. Considering that dung beetles are highly active throughout the year in tropical rainforests, including the Amazon (Iannuzzi et al., 2016; Ratclifffe, 2013), we believe that both the dry and rainy seasons could be an appropriate period to study the perching dynamics of these insects. To sample dung beetles, we performed active manual collections on two consecutive days during daylight hours (from 8:00 to 17:00 h) in a conserved *terra firme* forest. The total effort comprised ca. 4550 m of active linear sampling performed, during which we (three of us) (LVMPC, LAC, LLSA) spent 13 h of sampling. Collecting consisted of a visual search for all dung beetles that were perching on leaves from ca. 1 to 190 cm from the ground, and searches were performed mostly from the bottom to the top of the plants. There was no preference of plant species during the dung beetle samplings, and practically all plant species and individuals were observed. Since the objective was to analyse general spatial distribution trends in dung beetle species, plant species were not identified. As this research was a product of a postgraduation field course, we were unable to perform a stronger sampling effort or to select other seasons of the year. Nonetheless, the number of beetles and species collected allows us to perform trustworthy statistical analyses to achieve the goals of this research (see "Data analysis" section). Each time a beetle was observed perching, a photograph of the plant where the individual was located was taken, and the beetle was subsequently placed individually in an Eppendorf tube. After that the height at which the beetle was perching was estimated with the use of a measuring tape, which was set at the soil surface up to the leaf in which dung beetles perched. Leaves where beetles perched were photographed in the field to estimate the leaf area and shape. Each leaf was photographed with a measuring tape to provide a reference scale (following Noriega et al., 2020, see Figure S1).

To calculate the leaf area and leaf shape, as well as the beetles' body size, we used the software ImageMeter™. First, we took photographs of the leaves along with a reference scale. Then, we manually delimited the contour of the leaves in the application, and subsequently, the software calculated the leaf perimeter and area. We used the perimeter–area ratio (leaf perimeter/leaf area) to calculate the leaf shape. Dung beetles' body size was estimated as the maximum length between the apex of the clypeus and the pygidium, following Villada-Bedoya et al. (2019). To ensure accuracy, the body size measurement was standardized by placing all body parts of the dung beetles in a completely horizontal position during measurement, as this prevents artefacts that could result from variations in the positioning of the head and pronotum.

Specimens were identified by comparing them with reference material in the entomological collection of the *Instituto Nacional de Pesquisas da Amazônia*, in Manaus, by consulting the literature (particularly Silva & Valois, 2019), and with the aid of still unpublished information from the ongoing taxonomic investigations of one of us (MC; see, e.g. Cupello, 2022). Collected beetles were deposited in MC's personal collection and in the entomological collection of *Universidade Federal do Mato Grosso*, Cuiabá, Brazil.

Data analysis

To assess the effect of species on perching distribution among the most abundant dung beetles, we analysed the vertical distribution and leaf area at which each species perched. We used a generalized linear model (GLM) with a gamma distribution because it effectively handles continuous, positive-valued variables with skewness and non-normality. This distribution is suitable for modelling data such as the time until an event or rates, aligning well with the characteristics of our response variable. Perch height and leaf area where dung beetles perched were the response variable, and species was the predictor variable. In order to have a minimum adequate statistical power, we considered species with $N \geq 12$ for this analysis—namely, *C. bicolor* Boucomont, 1928, *Canthidium deyrollei* Harold, 1867, and *Canthon triangularis* (Drury, 1773).

To assess the effect of body size, leaf area, and leaf shape on the height of perching dung beetles, we performed generalized linear mixed models (GLMMs) with a gamma distribution, as well as GLMs with inverse-Gaussian, Gaussian, and gamma distributions. The gamma distribution was selected for the GLMMs due to its suitability for modelling positive, continuous response variables with skewness and varying dispersion. For the GLMs, the inverse-Gaussian distribution was chosen to address response variables with non-normal error structures and skewed distributions, while the Gaussian distribution was used for normally distributed data. The choices of distributions in our models were based on the characteristics of the response variable, aiming to ensure that the chosen models accurately represented the relationship between the predictor variables (height, leaf area, leaf shape) and the response variable (individual body size of perching dung beetles). Considering that perching dynamics in dung beetles may be species-specific (Feer, 2015; Noriega et al., 2020), statistical models were performed under two approaches: (i) using data from all individuals with species identity as a random variable to account for species-specific variation and improve model accuracy; (ii) analysing each species separately (using species with $N \geq 12$).

For all GLMs and GLMM, we checked the normality of the residuals by visually assessing normal q–q plots. We tested the presence of outliers using Cook's distance (Cook's distance <1) and the variance of the homogeneity using the Fligner-Killeen test. When variances were heterogeneous, different variance structures were tested. To select the predictor variables that best explain the variation in the response variables, we performed model selection (Johnson & Omland, 2004). The model with the best support was chosen based on the Akaike Information Criterion (AIC) value (Zuur et al., 2009). All analyses were carried out in R software version 4.2.1 (R Development Core Team, 2022). To explore the distribution of dung beetle assemblage throughout the different heights and leaf areas, we constructed compound graphs of species occurrence ordered by the predictors.

RESULTS

A total of 139 dung beetles were sampled, belonging to four genera and 10 species (Table 1). *Ateuchus* Weber, 1801, and *Canthidium* Erichson, 1847 were the most species-rich genera, with three and four species recorded, respectively. *C. deyrollei* and *Canthon triangularis* were the most abundant species, comprising 78% of the total amount recorded, while four species were singletons. Regarding mean body size, *C. triangularis*, *Canthidium* aff. *aurichalceum* Preudhomme de Borre, 1886, and *Canthon quadriguttatus* (Olivier, 1789) were the largest ones (see Table 1). *C. bicolor* Boucomont, 1928, *Ateuchus murrayi* (Harold, 1868), and *Ateuchus* sp. nov. aff. *murrayi* were the smallest species (Table 1).

The height at which beetles were observed perching ranged from 18 cm (by a *C. bicolor*) to 129.5 cm (*C. deyrollei*, Supplementary material). There was a statistical difference in the perching height between the most abundant species (*C. bicolor*, *C. triangularis*, *C. deyrollei*) ($F_2 = 22.11$, $p < 0.01$). *C. bicolor* perched at lower heights, *C. triangularis* perched at intermediate heights, and *C. deyrollei* perched at higher heights (Figure 1). The leaf area in which beetles perched varied widely, ranging from 2.19 mm^2 (perched by an *C. deyrollei*) to leaves measuring 981.68 mm^2 (perched by an *Ateuchus sulcicollis* [Harold, 1868], see Supplementary material). In contrast to the height, there was no difference in the leaf area among the three most abundant species ($F_2 = 0.33$, $p = 0.72$).

There was a significant relationship between the body size of the beetles and the perching height in the two tested approaches. When analysing all individuals with the species identity being considered as a random variable (i approach), larger individuals perched at lower heights than small

TABLE 1 Dung beetle species abundance, mean (±standard error) body size, leaf area, and height in which they were recorded perching in Vanessa RAPELD, Presidente Figueiredo, Amazonas, Brazil.

Species	Abundance	Body size (mm)	Perched leaf area (mm^2)	Perched height (cm)
Ateuchus murrayi (Harold, 1868)	5	4.58 ± 0.37	153 ± 146.8	66 ± 26.95
Ateuchus sp. nov. aff. *murrayi*	3	4.67 ± 0.4	122.12 ± 135.59	31.17 ± 14.8
Ateuchus sulcicollis (Harold, 1868)[a]	6	5.68 ± 0.49	368.22 ± 361.95	55.13 ± 24.46
Canthidium aff. *aurichalceum* Preudhomme de Borre, 1886	1	9.70 ± 0.00	32.3 ± 0.00	28 ± 0.00
Canthidium bicolor Boucomont, 1928	12	3.72 ± 0.28	43.4 ± 25.08	32.94 ± 14.62
Canthidium deyrollei Harold, 1867	60	5.27 ± 0.47	76.65 ± 118.62	67.49 ± 26.2
Canthidium sp.	1	4.00 ± 0.00	52.03 ± 0.00	65 ± 0.00
Canthon quadriguttatus (Olivier, 1789)	1	6.60 ± 0.00	34.97 ± 0.00	58 ± 0.00
Canthon triangularis (Drury, 1773)	49	10.27 ± 1.15	55.93 ± 40.25	48.03 ± 15.45
Scybalocanthon pygidialis (Schmidt, 1922)	1	5.90 ± 0.00	13.74 ± 0.00	29 ± 0.00

[a]Originally described as *Canthidium sulcicolle* Harold, 1868, this species was subsequently cited as *A. sulcicollis* by Feer (2008) and Génier (2010), but without explanation. Larsen (2012) correctly noted that the species still needs to be formally transferred to *Ateuchus*, a task that Mario Cupello will undertake in his forthcoming revision of the genus.

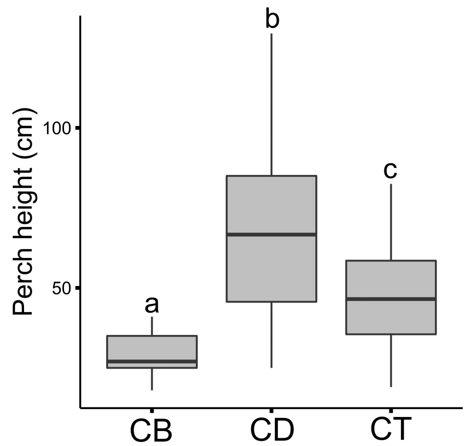

FIGURE 1 Distribution of heights at which beetles from the three most abundant species (CB, *Canthidium bicolor*; CD, *Canthidium deyrollei*; CT, *Canthon triangularis*), in increasing order of body size, perched in Vanessa RAPELD, Presidente Figueiredo, Amazonas, Brazil. Different letters indicate statistical differences among the treatments.

ones (Table 2; Figure 2a). In the analysis comprising each species separately (ii approach), larger individuals of *C. bicolor* perched higher than smaller ones (Table 2; Figure 2b). However, *C. deyrollei* and *C. triangularis* did not show a significant relationship between individual body size and perching height (Table 2).

There was a significant relationship between the leaf area and the height of the leaves where the dung beetles perched. The larger the leaf area, the higher the beetles perch in the analysis considering all individuals with the species identity being considered as a random variable (i approach) (Table 2; Figure 3a). For the analysis with all individuals of each species separately (ii approach), *C. bicolor* had a positive relationship between leaf area and perch height (Table 2; Figure 3b). There was no significant relationship between beetles' perch height and the leaf shape in any of the two tested approaches: (i) all individuals with the species identity being considered as a random variable, and (ii) considering all individuals of each species separately (Table 2).

TABLE 2 Statistical models assessing the effect of body size, leaf area, and leaf shape on perching height in Vanessa RAPELD, Presidente Figueiredo, Amazonas, Brazil.

	Perch height
All individuals ($N=139$; i approach)	
Leaf area	**$t=-3.00$, $p<0.01$ (+)**
Body size	NS
Leaf shape	NS
Canthidium bicolor ($N=12$; ii approach)	
Leaf area	**$F_1=12.66$, $p<0.01$ (+)**
Body size	**$F_1=7.23$, $p=0.02$ (+)**
Leaf shape	NS
Canthidium deyrollei ($N=60$; ii approach)	
Leaf area	NS
Body size	NS
Leaf shape	$F_1=1.7$, $p=0.19$
Canthon triangularis ($N=49$; ii approach)	
Leaf area	$F_1=3.18$, $p=0.08$
Body size	NS
Leaf shape	NS

Note: Approach i—analysis performed with all individuals considering species identity as a random factor; Approach ii—analysis performed with all individuals of each species separately. Significant effects are shown in bold. '(+)' indicates a positive relationship. NS, nonsignificant (variables not selected by the best-supported model).

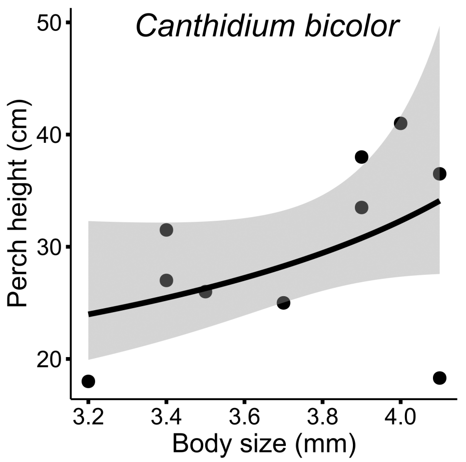

FIGURE 2 Relationship between individuals of *Canthidium bicolor*'s body size and height at which each beetle perched in Vanessa RAPELD, Presidente Figueiredo, Amazonas, Brazil.

According to the compound graphs, most species were recorded at low and intermediate heights (Figure 4a). The only species which were recorded at higher heights were *C. deyrollei* and *A. murrayi* (Figure 4a). When considering leaf area, all species were observed on small leaves (Figure 4b). The three *Ateuchus* species observed in this study (and a few *C. deyrollei* individuals) and *C. deyrollei* were the only ones recorded on larger leaves (Figure 4b).

DISCUSSION

The perching behaviour of dung beetles is important for their survival, helping them detect food, regulate body temperature, and reduce

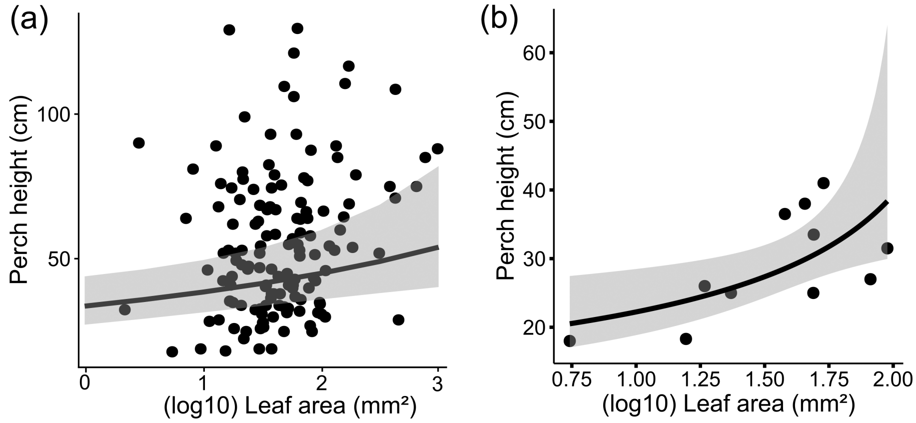

FIGURE 3 Relationship between all individuals leaf area and height at which each beetle perched (a) and between individuals of *Canthidium bicolor* leaf area and height at which each beetle perched (b) in Vanessa RAPELD, Presidente Figueiredo, Amazonas, Brazil.

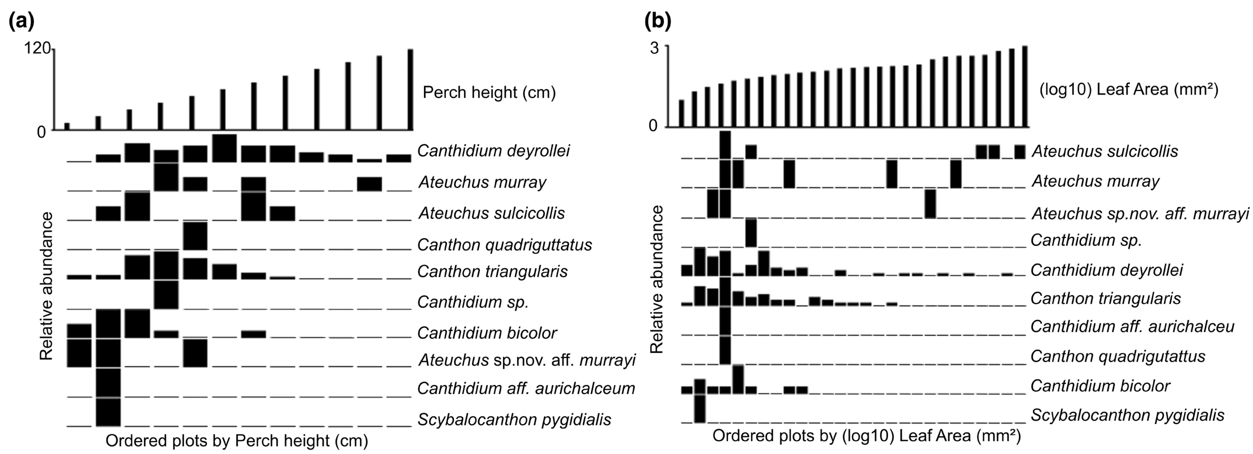

FIGURE 4 Relative abundance of dung beetle species recorded perching at different heights (a) and at different leaf areas (b) in Vanessa RAPELD, Presidente Figueiredo, Amazonas, Brazil.

competition (Noriega & Vulinec, 2021). This behaviour is particularly important in complex ecosystems like the Amazon rainforest, where resource competition is intense. Our findings show a spatial partitioning between perching dung beetles, which was dependent on the dung beetle species, intraspecific and interspecific body size, and leaf area, agreeing with what was initially proposed by Noriega et al. (2020). Corroborating with other studies (e.g. Noriega et al., 2020; Noriega & Vulinec, 2021), larger dung beetles perched at higher heights. However, perching height varied among species, suggesting that each one has different spatial perching strategies and vertical spatial distribution. Most studies regarding vertical stratification of terrestrial invertebrates focus on assemblage-level distribution, aiming at comparing vertical distribution among species, but rarely within species (e.g. Abdul Rahman et al., 2021; Salomon et al., 2010; Schal, 1982; Tanabe, 2002). The present study sheds light on both intra- and interspecific perching dynamics of dung beetle species that inhabit a region of central Amazonia.

Interestingly, larger individuals of *C. bicolor* perched at higher heights, but such a relationship was not observed for *C. triangularis* or *C. deyrollei*. Among other arthropods, resource partitioning and sexual dimorphism feature as important characteristics that explain intrapopulation segregation across vertical distribution (Salomon et al., 2010; Schal, 1982). Although we have limited knowledge regarding the biology of *C. bicolor*, we know that sexual pheromones and the presence of abdominal exocrine glands are more common in roller dung beetles than in tunneller dung beetles, like *C. bicolor* (see e.g. Pluot-Sigwalt, 1982). Therefore, although pheromone production is perhaps unlikely for *C. bicolor*, other mechanisms of sexual segregation may explain the vertical distribution of this species. For example, species that inhabit higher heights present specific morphological traits compared with those that inhabit lower-strata sites (Abdul Rahman et al., 2021; Cordero, 1995; DeVries et al., 2010), and this idea could be extrapolated to intraspecific level. Therefore, an alternative hypothesis for *C. bicolor* is that putative individual variation of morphological traits (e.g. wingspan, leg size, eye width) could explain the vertical distribution of these dung beetles. These traits could represent adaptations to different environmental pressures, such as flight efficiency (Bhat et al., 2018), mobility (Kelly et al., 2008), and visual acuity (Farnier et al., 2015), allowing individuals to better exploit resources and reduce competition across strata. Regarding the species that did not present clear correlation between body size and perching height, it is important to note that this body trait is also related to intraspecific competition (Chamorro-Florescano et al., 2011; Salomão et al., 2019; Sato & Hiramatsu, 1993) and that body size is a key driver of dung beetle response to environmental conditions (Scholtz et al., 2009). Thus, we suggest that perching at specific heights is not a determinant of the individual success of either *C. deyrollei* or *C. triangularis* individuals. The intraspecific approach suggests that body size may determine vertical distribution, but this relationship is species-dependent. Other biological (e.g. physiological condition, age, sex) and morphological traits should be analysed to better understand the dynamics of the vertical distribution of dung beetles.

For *C. bicolor* and the entire assemblage, individuals that perched at higher heights tended to perch at larger leaves. Interestingly, such a trend was similar to the one observed for the relationship between dung beetle body size and perch height. In lizards and in dragonflies, the area available for perching may explain intraspecific and interspecific distribution (Hykel et al., 2020; Rand, 1964). For example, odonatans tend to perch at higher perches whenever the perch area is large (Hykel et al., 2020), such behaviours being related to competitiveness. According to our results, we may suggest that *C. bicolor* presents foraging strategies that are strongly related to its spatial perching distribution. In one of the few studies focusing on perching behaviour among dung beetle species in the Colombian Amazonian, a *Canthidium* species (*C. gerstaeckeri* Harold, 1867) had the broadest vertical distribution range (Noriega et al., 2020). This study and our data on *C. bicolor* may indicate that the species of *Canthidium* tend to occupy wide intervals of vegetation strata. Since animals that perch at different strata tend to specialize on specific layers and occupy specific perching areas (Abdul Rahman et al., 2021; Rand, 1964; Robinson & Holmes, 1984), it is possible that this phenomenon also occurs in *C. bicolor*. Nonetheless, it is crucial to consider that vegetation and leaf structure may also modulate the patterns of perching, as observed in bird species (Robinson & Holmes, 1984). Therefore, we need to consider that the positive relationship between perch height and leaf area could be an effect of spatial availability. In other words, dung beetles could be perching at larger leaves in higher strata due to their higher availability compared with smaller leaves.

The pattern we found shows a segregation tendency between the species of the same genus. The three species of *Ateuchus* (*A. murrayi*, *A. sulcicollis*, and *A*. sp. nov. aff. *murrayi*), the four species of *Canthidium* (*C. deyrollei*, *C. bicolor*, *C*. aff. *aurichalceum*, and *C*. sp.), and the two species of *Canthon* (*C. quadriguttatus* and *C. triangularis*) present a low degree of overlap between them compared with species of other genera. This may be due to a spatial segregation strategy that prevents interspecific competition

(Davis, 1999; Feer, 2015; Noriega & Vulinec, 2021). We recorded less segregation at lower heights (20–50 cm), evidencing that there is potential greater competition for perches at these heights than on leaves at higher heights (>60 cm). Very few species use leaves above 100 cm. This may be related to the understory structure of the vegetation at this specific locality. However, it must be mentioned that our methodological limitation did not allow us to observe species perching above 190 cm.

Concerning the assemblage pattern related to leaf area and perching, we found several species that prefer a narrow range of leaf sizes, especially small leaves (*Canthidium* sp., *Canthidium* aff. *aurichalceum*, *C. quadriguttatus*, and *Scybalocanthon pygidialis* [Schmidt, 1922]) and a small group of species that have wider ranges in their leaf area preference. In this study, we did not record a clear segregation associated with the size of the leaves, unlike Noriega et al. (2020). For some species (*A. sulcicollis*, *A. murrayi*, and *A.* sp. nov. aff. *murrayi*), there is a clear gap in records associated with leaves of an intermediate area that could be related to a lack of plants in the area with these characteristics. The case of *C. deyrollei* demonstrates that individuals could perch at any height for some species and in any type of leaf.

When analysing the results and trends observed herein, it is important to take into consideration our limitations. Compared with the few studies performed with perching dynamics (Feer, 2015; Noriega et al., 2020), our research has a limited sampling effort and was conducted only during the daytime. Despite such limitations, the number of individuals used in the analyses performed herein allowed us to present relatively robust results. Moreover, our plant approach was generalized, and important plant characteristics that could drive perching patterns, such as plant species and turgor were not considered. This study provides preliminary data regarding perching dynamics in Amazonian forests of Brazil. Future studies with a broader sampling effort (e.g. comprising different seasons, periods of the day, and larger ranges of height) would disentangle and strengthen the patterns of perching found in this portion of the Amazon.

Perching behaviour in dung beetles has recently attracted the attention of researchers (Davis, 1999; Feer, 2015; Noriega & Vulinec, 2021), expanding our understanding of species vertical distribution, especially in tropical rainforests. The results presented herein suggest that perching dynamics may depend on individual body size but also depend on the species' life history. Given that the relationship between body size and perching height is species-dependent, our observed pattern apparently is particular and contrasts with previous findings (Feer, 2015; Noriega & Vulinec, 2021), presenting novel and unexpected data for perching in tropical rainforests. We believe that the next step is to deepen and develop more complex studies addressing the intra- and interspecific dynamics of life history, their potential associations with perching behaviour and a more extensive range of heights. Species phylogeny, age, sex, physiological condition, morphology, and dial period of activity are some traits that should be considered in future studies focused on perching dynamics.

AUTHOR CONTRIBUTIONS

Leonardo Vilas-Bôas M. P. de Cerqueira: Conceptualization (equal); data curation (equal); formal analysis (lead); investigation (equal); methodology (equal); project administration (equal); visualization (lead); writing – original draft (equal); writing – review and editing (equal). **Liara de Azevedo Cassiano:** Conceptualization (equal); data curation (equal); investigation (equal); methodology (equal). **Lucas Liesak Sant' Ana Santos:** Conceptualization (equal); data curation (equal); investigation (equal); methodology (equal); writing – review and editing (equal). **Jorge Ari Noriega:** Data curation (equal); writing – review and editing (equal). **Mario Cupello:**

Data curation (equal); writing – review and editing (equal). **Fernando Vaz-de-Mello:** Data curation (equal). **Renato Portela Salomão:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); project administration (lead); supervision (lead); writing – original draft (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The current research has no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the Supplementary material of this article.

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