

Life history patterns of coleopteran pollinators of *Annona crassiflora* Mart. in the Brazilian Cerrado

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ABSTRACT

The large floral chambers of the Neotropical Annonaceae are pollinated by large beetles of the tribe Cyclocephalini Laporte (Melolonthidae). Previous research indicates that, depending on the geographic area, the assemblage of Cyclocephalini pollinators may differ. In this study, pollinators of *Annona crassiflora* Mart. were surveyed in the Cerrado of Chapada dos Guimarães, Mato Grosso, Brazil, for the first time. The analysis of 74 flowers from 24 *A. crassiflora* individuals revealed that the principal pollinator was *Cyclocephala octopunctata* Burmeister. The secondary pollinator, *Cyclocephala celata* Dechambre, and *C. octopunctata* exhibited behaviour that may promote cross pollination, visiting both female- and male-phase flowers, touching stigmas and anthers and becoming coated in pollen during anthesis. This is the first record of *C. celata*, a species commonly found pollinating Araceae in the Atlantic Forest, as a pollinator of an Annonaceae species in the Cerrado. Additionally, an interim phase between the female and male phases of *A. crassiflora* is documented here for the first time.

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Introduction

The economic relevance of Coleoptera is mostly attributed to the role they play as pests in crops and stored products (Capinera 2001; Casari and Ide 2012). The last several decades have seen an increase in the number of studies concerning the role of beetles as pollinators in several plant families, many of which are economically important (Kono and Tobe 2007; Gottsberger 2012; Kishore et al. 2012; Meléndez and Ponce 2016; Lara et al. 2017).

Many herbivorous scarabs from the tribe Cyclocephalini, which includes nearly 500 described species, are important agricultural pests, especially in their immature stages, during which they feed on the living roots of crop plants such as soybean, sugarcane and pasture species (Casari et al. 1988; Santos and Ávila 2007; Coutinho et al. 2011; Nogueira et al. 2013; Souza et al. 2013, 2014; Albuquerque et al. 2014; Moore et al. 2018; Rodrigues et al. 2018). In contrast, adult Cyclocephalini rarely act as pests of agroecosystems, and they play a major role in the pollination of nearly 900 species of Neotropical plants (Moore et al. 2018).

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Cyclocephalini are known to pollinate basal angiosperms and monocotyledons from plant families such as Magnoliaceae, Nymphaeaceae, Annonaceae and Araceae (Dieringer and Spinosa 1994; Dieringer et al. 1999; Ervik and Knudsen 2003; Gottsberger 2012; Saravy et al. 2021a; Torezan-Silingardi et al. 2021). The species-rich plant family Annonaceae is mainly pollinated by beetles of the families Nitidulidae, Staphylinidae, Curculionidae and Scarabaeidae, although there are some records of Chrysomelidae (Andrade et al. 1996; Ratnayake et al. 2007; Gottsberger 2012; Aragão et al. 2019).

Current knowledge of the presence of Annonaceae in the Cerrado indicates the occurrence of 75 species (Mendonça et al. 2008). *Annona crassiflora* Mart., which is popularly known as *araticum-do-cerrado* or *marolo*, occurs mainly in *Cerradão* and *Cerrado sensu stricto* regions, from Ceará in the north to São Paulo in the south (Silva-Júnior et al. 2005; Lorenzi 2009). Figure 1 shows a distribution map for this

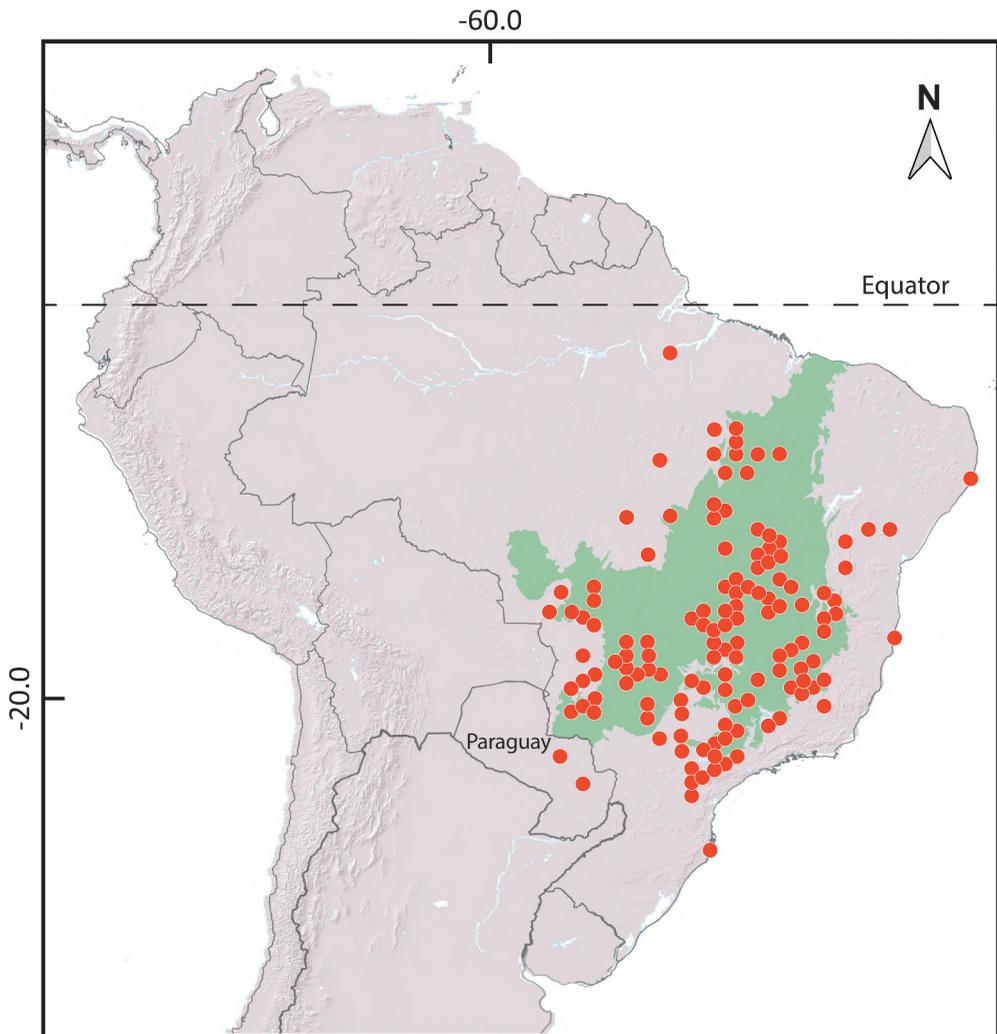


Figure 1. Global occurrence map of *Annona crassiflora* (araticum). Adapted from: Global Biodiversity Information Facility (GBIF 2021).

species. Although its fruits are greatly appreciated by traditional populations of central Brazil, the high economic potential of *A. crassiflora* remains largely unexplored (Lorenzi 2009; Rezende and Malafaia 2012). Data on the pharmacological potential of its different plant parts is scant. However, studies have shown a high nutritious content of the fruit pulp and potential for the extraction of antioxidant compounds from the fruit peel (Cardoso et al. 2013). Leaf extracts of *A. crassiflora* have shown antioxidant activity when included in a phytocosmetic gel and *in vitro* anthelmintic activity (Costa 2017; Caldeira et al. 2019).

Gottsberger and Silberbauer-Gottsberger (2006) mentioned three species of Cyclocephalini as pollinators of *A. crassiflora* in the Brazilian Cerrados of the states of Minas Gerais, São Paulo, Goiás and Distrito Federal: they are *Cyclocephala atricapilla* Mannerheim, *Cyclocephala quatuordecimpunctata* Mannerheim and *Cyclocephala literata* Mannerheim, the latter of which was found only once as a flower visitor. In a Cerrado area in the state of Goiás, Cavalcante et al. (2009) found three *Cyclocephala* species visiting flower chambers of *A. crassiflora*: *C. atricapilla*, *Cyclocephala latericia* Hohné and *Cyclocephala octopunctata*. These are relatively large, nocturnal beetles often found in the large, thermogenic flower chambers of *A. crassiflora* (Gottsberger, 1989a, 1989b, Gottsberger 1994; Gottsberger and Silberbauer-Gottsberger 2006). Oliveira and Gibbs (2000) cited *Cyclocephala* cf. *atricapilla* as visitors of *araticum* flowers in a Cerrado area of the Brasília Botanic Garden (Distrito Federal). Two species of Cyclocephalini are constant pollinators throughout the geographic range of *A. crassiflora*: *C. atricapilla* and *C. quatuordecimpunctata*. However, other *Cyclocephala* species are occasional pollinators in different geographic sites.

Given that the pollinator assemblage of *A. crassiflora* varies according to the geographic location despite how specialised its pollination syndrome is, this study aimed to (1) determine the floral visitors of *A. crassiflora* in a Cerrado area in the municipality of Chapada dos Guimarães, Mato Grosso, Brazil, and (2) identify their behaviour to determine whether it is likely to promote pollination.

Material and methods

Study area

The study was carried out in two flowering seasons of *A. crassiflora*: during 2019, over 13 days in the months of September and October; and during the flowering event of 2020, over eight days between October and November. Both sampling periods were during the beginning of the rainy period. The study area in the Chapada dos Guimarães measured nearly 7 ha (15.27°S, 55.47°W). According to the key of Cerrado vegetation physiognomies of Ribeiro and Walter (2008), the area in which the individuals of *A. crassiflora* were sampled was characterised as 'Cerrado Denso' and was bordered in the north-west by a patch of 'Mata de Galeria Não-Inundável' and in the south-east by a strip of 'Mata Seca' (Figure 2). The climate in the region is type Aw (tropical with dry winter), according to the Köppen classification (Alvares et al. 2013). The mean annual temperature is 21.5°C, and the mean annual rainfall may reach 2100 mm at higher elevations (Vieira-Júnior et al. 2012). The individuals of *A. crassiflora* (n = 24) selected for this study were located at elevations of 774 to 822 m.



Figure 2. Study area located in the Cerrado of the municipality of Chapada dos Guimarães, MT, with the positions of the 24 individuals of *Annona crassiflora* analysed in this research (red circles). Source: Google Earth.

Sampling of flower chamber visitors

Twenty-four blossoming individuals of *A. crassiflora* were randomly selected in the study area. Observations and the collection of flowers and their visitors were accomplished at the time of day in which the flowers were anthetic (i.e. from dusk until just before dawn). Flowers were considered in the female phase when the stigmatic head was covered with stigmatic exudate and in the male phase when anthers were open and detached from the receptacle. The external petals of *A. crassiflora* flowers delimit a semi-open flower chamber. The handling of such chambers scares off their flower visitors. Hence, flowers were hand-picked and promptly photographed. Immediately afterwards, the flowers were individually placed in labelled vials with 90% alcohol to prevent visitors' escape. The sampled flowers were taken to the Laboratório de Ecologia e Taxonomia de Artrópodes (LETA) of the Instituto de Biociências in the Universidade Federal de Mato Grosso (UFMT). In total, the contents of the flower chambers of 74 flowers were analysed. Specimens are deposited in the Collection of Arthropods of LETA and Setor de Entomologia da Coleção Zoológica da UFMT.

The behavioural characteristics of visiting insects were considered appropriate for pollination when they (1) were found inside the floral chambers, (2) were found inside the floral chambers in either the female phase or the male phase, which favours cross pollination and/or (3) pollen adhered to the flower visitors' bodies.

Thermogenesis measurements

During nine days in September and October 2019, the floral thermogenesis of *A. crassiflora* flowers was assessed on 71 flowers from 14 individuals. The temperature was taken by inserting a digital thermal sensor device (GTH 175 PT, Germany) in the floral chamber until it touched the base of the petals' inner surface. The obtained value was then subtracted from the ambient temperature to calculate thermogenesis in degrees Celsius.

Imaging procedures

Digital photographic field records were obtained with a Sony NEX-F3 camera. Photographs of the material examined in the laboratory were obtained with a Leica CH-94335 microscope camera attached to a Leica L2 stereomicroscope (Leica Microsystems) and were captured with Leica Application Suite v. 3.8 software. When necessary to highlight particular aspects of the plant structures and/or their visitors, images were obtained via multifocal sequences, stacked and grouped with Adobe Photoshop 2020 v. 21.0.2 software.

Taxonomic analysis

Non-coleopteran floral visitors of the subphylum Hexapoda were identified at the order level (with the exception of Hymenoptera, belonging to Formicidae, and Hemiptera, belonging to Aphidae). Flower visitors of the order Coleoptera were identified to the lowest taxonomic level possible. Photographs were sent to taxonomists of Scarabaeoideae (*sensu* Cherman and Morón 2014). The classification in higher taxonomic categories of Coleoptera follows Bouchard et al. (2011). The familial and subfamilial classification of scarabs followed Cherman and Morón 2014. The species-level classification of Scarabaeidae followed Endrödi (1985). The classification of Curculionidae at the supra-species level was in accordance with Alonso-Zarazaga and Lyal (1999).

Results

Flower buds of *Annona crassiflora* may take up to four months to fully develop (Figure 3a). On the day of anthesis, the pendant flower chambers open up during the day, and the colour of the external petals changes from a greener tone to a more ferruginous hue (Figure 3b). However, anthesis only starts during the evening, when the flowers ($n = 26$, Figure 5a) enter the female phase (7.30pm–11.00pm), which is perceived based on the presence of a sticky, transparent, glossy stigmatic exudate covering the entire surface of the gynoecium (Figure 3c).



Figure 3. Some steps in the floral cycle of *Annona crassiflora* in a Cerrado area in the municipality of Chapada dos Guimarães, MT. (a) Developing flower buds photographed in early August, almost two months before the flowering season of *A. crassiflora*. (b) Open flower chamber photographed in the morning before the onset of anthesis. (c) Flower entering the female phase, photographed from below during crepuscule. Note the sticky, transparent, glossy substance on the gynoecium (the stigmatic exudate; arrow). Petals were spread open to show internal structures.

There appears to be a brief interim phase in anthesis during which flowers ($n = 4$, [Figure 5a](#)) are neither in the female phase nor in the male phase. Depending on the tree, this phase may occur between approximately 10.00pm and 11.00pm. This stage is



Figure 4. Some steps in the floral cycle of *Annona crassiflora* in a Cerrado area in the municipality of Chapada dos Guimarães, MT. (a) Interim in the floral cycle. Note that the stigmatic head is detached from the receptacle (arrow). Petals were spread open to show the flower chamber interior. (b) Flower found on the ground in the morning close to anthesis, showing the aspect of the flower during the male phase, with detached stamens filling the floral chamber.

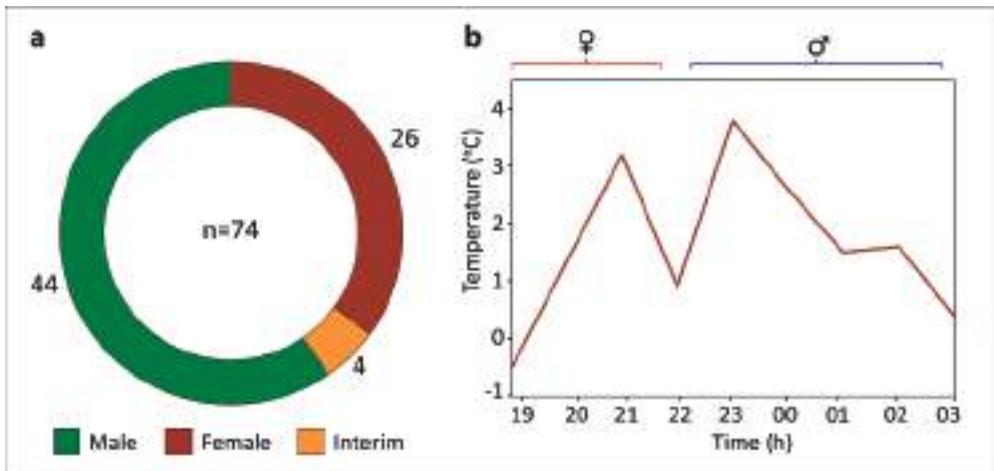


Figure 5. Aspects of floral biology of *Annona crassiflora* in a Cerrado area in the municipality of Chapada dos Guimarães, MT. (a) Number of sampled flowers ($n = 74$) according to the floral phase. Note the greater number of male flowers collected in the field relative to the female-phase flowers sampled. (b) Floral thermogenesis during one floral cycle. Note that there are two heat production peaks during the night, one at approximately 7.00pm, when the flowers are in the female phase, and another at approximately 11.00pm, when they are in the male phase. During the interim phase, heat production diminishes without ceasing altogether.

perceivable when the stigmatic head is either darkened and/or detached from the receptacle but anthers are not yet open (Figure 4a). Flowers in the male phase were found from 8.45pm to 3.50am ($n = 44$, Figure 5a). The beginning of the male phase is marked by the opening of anthers and their detachment from the receptacle (Figure 4b). After 3 h, corollas start dropping as a whole unit, marking the end of anthesis.

In the course of anthesis, flowers give off a sweet, fruity scent with a faint background of acetone. This smell is enhanced by floral thermogenesis, which starts during the female phase and intensifies during the male phase. During the interim, however, between the female and male phases, floral heat production decreases. After 3 h, corollas start dropping as a whole unit, marking the end of anthesis (Figure 5b).

As shown in Figure 6a and Table 1, among the 119 visitors collected from the anthetic flowers of *A. crassiflora*, 74 belonged to the order Coleoptera. The remainder, as demonstrated in Figure 6b, were insect members of the orders Thysanoptera ($n = 12$), Diptera ($n = 8$, all in larval stages), Hymenoptera ($n = 4$, all from the family Formicidae) and Hemiptera ($n = 3$). The individuals found in the flowers of *A. crassiflora* came from only two families of Coleoptera (Figure 6c): Melolonthidae ($n = 82$ individuals) and Curculionidae ($n = 10$ individuals). From the former taxon, only two species were collected, *Cyclocephala octopunctata* ($n = 66$; Figure 7a, b) and *Cyclocephala celata* Dechambre ($n = 16$; Figure 7c, d), and all of these specimens were found inside the floral chambers during anthesis (Figure 6d; Table 1).

The three most significant taxa collected on the flowers of *A. crassiflora* were *C. octopunctata*, *C. celata* and *Lydamis* sp. 1 Pascoe. All individuals of both *Cyclocephala* species were found within the floral chambers (Table 1). However, it was unclear whether, at the time of flower collection in the field, the small individuals of *Lydamis* sp. 1 were

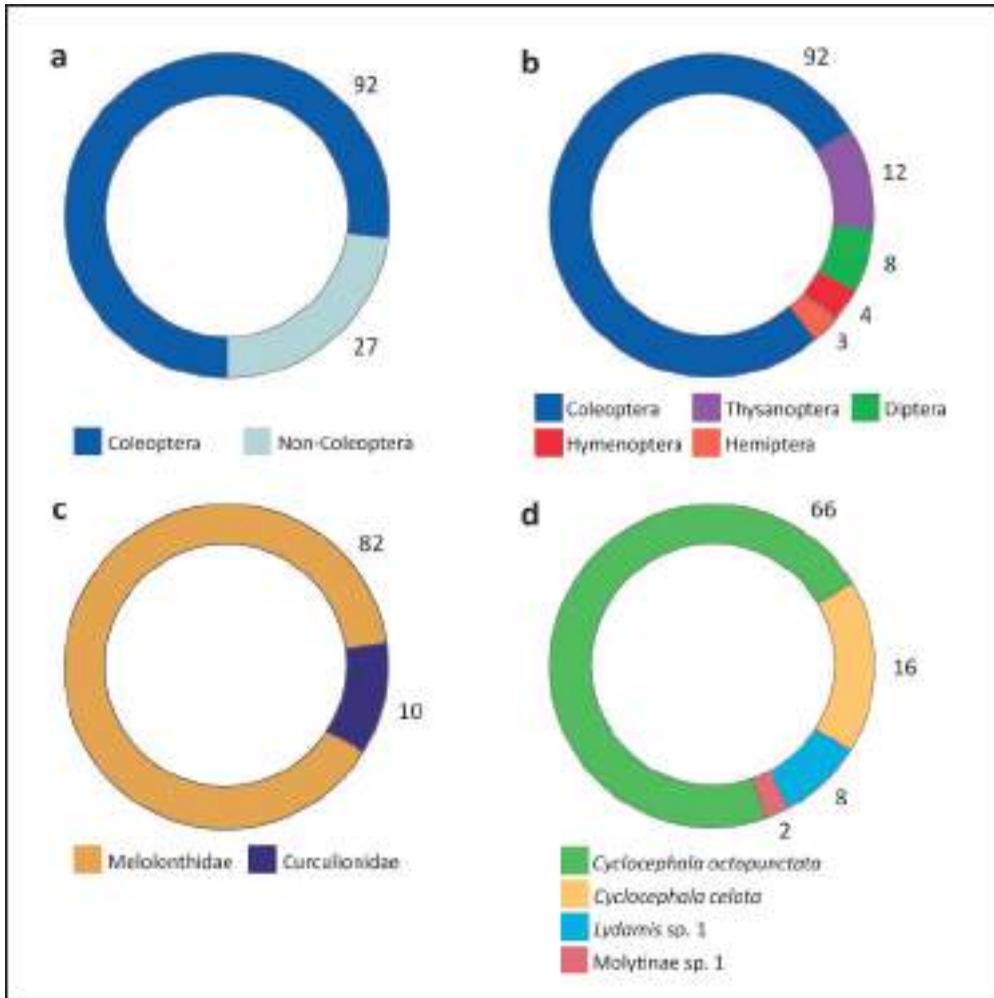


Figure 6. Quantitative data on the visitation of *Annona crassiflora* flowers in a Cerrado area in the municipality of Chapada dos Guimarães, MT. (a) Number of coleopteran and non-coleopteran visitors of anthetic flowers. (b) Number of insect flower visitors sorted by order. (c) Number of beetles visiting anthetic flowers, classified at the family level. (d) Number of beetles visiting anthetic flowers classified at the species and morphospecies levels.

located inside the flower chambers. These specimens were unknowingly collected during the nocturnal field work. The *Lydamis* sp. 1 specimens were identified only in the laboratory, when the alcohol containing the samples was observed under a stereomicroscope (Table 1). Additionally, the two identified specimens of *Molytinae* sp. 1 (Curculionidae) were found outside the floral chambers, feeding on the adaxial surface of the outer petals.

The two most abundant species found in the flower chambers of *A. crassiflora*, *C. octopunctata* and *C. celata*, exhibited very similar behaviour during visitation. They were present in both female- and male-phase flowers (Figures 8, 9, 10a, b), fed on the basal lobes of the inner petals, and touched the androecium as well as the gynoecium

Table 1. List of floral visitors of 74 anthetic *Annona crassiflora* flowers in a Cerrado area in the municipality of Chapada dos Guimarães, MT. Ni = total number of individuals in each morphospecies found on the flowers. Nf (%) = percentage of flowers in which each listed morphospecies was found. Ni/f = average number of individuals of each morphospecies per flower. PFC (%) = percentage of each morphospecies individual found inside floral chambers. All other specimens were found in the alcohol samples.

Flower visitor	Subfamily	Ni	Nf (%)	Ni/f	PFC (%)
Coleoptera					
Melolonthidae					
<i>Cyclocephala octopunctata</i>	Dynastinae	66	54.05	1.65	100
<i>Cyclocephala celata</i>	Dynastinae	16	14.86	1.45	100
Curculionidae					
<i>Lydamis</i> sp. 1	Baridinae	8	6.75	1.6	0
Molytinae sp. 1	Molytinae	2	0.37	1	0
Thysanoptera	–	12	8.1	2	0
Diptera	–	8	4.05	2.66	0
Hymenoptera	–	4	4.05	1.33	0
Hemiptera	–	3	2.7	1.5	0

with their large bodies (Figures 8, 9). In some cases, more than one individual was present in the same floral chamber (Figures 8c, 9c). Individuals of both *Cyclocephala* species, whose activity was observed only during the night, when the flowers of *A. crassiflora* are anthetic, were seen moving about inside the floral chambers with their elytra covered in pollen (Figures 8b, 9b, c, d). Under the stereomicroscope, tetrads of conspecific pollen were found to be adhered not only to the elytra of *Cyclocephala* but also to their conspicuous ventral setae. The sticky stigmatic exudate produced during the female phase of the flowers can mediate the adherence of pollen tetrads to the smooth surfaces of the beetles' bodies (Figures 8b, 9d).

At the end of anthesis, the thick gamopetalous corolla drops as a whole unit, which provides *Cyclocephala* individuals with shelter from desiccation and predators throughout the day after anthesis (Figures 9c, 11b). Two post-anthetic flowers were found on the ground beneath the crowns of two *A. crassiflora* trees at approximately 10.00am, each associated with an individual of *C. celata* covered with pollen. A third post-anthetic flower was collected in the afternoon after anthesis and was surprisingly still attached to the pedicel; this flower contained two individuals of *C. octopunctata*, covered with pollen (Figure 11b).

The relatively ample floral chambers allow Cyclocephalini beetles to encounter conspecifics foraging in the same flower (Figures 8c, 9c; Table 1). Up to four specimens of *C. octopunctata* were found inside single floral chambers of *A. crassiflora* (Figure 10c). More than one individual of *C. celata* was found inside six floral chambers (Figure 10d). We concluded that within the study area, both sampled species of *Cyclocephala* (*C. octopunctata* and *C. celata*) are pollinators of *A. crassiflora*.

Discussion

Protogyny is a common condition of plant species pollinated by beetles, regardless of the pollinators' circadian rhythms. Cantharophilous flowers and inflorescences whose anthesis is diurnal show protogynous flower cycles, not only in Annonaceae species but

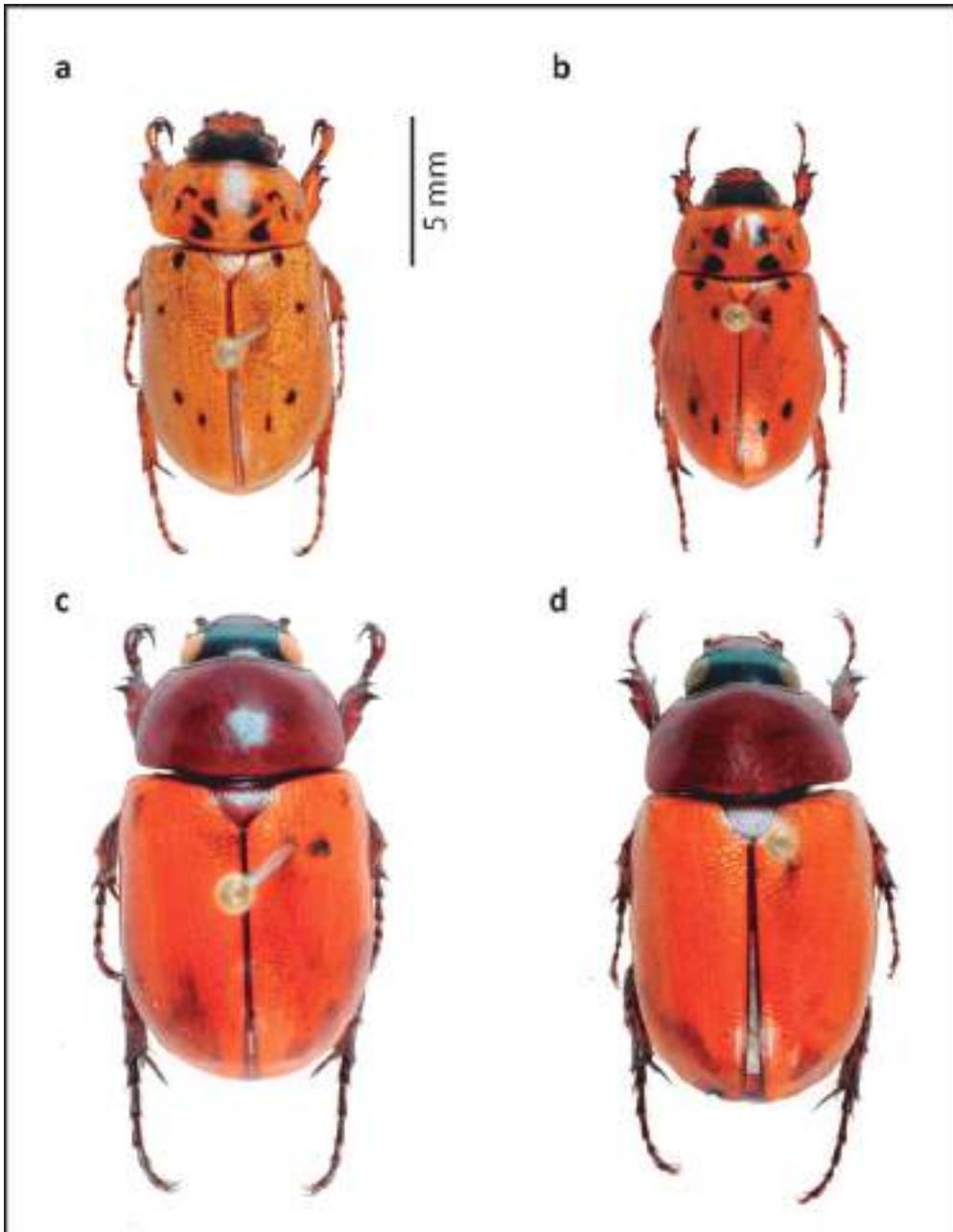


Figure 7. Pollinators of *Annona crassiflora* in a Cerrado area in the municipality of Chapada dos Guimarães, MT. (a) Dorsal habitus of *Cyclocephala octopunctata* (male). (b) Dorsal habitus of *Cyclocephala octopunctata* (female). (c) Dorsal habitus of *Cyclocephala celata* (male). (d) Dorsal habitus of *Cyclocephala celata* (female).



Figure 8. *Cyclocephala octopunctata* visiting flowers of *Annona crassiflora* in a Cerrado area in the municipality of Chapada dos Guimarães, MT. (a) A male individual found inside the floral chamber during the female phase. Note the darkening gynoecium, characteristic of an advanced female phase. (b) A specimen covered in pollen found in a male-phase flower. (c) Two individuals inside a female-phase flower. Note that their heads are directed towards the base of the inner petals, where basal alimentary lobes are located. (d) One individual feeding on one basal lobe of an inner petal in a female-phase flower.

also in palms (Oliveira et al. 2003; Gottsberger 2012; Paulino-Neto 2014a). Protogyny in nocturnal blossoms, such as *A. crassiflora*, has been described in water lilies, aroids and Annonaceae, especially within the genus *Annona* (Ervik and Knudsen, 2003; Silberbauer-Gottsberger et al. 2003; Paulino-Neto 2014a, 2014b; Costa et al. 2017).



Figure 9. *Cyclocephala celata* visiting flowers of *Annona crassiflora* in a Cerrado area in the municipality of Chapada dos Guimarães, MT. (a) Here, the elytra (arrow) of one individual of *C. celata* are visible inside a female-phase flower. (b) Individuals of *C. celata* covered in pollen exiting a male-phase flower. (c) Two individuals of *C. celata* covered in pollen inside a recently fallen corolla that was picked from the ground beneath an *A. crassiflora* tree. Note that their heads are directed towards the base of the petals, where the nutritious basal lobes are located. (d) This individual of *C. celata* had just escaped from inside a corolla that was found on the ground under an *A. crassiflora* individual on the day following flower anthesis.

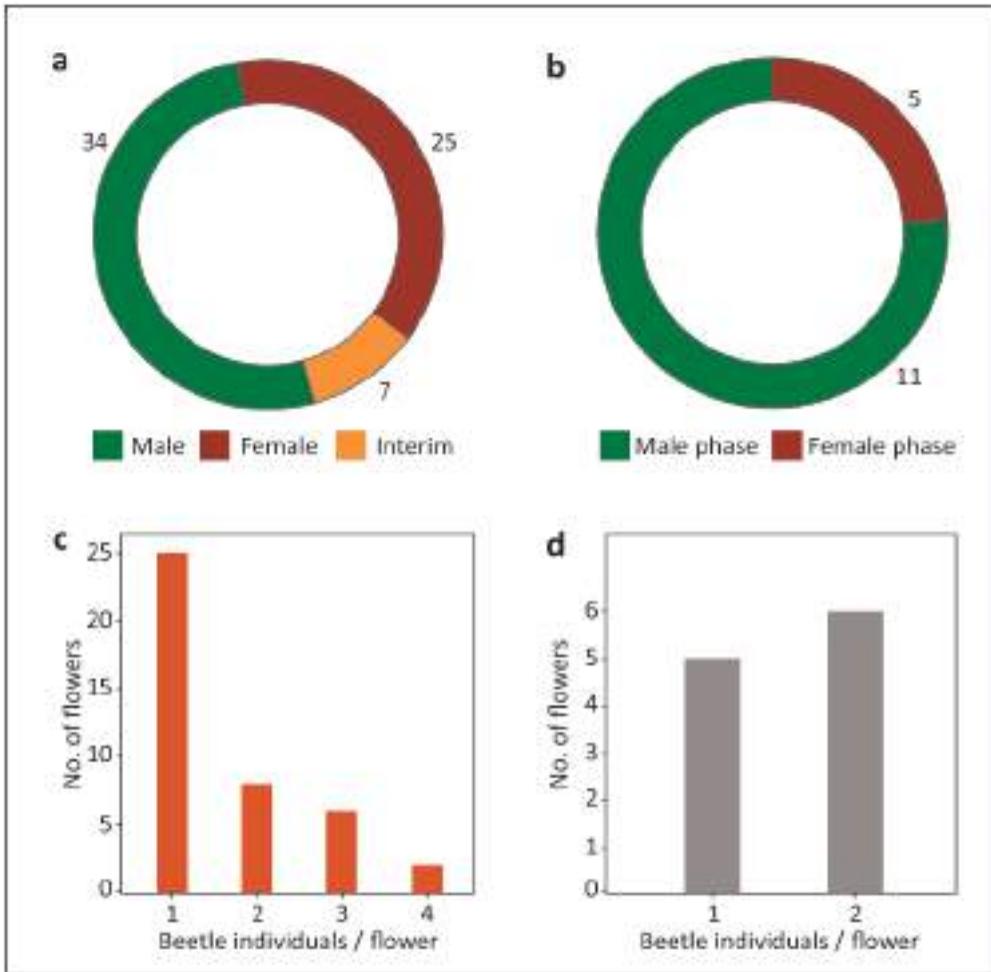


Figure 10. Quantitative data on the visitation of *Annona crassiflora* flowers by both *Cyclocephala* species sampled in this study. (a) Number of individuals of *Cyclocephala octopunctata* ($n = 66$) classified according to the anthesis phase of the flowers in which they were found. (b) Number of individuals of *Cyclocephala celata* ($n = 16$) classified according to the anthesis phase of the flowers in which they were found. (c) Distribution of the number of individuals of *C. octopunctata* per sampled flower ($n = 41$ flowers). (d) Distribution of the number of individuals of *C. celata* per sampled flower ($n = 11$ flowers).

During the female phase, the stigmatic exudate (Figure 3c) of Annonaceae seems to play a threefold role in pollination: it serves as an alimentary resource for beetles and a pollen germination medium, and facilitates pollen adhesion to pollinators' bodies (Lau et al. 2017b). For example, although the indumentum of *C. octopunctata*, the principal pollinator of *A. crassiflora* in our study area, is less dense than that of *C. celata*, pollen adheres to the smooth surfaces of the former, probably with the aid of the sticky stigmatic exudate (Figures 8b, 9 b–d, 11a). Further tests need to be carried out to

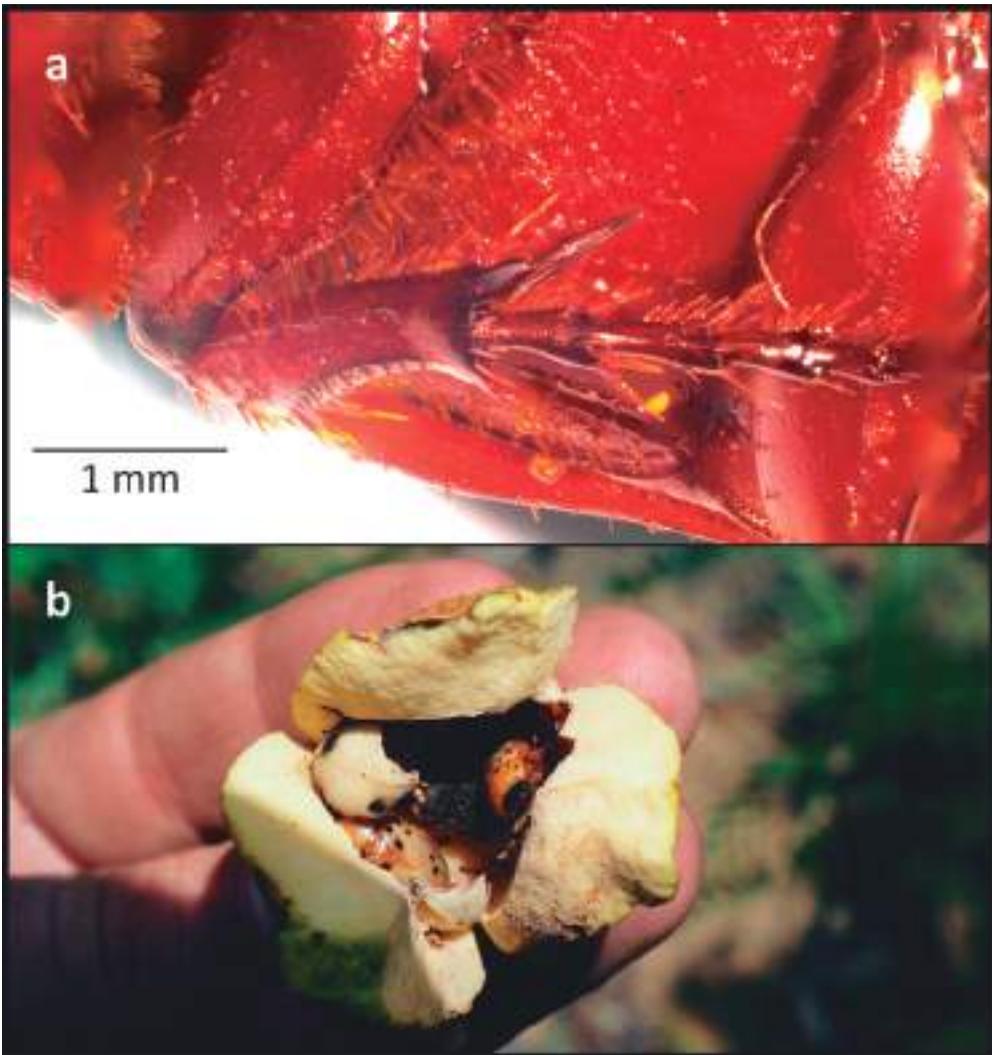


Figure 11. Individuals of Cyclocephalini found in post-anthetic flowers of *Annona crassiflora* in a Cerrado area in the municipality of Chapada dos Guimarães, MT. (a) A specimen of *Cyclocephala celata* from a flower found on the ground under the tree crown in the morning after anthesis. Note the pollen tetrads adhered to the tibial and tarsal setae of the right mesothoracic leg. (b) Individuals of *C. octopunctata* collected in the morning after anthesis from a flower still attached to the pedicel.

evaluate the two other possible roles that the stigmatic exudate may play in the pollination of *A. crassiflora*: as an alimentary resource for beetles and as a pollen germination medium.

During the male phase, however, Annonaceae flowers offer pollen, which is produced in massive quantities, as an alimentary reward for beetles (Gottsberger 2012). In a Cerrado area in the municipality of Marilândia, in the state of Mato Grosso, Costa et al. (2017) observed *Cyclocephala* species feeding on stamens still attached to the receptacle, providing evidence of pollinivory. In the field, during our nocturnal observations, when

insect-visited male flowers were removed from the trees, beetles were found immersed in the pollen and stamens, such that even the accidental ingestion of pollen could not be prevented. However, to our knowledge there has been no reported gut content analysis of *Cyclocephala* that visit *Annona* spp. flowers searching for pollen traces, and the present study did not undertake such an endeavour. Gut content analyses need to be accomplished to confirm pollen ingestion by the Cyclocephalini that visit *A. crassiflora* in our study areas.

Some rewards are present during the flower cycle (and even afterwards): for instance, the flower chamber offers the Cyclocephalini beetles shelter from desiccation and predators and a mating site, even after the flower drops, which was verified in the field by the observation of both *C. octopunctata* and *C. celata* inside post-anthetic floral chambers collected from the ground (Figures 9c, 11b). The relatively large size of the floral chamber also allows conspecific beetles to aggregate and mate, which was verified by the numerical distribution of individuals per flower chamber (Figure 10c, d). Furthermore, the basal lobes on the abaxial surface of the inner petals provide constant alimentary rewards for Cyclocephalini during and even after the floral cycle. Gottsberger and Webber (2018) verified that these nutritious tissues are rich in starch and lipids in five species of Amazonian Annonaceae from four genera, all of which are pollinated by Cyclocephalini. Nutritious tissue at the base of the inner petals in Annonaceae has also been reported in species pollinated by small, diurnal beetles (Olesen 1992).

The role of thermogenesis in cantharophilous blossoms has been the subject of controversial debate regarding whether it functions solely as a means of attraction or also provides resources (Meeuse and Raskin 1988; Seymour and Schultze-Motel 1997; Seymour and Shultze-Motel 1998; Dieringer et al. 1999; Seymour et al. 2003, 2009; Rands and Whitney 2008). There has been a consensus in the literature regarding the concept of floral heat production as a means of attracting pollinators, which suggests that heat serves to spread odour over longer distances, especially during the night (Gottsberger 1990; Seymour and Schultze-Motel 1997; Küchmeister et al. 1998; Dieringer et al. 1999). There is even a hypothesis that the thermogenicity of one Annonaceae species, *Xylopia championii* Hook. f. and Thomson, may be perceived by infrared (IR) organs of beetles, but this remains strictly conjectural, since such organs have not been confirmed in the taxa of this species' pollinators (Ratnayake et al. 2007). Dieringer et al. (1999) concluded that the heat produced by the protogynous flowers of *Magnolia tamaulipana* A. Vázquez (Magnoliaceae) did not affect the endothermy cost of its Cyclocephalini pollinator. In contrast, Seymour et al. (2009) discovered that the scarabs that pollinated *Philodendron solimoesense* A.C. Sm. (Araceae) did not exhibit thermoregulation inside the floral chambers, thus avoiding the costs of endothermy.

It becomes quite obvious when considering blossoms pollinated by nocturnal scarabs across different plant families that there is remarkable evolutionary convergence towards thermogenicity in phylogenetically distant taxa. Such convergence might have occurred due to the twofold roles that thermogenesis may play as both an odour intensifier and an energetic reward for pollinators (Bernhardt 2000; Seymour et al. 2003, 2009).

In the present study, thermogenicity in *A. crassiflora* was shown to be intermittent. There were two peaks of heat production: one during the female phase and another, slightly longer and more intense, peak during the male phase, between 11.00pm and 12.00am (Figure 5b). These results are not entirely consistent with those of Gottsberger (1989a), who found that the heat production peak of *A. crassiflora* flowers occurred during the female phase between 7.00pm and 8.00pm. This difference may be due to the climatic conditions of the region of the study, in the municipality of Botucatu, in the state of São Paulo. The author pointed out that thermogenesis in *A. crassiflora* seems to be temperature-dependent and that the conditions under which the flowers reach higher temperatures are more likely to occur in northern regions of the Cerrado, such as our study area. The heat production peak in the male-phase flowers of *A. crassiflora* in the Cerrado of Chapada dos Guimarães may therefore be explained by the lower decline in ambient temperature during late night relative to the cooler Cerrados in the state of São Paulo.

Thermogenesis is a common feature of cantharophilous blossoms and also occurs in other Annonaceae genera. Küchmeister et al. (1998) observed thermogenesis events in both female- and male-phase flowers of Amazonian *Anaxagorea* spp., the most basal genus within Annonaceae. The three *Anaxagorea* species analysed in their study show diurnal anthesis and are pollinated by small Staphylinidae and Nitidulidae. In the same study, these authors also detected thermogenesis in two *Duguetia* (Annonaceae) species pollinated by Cyclocephalini. These species present nocturnal anthesis, in accordance with their pollinators' active period, in a two-day flowering cycle, with a long interim between the two nights of anthesis and heat production events in both male and female flowers (Küchmeister et al. 1998).

Regarding the dichogamy observed in *A. crassiflora* in the Cerrado of Chapada dos Guimarães, more male-phase flowers were collected, which reflects the fact that the male phase is longer rather than sampling effort bias (Figure 5a). The short interim phase was accordingly the least sampled in the field (Figure 5a). Unlike the present study, Gottsberger (1989a, 1989b) and Silberbauer-Gottsberger and Gottsberger (2006) did not detect an interim phase in *A. crassiflora* flowers. Long interim phases of approximately one day were found in *Annona* spp. with a two-day flowering rhythm in the Cerrado, such as *Annona coriacea* Mart. and *Annona cornifolia* A. St.-Hil. (Gottsberger 1989a; Silberbauer-Gottsberger and Gottsberger, 2006; Costa et al. 2017), but this was not observed in *A. crassiflora*. The present study is the first to describe an interim phase in *A. crassiflora*, which highlights the role that dichogamy plays in avoiding self-pollination.

Sweet, fruity smells, such as those given off by *A. crassiflora* during anthesis, have been reported in other *Annona* species pollinated by Cyclocephalini, such as *Annona tomentosa* R.E. Fr., *Annona aurantiaca* Barb. Rodr., *A. coriacea* and *A. cornifolia*, all of which are found in the Cerrado (Gottsberger 1989a, 1989b; Gottsberger and Silberbauer-Gottsberger 2006; Mendonça et al. 2008). Similar smells have been described in *Annona* species pollinated by small beetles, such as *Annona squamosa* L., a very economically important species pollinated by Nitidulidae (Gottsberger 1989a; Kishore et al. 2012), and Amazonian species *Annona glabra* L., pollinated by small Chrysomelidae (Gottsberger, 1999).

Curiously, although Gottsberger (1989a) described the floral scent of *A. crassiflora* as 'disagreeable', Gottsberger and Silberbauer-Gottsberger (2006) mentioned further nuances acquired by the fruity bouquet when floral temperature rises, describing it as predominantly 'unpleasant and cyanide-like'. The perception recorded in the present study

was that the background smell that intensifies during thermogenesis is reminiscent of acetone. These discrepancies are the result of the subjectivity of scent perception by researchers, indicating the need to carry out scent extraction and chemical analyses of blossoms to assess their sensorial effects on pollinators and other evolutionary implications.

Plant evolutionary convergence towards the production of fruity floral scents in Cyclocephalini-pollinated angiosperms is worth noting when the floral bouquet of unrelated genera of Annonaceae and other angiosperm families is taken into account. Cantharophilous *Magnolia* species tend to emit fruity scents, as observed in *Magnolia schiedeana* Schltld. and *Magnolia ovata* (St.-Hil.) Spreng., whose scent has been described by Gottsberger et al. (2012) as 'fruit-like, reminiscent of apples and/or cherimoya (*Annona cherimola* Mill.) and melon fruits' (Gottsberger 1989a, 1989b; Dieringer and Espinosa 1994; Gottsberger et al. 2012). Regarding the role of the background acetone or 'cyanide-like' scent, the question arises of whether it plays the role of a sexual pheromone, as suggested by Schatz (1990) when reviewing aroid scent emissions, or deters visitation by less efficient or pillaging visitors, an evolutionary mechanism envisioned in a review by Schiestl and Johnson (2013).

After scent emission draws pollinators close to flowers, visual cues seem to be the ultimate attractant to plant reproductive parts (Pellmyr and Patt 1986; Ervik et al. 1999). Similar to most blossoms pollinated by nocturnal beetles, *A. crassiflora* flowers possess pale corollas, with light yellow inner and outer petals (Pellmyr and Patt 1986; Bernhardt 2000; Gottsberger and Silberbauer-Gottsberger 2006; Gottsberger et al. 2012). In distinct contrast, the outer petals bear semicircular purple spots on their basal half (Figure 4a). The pigment from these spots was immediately solubilised when petals were placed in 90% alcohol. Similar spots have been found in floral chambers from Annonaceae visited not only by nocturnal Cyclocephalini but also by diurnal beetles such as *A. squamosa*, *Anaxagorea dolichocarpa* Sprague and Sandwith, and *Xylopiia aromatica* (Lam.) Mart. (Bernhardt 2000; see fig. 3a in Kishore et al. 2012 for *A. squamosa*; fig. 1b in Gottsberger 2012 for *A. dolichocarpa*; fig. 5d in Aragão et al. 2019 for *X. aromatica*, and fig. 3 in Saravy et al. 2021b). Given the scarcity of knowledge on the interaction between these visual floral signals and the coleopteran sensorial system, one can only speculate about the effect this arrangement (reddish-purple-over-yellow in *A. crassiflora* flowers) has on the perception of beetles.

Unlike the other two Annonaceae species present in the study area, *Cardiopetalum calophyllum* Schltld. and *Xylopiia aromatica* (Lam.) Mart., in which dozens of anthetic flowers occur on each individual every day, relatively few flowers of *A. crassiflora* blossom each day on each tree, rendering the sampling task a more reasonable endeavour. The flower chambers of *A. crassiflora* are semi-open, which allows beetles mobility from flower to flower. Therefore, assessing the visitation rate by counting the number of visited flowers at any given time of anthesis would provide a misleading notion of the total percentage of flowers visited on a tree during one night. The paucity of blossoming flowers on each tree on each night (rarely over 10 flowers) also constrains their collection. For example, by collecting flowers both with and without beetles, we would prevent the floral scent from attracting beetles to the trees and remaining therein. Moreover, beetle

permanence on trees also depends on the presence of shed corollas. Therefore, only flowers with beetles were collected so that we could more accurately estimate the taxonomic composition of flower visitors.

Quantitative data on flower visitors during the nocturnal anthesis of *A. crassiflora* flowers show the prevalence of visitations by Coleoptera, with a residual presence of other orders of Insecta (Figure 6a; Table 1). Despite the extraordinary diversity of the order Coleoptera, it is difficult to draw robust conclusions regarding the specialisation of the relationship between the beetles sampled in the present study and *A. crassiflora* flowers due to undersampling and a lack of research on natural history and taxonomic constraints, especially in the Cerrado (Pinheiro et al. 1998; McKenna et al. 2015; Monné and Costa 2021). Nevertheless, members of only two families of beetles (Melolonthidae and Curculionidae) were present in anthetic flowers (Figure 6c; Table 1). When inferior taxonomic categories are put in perspective, specialisation emerges even more clearly: within these two families, only four species from three genera of beetles were found (Figure 6d; Table 1).

The two identified *Cyclocephala* species differ greatly in their morphology and behaviour from the two weevil species (Table 1). In addition to being present in female and male flowers, both *C. celata* and *C. octopunctata* were found in relatively large numbers inside floral chambers (Figure 6d; Table 1), touching the stigmas and open anthers. In male-phase flowers, *Cyclocephala* individuals coated in pollen were observed (Figures 8b, 9 b–d, 11a). Both species are relatively large and possess dense vestitures (especially *C. celata*, on its ventral surface), to which pollen can adhere (Figure 11a). Regarding the weevil species, *Lydamis* sp. 1 was seen frequently in the field on flower buds during the day, engaged in drilling holes, mating and ovipositing, which indicates that it probably shows only diurnal activity. It is therefore likely that the *Lydamis* sp. 1 individuals collected in anthetic flowers during the night were only sheltering inside them. Furthermore, no pollen loads were detected on *Lydamis* sp. 1 or Molytinae sp. 1. In conclusion, in the Cerrado in our study area, the putative pollinators of *A. crassiflora* were identified as *C. celata* and *C. octopunctata*, which indicates a specialised pollinator–plant relationship (Johnson and Steiner 2000).

A review undertaken by Moore and Jameson (2013) estimated that at least 97 species of Cyclocephalini were associated with flowers of at least 191 plant species from 17 families, especially Magnoliales and monocots. Associations with dicots were also reported therein, but most of them were of destructive rather than symbiotic in nature (Moore and Jameson 2013). Distant families such as Magnoliaceae and Araceae have developed analogous structures that attract and shelter Cyclocephalini, referred to as ‘floral chambers’ in both cases (Gibernau 2003; Gottsberger et al. 2012). Convergent evolution seems to drive not only analogous floral features, such as odour and colour, as previously observed, but also size and shape, even though these characteristics are formatted by different constraints in phylogenetically distant taxa. In Araceae, for instance, the Cyclocephalini-bearing floral chamber is formed by a constriction of the spathe, delimiting a basal space in the inflorescence where beetles remain concealed during anthesis (Gottsberger 1990; Gibernau et al. 1999; Gibernau 2003). In the genus *Magnolia* (Magnoliaceae) and in water lilies (Nymphaeaceae), which belong to the order Magnoliales, flower chambers visited by Cyclocephalini are delimited by the closing of petals (Prance and Arias 1975; Prance 1980; Ervik and Knudsen 2003; Gottsberger 2012).

Among the 15 species of *Cyclocephala* that have been catalogued in the Cerrado, only two were collected in our study area: *C. octopunctata* and *C. celata* (Gonçalves et al. 2020). In the Cerrado, Annonaceae flower chambers with nocturnal anthesis are visited by a relatively constant group of *Cyclocephala* species, regardless of their geographical distance from each other. For instance, *C. atricapilla* is the principal pollinator of *A. crassiflora* and *A. coriacea* in Cerrado areas located in the states of São Paulo, Maranhão, Minas Gerais, Goiás and Mato Grosso and the Federal District (Gottsberger 1989b, 1990, 1994; Oliveira and Gibbs 2000; Silberbauer-Gottsberger et al. 2003; Gottsberger and Silberbauer-Gottsberger 2006; Cavalcante et al. 2009; Paulino-Neto 2014b; Costa et al. 2017).

In the present study, the most abundant *Cyclocephala* species in the Cerrado area of Chapada dos Guimarães collected inside the floral chambers of *A. crassiflora* was *C. octopunctata* (Figures 6d, 7a, b; Table 1), which is also known to be associated with another *Annona* species from the Cerrado, *Annona coriacea* (Costa et al. 2017). The present study provides the first record of *C. octopunctata* as the main pollinator of *A. crassiflora* and the first investigation of the associated pollinator fauna of this plant species in the Cerrado of Chapada dos Guimarães, MT.

The secondary pollinator of *A. crassiflora* in Chapada dos Guimarães, *C. celata*, is very rare in lists of associations between beetles and Annonaceae (Figures 6d, 7c, d; Table 1). However, associations between this scarab and aroids have been described in the literature (Maia et al. 2010; Moore and Jameson 2013). The only record of *C. celata* as a flower visitor of Annonaceae comes from an introduced species that was probably native to Central America (*Annona muricata* L., locally known as *graviola*) in a study performed at a commercial orchard in the state of Pernambuco surrounded by a native fragment of Atlantic rainforest. There are thus far two accounts of *C. celata* as a pollinator of two species of Araceae in Atlantic rainforests in Pernambuco, which is very suggestive of the possibility of cooption of native scarab species by introduced cantharophilous crops, despite their phylogenetically distant relationships (Junqueira et al. 1996; Maia et al. 2010; Parizotto and Grossi 2019). The cooption of native beetle species by introduced cantharophilous plants of economic importance has been reported in one *Annona* hybrid in Australia and oil palms in tropical America (Blanche and Cunningham 2005; Meléndez and Ponce 2016). Hence, the maintenance of local *Cyclocephala* populations through habitat conservation might prove financially beneficial, especially in cases where pollination deficiency causes a reduction in productivity, as observed on *Annona* spp. plantations around the globe (Pinto 2005). Although there is only one dubious available record of *C. celata* occurrence in the Cerrado, the present study provides the first record of this species as a pollinator of an Annonaceae (Gonçalves et al. 2020).

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