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ORIGINAL PAPER

Dietary habits of the giant armadillo (*Priodontes maximus*) in the Brazilian wetlands

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Abstract

Trophic ecology has major implications for understanding species' natural history and functional role in ecosystems. This type of information is key to define resource requirements and constraints for conservation planning, especially for threatened specialist species. Here we describe the items that compose the diet of giant armadillos (*Priodontes maximus*) in the Brazilian wetlands, characterizing their functional role and evaluating if they are true myrmecophages. We sorted 113 fecal samples collected throughout 10 years of monitoring of 29 individuals to identify prey items to the finest possible taxonomic level. Then we estimated the Relative Frequency of Occurrence of each item. The sampling effort was shown to closely represent the expected local prey diversity. Giant armadillos preyed on a diverse array of invertebrates and plants: 23 morphotypes of Isoptera, 50 morphotypes of Hymenoptera, 14 types of seeds, one vertebrate (bone), unidentifiable fragments of Arthropoda, Scarabaeidae fragments, invertebrate eggs, and Acari. All individuals consumed termites (*Cornitermes* sp. and Nasutermitinae) and plant fragments. There was a high variation on the occurrence of ant morphotypes among samples, most being consumed by few individuals. The most consumed ants were *Carebara coeca* and *Atta vollenweideri*, considered crop pests, highlighting armadillo's importance to society through pest control. Fruits were consumed opportunistically by multiple individuals, likely not incidentally as previously hypothesized, and the role of this large mammal as a seed disperser should be further explored. Although giant armadillo's diet is more diverse than expected, the high prevalence of termites and ants confirms its myrmecophagous specialization, making them the largest Neotropical specialist insectivore.

Keywords Cingulata · Trophic Ecology · Myrmecophagy · Dietary specialization · Brazilian Pantanal

Introduction

Trophic ecology has major implications in the understanding of species' natural history and their functional role in ecosystems. That is because species feeding habits are one of the main factors defining their relationship with other organisms and their habitat (Duffy et al. 2007). Furthermore, information on dietary habits can provide key insights into resource constraints and requirements of a species, which are related to their population dynamics, habitat use, and response to habitat degradation, amongst others. Hence, understanding species dietary requirements can aid in

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building more effective conservation plans for threatened species (Dunlop et al. 2017).

Dietary habits can vary according to spatial (e.g., ecoregions along a species distribution) and temporal factors (e.g., seasonality in environmental conditions) that can influence prey availability and individual behavior (Díaz-Ruiz et al. 2013). Hence, the identification of the items that compose a species diet can help deepen the understanding of the relationship between species and their environment and is especially important to understand the biology and ecology of species with broad distributions that are subject to a broad array of environmental conditions (Dunlop et al. 2017)).

The superorder Xenarthra is a basal clade of placental mammals exclusive to the Neotropics composed of sloths, anteaters (Pilosa) and armadillos (Cingulata; Wilson and Reeder 2005). Xenarthrans have low basal metabolic rates that are associated with their specialized low-energy diets. Armadillos, in particular, have previously been classified according to the level of specialization of their diet being separated in four groups: (1) carnivore-omnivore (can consume any type of animal matter as well as many different types of fruit and tubers, *e.g.*, *Euphractus* sp.); (2) fossorial and (3) terrestrial generalist insectivores (consume insects and possibly some plant material, e.g., *Calyptophractus* sp. and *Dasypus* sp., respectively); and (4) ant and/or termite specialists (eat almost exclusively ants and termites, e.g., *Priodontes* sp. (Redford 1985). Nevertheless, because Xenarthra are a generally understudied group, an increasing variation in dietary habits has been described as the number of published studies increased in the past two decades (e.g., Anacleto 2007; Campos et al. 2016; Foster et al. 2017).

The giant armadillo *Priodontes maximus* (Kerr, 1792) is the largest living armadillo and has been classified as an ant and termite specialist, i.e., a myrmecophage (Redford 1985). Previous studies corroborate that termites (Isoptera) are the most common prey of the species, followed by ants (Hymenoptera), but plant fragments and other invertebrates (e.g., Araneae, Blattaria, Coleoptera, Diplopoda and Scorpiones) have also been consumed at small frequencies (Anacleto and Marinho-Filho 2001). The species possess specialized morphological adaptations that enable their myrmecophagous habits such as large scimitar front claws, vermiform tongue and large salivary glands (Carter et al. 2016; Desbiez et al. 2019). Adult giant armadillos can have a body length of up to 1.5 m and weigh up to 60 kg (Carter et al. 2016; Desbiez et al. 2019). However, they are rarely seen in the wild due to their nocturnal, fossorial, and solitary habits, associated with the species naturally low population densities (Silveira et al. 2009; Carter et al. 2016; Desbiez et al. 2020a, c). The species has a wide distribution, occurring in eleven South American countries (Carter et al. 2016). This species is classified as 'Vulnerable' (A2cd) by the Red List of threatened species of the International Union for Conservation of Nature (IUCN; Anacleto et al. 2014) and in Brazil by the Chico Mendes Institute for Biodiversity Conservation (ICMBIO; Chiarello et al. 2015). The main threats to the species are habitat loss and degradation, roadkill, hunting, illegal trade, poisoning, and fires (Chiarello et al. 2015; Desbiez and Attias 2021).

Giant armadillo biology was poorly known until recently, as most studies were based on a relatively small number of individuals (Carter and Encarnação 1983; Encarnação 1987; Anacleto 1997; Pitman et al. 2004; Silveira et al. 2009). However, in recent years, several individuals of the species have been monitored and studied in a location in the Brazilian Pantanal (Desbiez and Kluyber 2013; Desbiez et al. 2020b, a; Luba et al. 2020). This location harbors the highest known population density of the species (Desbiez et al. 2020c). There, giant armadillos have been shown to select mainly areas of closed savanna and forest edges during activity, performing local searches, presumably associated with foraging activities, mostly in closed savannas (Desbiez et al. 2020b; Cullen et al. 2023). Furthermore, stable isotope analysis showed that most giant armadillos have a mixed diet (C3/C4 resources, forests/open areas), but there is a wide variation in resource use by giant armadillos, indicating that there is individual variation in foraging behavior (Magioli et al. 2023).

Although there has been a recent increase in our knowledge of the species' habits and resource use, most of it has been generated through indirect evidence, and the species diet composition has yet to be explored in this region. Furthermore, despite being once considered the most myrmecophagous of armadillos (Redford 1985), specific observations in more recent studies indicate that the diet of this species may be broader than previously described, and that they can feed on seeds and even vertebrates (e.g., cayman eggs; Wallace and Painter 2013; Campos et al. 2016). However, we still lack understanding if these are opportunistically consumed prey or important items in the species diet. Therefore, long-term studies with a broad sampling (with a larger number of individuals and samples) may allow the composition of the species' diet to be reliably characterized, enabling the detection and characterization of seasonal or intrapopulation variations in the species' dietary composition (Trites and Joy 2005). Hence, the aim of the present work is to describe the items that make up the diet of the giant armadillo in the Nhecolândia Pantanal subregion and evaluate if the species is a true myrmecophage as suggested by their morphology and the literature.

Materials and methods

This study was carried out between 2010 and 2021, in a 350-km^2 area that includes ten extensively managed cattle ranches (19°16′60″S, 55°42′60″W) in the Brazilian Pantanal

(Nhecolândia subregion, Mato Grosso do Sul state). The landscape is a mosaic of different habitats that include open grassland, scrub grassland, scrub forest, and semi-deciduous forest. The historical mean temperature is 25.4 °C, climate is classified as semi-humid tropical (Aw), with a hot, rainy season (October to March), and a warm drier season (April to September) during which temperatures may drop due to cold fronts from the South (Alvares et al. 2013). The area lacks watercourses but has permanent lakes and experiences widespread flooding during the rainy season. Traditional extensive cattle ranching is practiced in the area and, overall, anthropogenic threats to biodiversity are low.

Capture and handling

This study was performed under License No. 27587 from the Chico Mendes Institute for Biodiversity Conservation, granting permission to capture, immobilize, and manipulate armadillos, and collect and store biological samples. All procedures followed the Guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016).

The collection of fecal samples for this study was undertaken as part of the Giant Armadillo Conservation Program (GACP), which was set up in July 2010 as a long-term multidisciplinary initiative that uses a broad array of approaches to study the biology and ecology of *P. maximus* to foster its conservation (www.icasconservation.org.br). Capture and handling procedures were accomplished by following the procedures described in Kluyber et al. (2020). Armadillos were captured using an iron funnel trap placed in front of their burrows and then chemically immobilized to enable the collection individual information such as sex, age class and body mass (Kluyber et al. 2020). Fecal samples were collected from 29 radio tagged individuals (12 M, 17 F; Sup. Mat. 1) either during captures or during telemetry monitoring, when fresh feces could be encountered in front of burrows occupied by tagged armadillos. All fecal material was stored in alcohol 70% between the collection date and its sorting.

Sampling of dietary items

Fecal samples were oven dried (at 60 ℃) and weighed. We used a point sampling method (Ciucci et al. 2004) to define random subsamples with a total mass of 8 g from each fecal sample. The point sampling method consists of homogenizing and spreading the fecal sample on a metal tray marked with distance measurements (here, every 0.5 cm; Ciucci et al. 2004). At the top of the metal tray, we placed a sliding device, the point sampling frame, which contains two vertical rods at a 45° inclination in relation to the tray, connected by a horizontal rod. On the horizontal rod, there are five movable metal pins equally spaced (Sup. Mat. 2). While we slide the horizontal rod above the sample, the five movable pins fall at a random order, touching a random part of the sample that is then collected to form the subsample that will be sorted for dietary items. The method assumes a random distribution of the food items in the sample (Ciucci et al. 2004). In order to ensure that subsamples represented the prey diversity contained in each fecal sample, we inspected a species accumulation curve to define the minimum appropriate mass of the subsample (Sup. Mat. 2). In addition, because seeds tend to present a higher mass and surface area than other dietary items, we removed all seeds from the fecal sample before applying the point sampling method to avoid biasing the representativeness of the 8 g subsamples due to the presence or absence of seeds in a given fecal sample. All seeds encountered were sorted and identified with expert's assistance through external morphology. Information regarding types of fruits and dispersal syndromes was based on Lorenzi (1992).

The subsamples were subsequently washed under running water using 0.297 mm and 0.150 mm mesh sieves. We analyzed the processed material with the use of a stereoscopic microscope and separated the items according to identified morphotypes. With the help of expert entomologists and identification keys (Mathews 1977; Baccaro et al. 2015), we classified items to the lowest possible taxonomic level based on anatomical features such as the mandible and head. Nevertheless, item identification was constrained by the integrity of the material found in the fecal samples. We used a precision scale (Shimadzu Analytical Balance AUW220) to weigh the biomass of each identified genus or species to the nearest 0.1 mg.

Prey richness accumulation curve

To evaluate the efficiency of our sampling method, we estimated prey species accumulation curves in relation to the absolute number of fecal samples and to the number of giant armadillo individuals sampled using the function 'specaccum' from Vegan R package (Oksanen et al. 2022). We used the "random" method, with 1000 permutations, weighed by the mass of the evaluated subsample (excluding the mass that was represented by sediments), which generated the species accumulation curve and its standard deviation (Gotelli and Colwell 2001). We also applied the "collector" method to generate the observed species accumulation curve according to our sampling history. Then we fitted a Lomolino model to the "collector" method to allow the comparison between the observed and expected patterns of prey species richness in relation to the sampling effort. Finally, we calculated Chao's extrapolated species richness using the function "specpool" from the same package to estimate the potential number of undetected prey items. This is an incidence-based estimate that uses the frequency of occurrence of the detected prey items, especially the rare items, to estimate an extrapolated species richness (i.e., how many species might not have been detected through our sampling). For this analysis we evaluated the richness of all prey items found in the giant armadillo's diet, including both invertebrates and plants.

Frequency of occurrence

To determine the contribution of each item to the diet of giant armadillos, we used the Relative Frequency of Occurrence (FO), expressed as the number of samples where an item was found (n) divided by the total number of samples and multiplied by 100 (Korschgen 1987). The consumption frequency of each food item (expressed in percentage) was based on the number of samples presenting the category in question. Fecal samples were defined as all fecal pellets produced by a single identified individual in a day. To avoid pseudo-replication while evaluating population patterns, we grouped all fecal samples collected for each of the 29 identified individuals throughout the study period into a single sample.

Results

Prey richness accumulation curve

Our species accumulation curves showed an asymptotic tendency (Fig. 1) indicating that the number of fecal samples (N = 113; Fig. 1a) and individuals (N = 29; Fig. 1c) used in this study closely represents the expected prey diversity in the diet of giant armadillos in the study site. The similarity between the observed and modeled patterns of species accumulation further increases our confidence in our sampling efficiency (Moreno and Halffter 2000); Fig. 1b,d). We encountered 92 prey types in the diet of giant armadillos and estimated an extrapolated prey item richness of up to 114 (SE = 12).

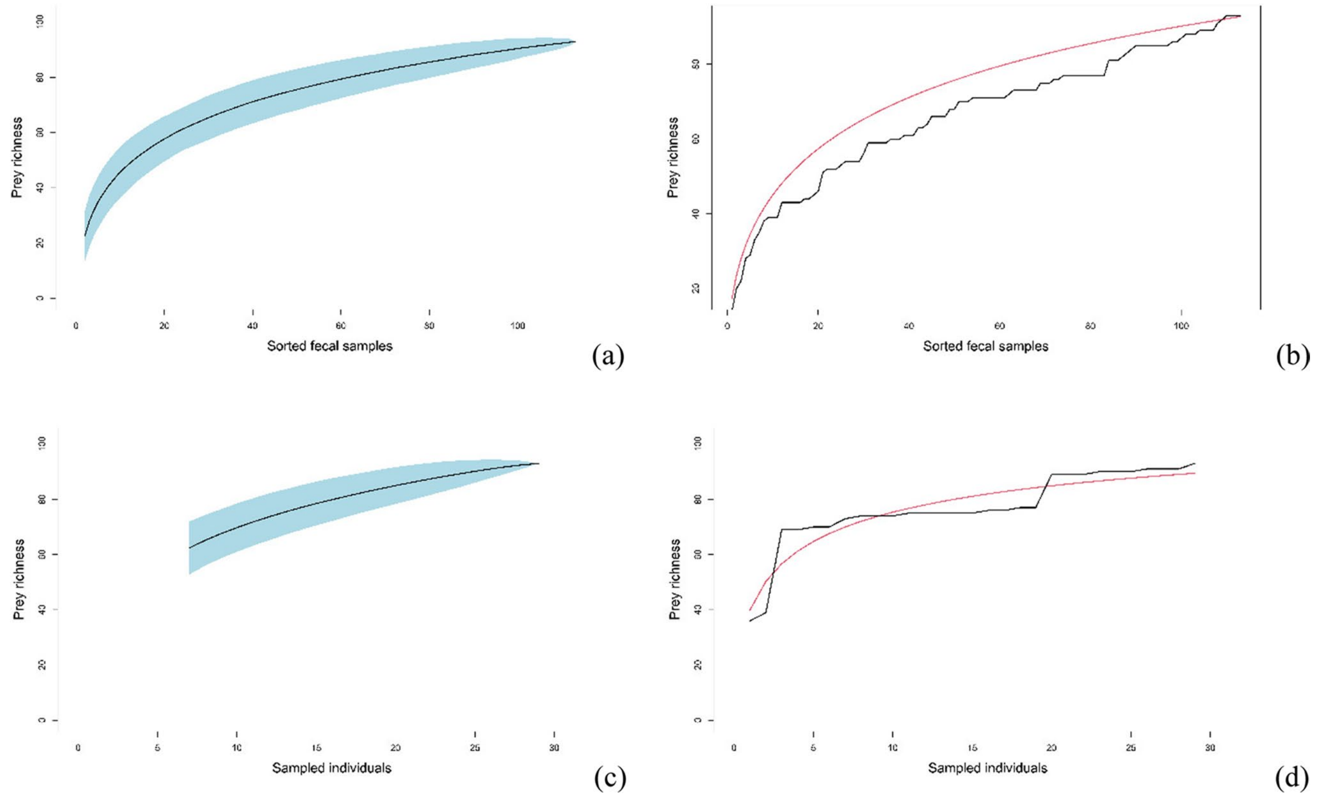

Fig. 1 Species accumulation curve according to sample size. (**a**) Prey species accumulation curve according to the number of fecal samples sorted. (**b**) Collector curve (black) and fitted Lomolino model of estimated species accumulation curve (red) according to the number of fecal samples sorted. (**c**) Prey species accumulation curve according to the number of individual giant armadillos sampled. (**d**) Collector curve (black) and fitted Lomolino model of estimated species accumulation curve (red) according to the number of individual giant armadillos sampled. Light blue bands in figures (**a**) and (**c**) represent confidence intervals. Individual fecal samples are defined as fecal pellets collected from an individual armadillo on a given day, hence multiple samples may have been collected from a single individual. All fecal samples collected for an individually identified armadillo were grouped to generate figures (**c**) and (**d**)

Diet composition and frequency of occurrence

Prey items included 23 morphotypes of termites (Isoptera; Table 1), 50 morphotypes of ants (Hymenoptera; Table 2), 14 types of seeds (Table 3), besides one vertebrate bone, unidentifiable insect fragments (Arthropoda), Scarabaeidae (beetle) fragments, invertebrate eggs and Acari (Fig. 2). Termite parts were mainly composed of cephalic capsules and mandibles of workers and soldiers that allowed the identification of individuals belonging to two families and seventeen genera. Thirteen of the termite morphotypes were identified to the genus level and 7 to the species level (Table 1). For the ants, 20 of the morphotypes were identified to the genus level and 25 to the species level (Table 2).

Termites and plant fragments were part of the diet of all studied giant armadillos (Fig. 2). Nevertheless, there was a high variation in the frequency of occurrence (FO) of termite morphotypes (mean ± SD = 46 ± 36%, range = 3.4 to 100%) and only *Cornitermes* sp. and Nasutermitinae were consumed by all individuals. Meanwhile, ant morphotypes were consumed on average by 18.8% of the individuals. There was a high variation on the occurrence of ant morphotypes among samples (SD = 20.1, range = 3.4 to 72.4%), and many of those were consumed by few individuals (Fig. 2). *Carebara coeca* and *Atta vollenweideri* were the ants with the highest FO, being consumed by 72.4% and 68.9% of the individuals, respectively. All identified seeds were consumed by less than half of the individuals (Fig. 2). On average, each seed morphotype was consumed by 19% of the individuals (SD = 15.1, range = 3.4 to 41.3%). The most common seeds found in the fecal contents were from *Cyperaceae* and another unidentified plant (seed morphotype #11; Table 3). Unidentified insect fragments and beetle fragments were found in the diets of 89.6% and 62% of the individuals, respectively. Invertebrate eggs were also found in the diets of more than half of the individuals (62.1%). In contrast, Acari and vertebrate bones were rarely consumed by individuals (two and one individual, respectively). Finally, even after being washed under running water using fine mesh sieves, on average, 25% of the subsample mass was composed of sediment (soil particles).

Table 1 Frequency of occurrence (FO%) of termite species (Isoptera) encountered in fecal samples ($N = 113$) of individuals ($N = 29$) of giant armadillo *Priodontes maximus*. The frequency of occurrence (FO%) was estimated as the percentage of individuals that consumed each item. Samples collected in the Pantanal wetlands, Mato Grosso do Sul state, Brazil between 2010 and 2021

FAMILY	SUBFAMILY	GENUS	SPECIES	FO%
Termitidae				
		-	-	89.6
		Embiratermes	*Embiratermes festivellus*	65.5
		Silvestritermes	*Silvestritermes euamignathus*	86.2
		Cornitermes	*Cornitermes* sp.	100
			Cornitermes cumulans	72.4
			Cornitermes bequaerti	86.2
		Rhynchotermes	*Rhynchotermes nasutissimus*	58.6
		Termes	*Termes* sp.	37.9
		Spinitermes	*Spinitermes* sp.	6.9
		Dihoplotermes	*Dihoplotermes* sp.	6.9
		Orthognathotermes	*Orthognathotermes* sp.	3.44
		Labiotermes	*Labiotermes* sp.	3.44
		Syntermes	*Syntermes* sp.	17.24
		Microcerotermes	*Microcerotermes* sp.	24.1
		Vaninitermes	*Vaninitermes ignotus*	48.3
		Curvitermes	*Curvitermes* sp.	6.9
	Termitinae			41.4
		Genuotermes	*Genuotermes* sp.	3.44
	Apicotermitinae	-	-	41.4
	Nasutitermitinae	-	-	100
		Nasutitermes	*Nasutitermes* sp. *#1*	96.5
			Nasutitermes sp. #2	13.8
		Angularitermes	*Angularitermes pinocchio*	10.3
Rhinotermitidae				
		Coptotermes	*Coptotermes* sp.	79.3

Table 2 Frequency of occurrence (FO%) of ant species (Hymenoptera) encountered in fecal samples ($N=113$) of individuals ($N=29$) of giant armadillo *Priodontes maximus*. The frequency of occurrence (FO%) was estimated as the percentage of individuals that consumed each item. Samples collected in the Pantanal wetlands, Mato Grosso do Sul state, Brazil between 2010 and 2021

FAMILY	SUBFAMILY	GENUS	SPECIES	FO%
Formicidae				
		-	Formicidae fragments	72.4
	Dorylinae			
		Nomamyrmex	*Nomamyrmex esenbeckii*	62.1
			Nomamyrmex hartigii	6.9
			Nomamyrmex sp.	20.7
		Eciton	*Eciton* sp. #1	6.9
			Eciton sp. #2	3.4
		Neivamyrmex	*Neivamyrmex* sp. #1	37.9
			Neivamyrmex sp. #2	3.4
		Neocerapachys	*Neocerapachys* sp.	3.4
		Labidus	*Labidus* sp.	3.4
			Labidus mars	3.4
	Myrmicinae			
		Carebara	*Carebara coeca*	72.4
		Atta	*Atta vollenweideri*	69
			Atta sexdens	48.3
		-	*Myrmicinae* sp. #1	20.7
		-	*Myrmicinae* sp. #2	17.2
		-	*Myrmicinae* sp. #3	24.1
		-	*Myrmicinae* sp. #4	10.3
		Camponotus	*Camponotus balzani*	17.2
			Camponotus crassus	62.1
			Camponotus melanoticus	10.3
			Camponotus punctulatus	44.8
			Camponotus sp. #1	6.9
			Camponotus sp. #2	10.3
			Camponotus sp. #3	3.4
		Crematogaster	*Crematogaster* sp.	20.7
		Pheidole	*Pheidole* sp1	20.7
			Pheidole fimbriata	10.3
			Pheidole oxyops	6.9
		Wasmannia	*Wasmannia auropunctata*	6.9
			Wasmannia lutzi	3.4
		Cephalotes	*Cephalotes pusillus*	3.4
		Acromyrmex	*Acromyrmex* sp.	31
		Pogonomyrmex	*Pogonomyrmex* sp.	24.1
		Mycetomoellerius	*Mycetomoellerius* sp. #1	20.7
			Mycetomoellerius sp. #2	10.3
		Strumigenys	*Strumigenys eggersi*	3.4
		Solenopsis	*Solenopsis* sp.	3.4
	Ponerinae			
		Odontomachus	*Odontomachus meinerti*	13.8
	Dolichoderinae			
		Forelius	*Forelius brasiliensis*	13.8
		Linepithema	*Linepithema* sp.	3.4
		Dorymirmex	*Dorymirmex brunneus*	10.3
	Pseudomyrmecinae			
		Pseudomyrmex	*Pseudomyrmex gracilis*	37.9
			Pseudomyrmex acanthobius	6.9
	Paraponerinae			

Table 2 (continued)

FAMILY	SUBFAMILY	GENUS	SPECIES	FO%
		Paraponera	*Paraponera clavata*	3.4
	Ectatomminae			
		Ectatomma	*Ectatomma tuberculatum*	3.4
			Ectatomma planidens	3.4
			Ectatomma edentatum	3.4
	Dorylinae			
		-	*Dorylinae* sp. #1	3.4
		-	*Dorylinae* sp. #2	31

Table 3 Frequency of occurrence (FO%) of plant morphotypes encountered in fecal samples ($N=113$) of individuals ($N=29$) of giant armadillo *Priodontes maximus*. The frequency of occurrence (FO%) was estimated as the percentage of individuals that consumed each item. Samples collected in the Pantanal wetlands, Mato Grosso do Sul state, Brazil between 2010 and 2021

FAMILY	GENUS	SPECIES	TYPE OF FRUIT	DISPERSAL SYNDROME	FO%
Rubiaceae					
	Alibertia	*Alibertia* sp.	berry	zoochoric	31
Annonaceae					
	Annona				
		Annona sp. #1	syncarp	zoochoric	10.3
		Annona sp. #2	syncarp	zoochoric	6.9
Malpighiaceae					
	Byrsonima	*Byrsonima orbignyana*	drupe	zoochoric	13.8
Cyperaceae					
		Cyperaceae sp. #1	achenes		41.4
		Cyperaceae sp. #2	achenes		37.9
Meliaceae					
	-	*Meliaceae* sp.			3.4
-					
		Seed #2			24.1
		Seed #8			3.4
		Seed #9			27.6
		Seed #10			3.4
		Seed #11			41.4
		Seed #12			6.9
Plant Fragments					100

Discussion

The dietary composition described in this study was based on the largest number of fecal samples ever collected for giant armadillos in a single location. Based on this comprehensive sampling scheme we identified that termites were the prey type most broadly consumed by giant armadillos in the Pantanal wetlands (Fig. 2). In particular, termites from the genus *Cornitermes* and from the subfamily *Nasutitermitinae,* which were found in samples from all individuals. This predominance of termites corroborates the observations made by (Anacleto and Marinho-Filho 2001) for giant armadillos in the Cerrado, a savanna ecoregion neighboring the floodable Pantanal wetlands. Nevertheless, in another area of the Cerrado savanna, (Anacleto 2007) found that ants were the most common item consumed by individuals, being present in all samples. Redford (1987) states that most myrmecophages eat ants opportunistically and hence, this difference could be due to differences in ant availability among localities. Furthermore, ant abundance in local invertebrate fauna tends to increase with habitat dryness (Pisarski 1978 *apud* Redford 1986), which could explain the different patterns of ant prevalence in the diet of individuals occupying savannas with different hydrological patterns, such as the Cerrado and the Pantanal.

The termite *Cornitermes* sp. counts with both chemical and mandibular defenses, however those seem ineffective in preventing their predation by giant armadillos, which have

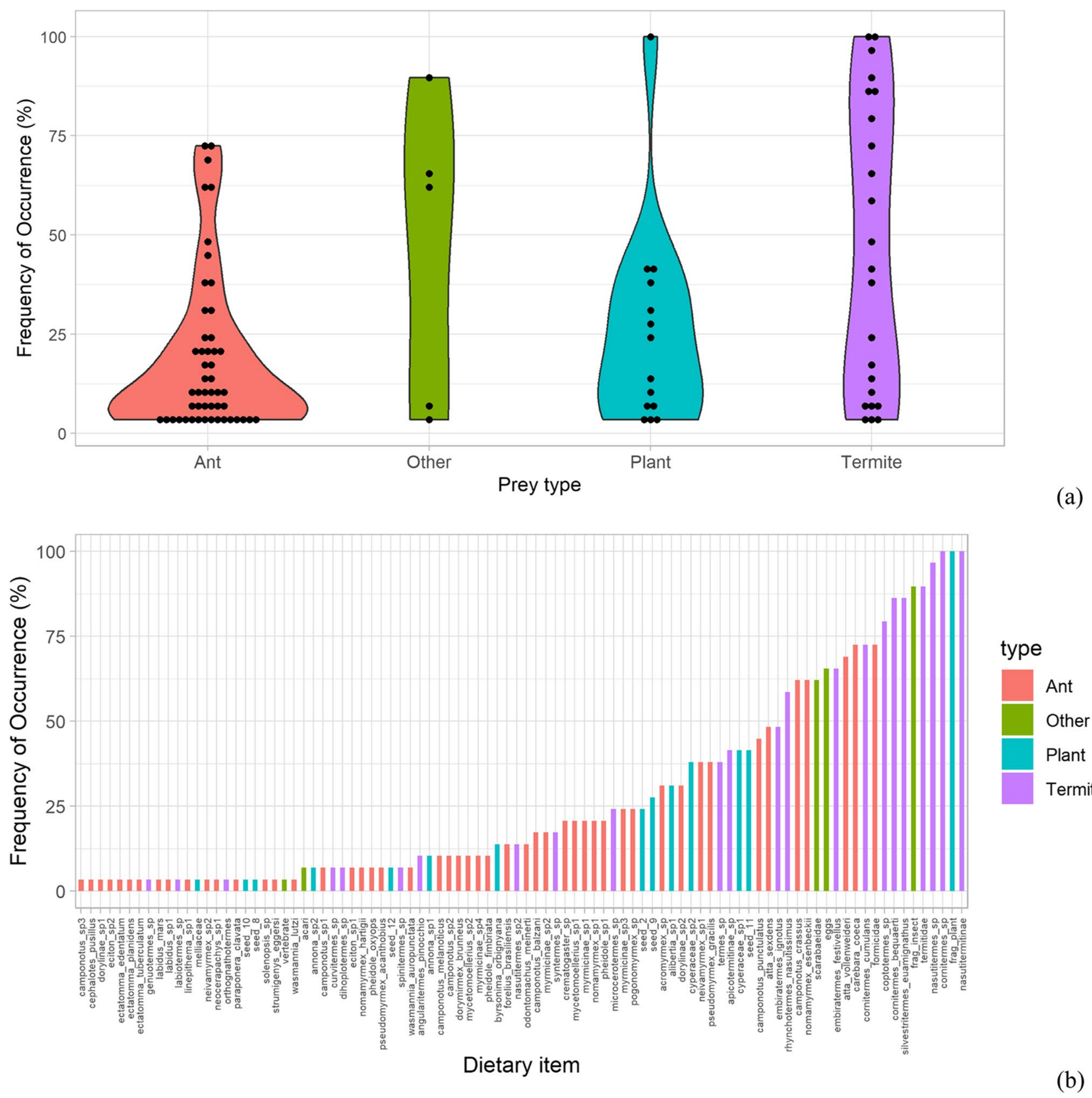

Fig. 2 Frequency of occurrence of each prey type (**a**) and of the items (**b**) identified in the giant armadillo (*Priodontes maximus*) diet. Prey items are color coded according to their type: ants (orange), termites (purple), plant seeds and fragments (turquoise blue), and other (encompassing vertebrate fragments, insect fragments, Scarabaeidae, invertebrate eggs and Acari; green). Patterns based on 29 individuals (113 samples) collected between 2010 and 2021 at Baía das Pedras ranch, Mato Grosso do Sul, Brazil

their back covered by a carapace and their ventral portion covered by relatively thick skin (Desbiez et al. 2019). Termite mounds built by the genus *Cornitermes* are abundant in the Cerrado savanna and are known for having a very hard consistency (Redford 1985). Hence, giant armadillo's morphological adaptations, such as their large scimitar front claws, developed musculature, elongated snout, vermiform tongue and large salivary glands are key to their myrmecophagous feeding habits (Carter et al. 2016; Desbiez et al. 2019).

Due to *Cornitermes* mound's structure and size, they can harbor other species in search for shelter from predators and unfavorable thermal conditions, contributing to the increase in invertebrate richness in the areas where they occur (Redford 1984; Gallego-Ropero et al. 2013; Marins et al. 2016). Over 200 species of termites and ants have been recorded inside *Cornitermes* mounds (Redford 1984; Gallego-Ropero et al. 2013). The cohabitation of termite mounds by multiple species could explain the pattern observed here where almost half of the prey species, particularly ants, were consumed at low frequencies (< 30%) by the giant armadillo (Fig. 2). These rarer prey species could have been cohabitating nests of preferred prey species and been eaten incidentally. Giant armadillos are guided mainly by chemical signals and forage by breaking into colonial insects' nests with their fore claws and inserting their sticky tongue in the natural cavities of the colonies, hence, any insect inhabiting the colony and within reach, could be consumed.

All ant morphotypes found in the fecal samples were consumed at relatively lower frequencies when compared to termites. The ant species with the highest frequency of occurrence in individuals' diets, *Carebara coeca*, is one of the most common hypogeic ant species in the study region, being encountered in both flooded and non-flooded areas (Lange et al. 2008). *Carebara* ants are very small ants with massive recruitment that are found in the leaf litter of forested areas (Fernández 2004; Baccaro et al. 2015). Although *Carebara*'s common occurrence in the biome could suggest an opportunistic feeding behavior by giant armadillo's, it is worth highlighting that ants of the genus *Solenopsis* are found even more frequently in the leaf litter (Lange et al. 2008) but were only consumed by one of the studied giant armadillos. The second most common ant species found in giant armadillos' feces was *Atta vollenweideri*. This is a fungus growing species that uses grass for its gardens. *Atta* nests are built in the ground and can have several underground chambers, distributed at a depth of up to eight meters. The excavation and cleaning of their nests generates a conspicuous accumulation of dirt around the colony up to two meters high (Baccaro et al. 2015), which could facilitate their detection by predators such as the giant armadillo.

Some of the termite species most commonly consumed by giant armadillos, such as *Cornitermes* spp. And *Nasutitermes* spp., have been classified as potential pests in South America affecting mainly sugarcane, rice and eucalyptus plantations (Constantino 2002). Similarly, ants of the genus *Atta* cause considerable economic damage, affecting agriculture and livestock in different regions of the Americas by cutting large amounts of plant biomass in pasture areas, forests, and commercial crops (Baccaro et al. 2015). Although giant armadillos select mainly native savanna vegetation (Desbiez et al. 2020b), they have been reported to use eucalyptus stands in Mato Grosso do Sul state (pers. obs.), and pastures and cropland edges near Emas National Park, in Central Goiás state (Silveira et al. 2009). Therefore, giant armadillos provide an important benefit to society (i.e., ecosystem service; Pascual et al. 2017; Vale et al. 2023) by controlling ant and termite populations that can act as pests in crops and plantations.

Redford (1987) proposes that if ants and/or termites compose more than 91% of the diet of a species (either considering the percent volume or percent occurrence) it can be classified as a specialized myrmecophage. The results encountered here are congruent with the patterns observed in previous studies, with a high prevalence of termites and ants in giant armadillo's diet (Anacleto and Marinho-Filho 2001; Anacleto 2007), confirming giant armadillo's myrmecophagous dietary specialization (Redford 1985). Giant armadillos are likely one of the armadillos with the most specialized dietary habits, with a myrmecophagous diet comparable to some of the most specialized insectivorous mammals of the tropics such as aardvarks, pangolins and aardwolves (Cooper and Skinner 1979; Taylor et al. 2002; Panaino et al. 2022). Nevertheless, the giant armadillo's diet is composed by a relatively high diversity of ant and termite species (73 prey morphotypes), while the African aardvarks and aardwolves consume a smaller diversity of prey, 15 and 7 prey morphotypes, respectively (Cooper and Skinner 1979; Taylor et al. 2002; De Vries et al. 2011). Whether this is related to prey availability, dietary preferences or other factors should be further explored in future comparative studies.

The consumption of fruits by giant armadillos is another point that should be further explored in future studies. The consumption of fruits by the species has seldom been recorded in previous studies and was generally recorded for a single individual. One individual was recorded with *Ficus* sp. seeds in its stomach in the Bolivian Amazon (Wallace and Painter 2013), while another one presented Annonaceae seeds in its feces in Central Brazil (Anacleto and Marinho-Filho 2001), and another one was found with 300 seeds of an unidentified plant in its stomach in the dry forests of Colombia (Barreto et al. 1985). Hence, it was not possible to define if this was part of the species dietary habit, an opportunistic behavior, or due to individual personality traits. Our extensive sampling effort allowed the detection of multiple seed morphotypes in the species diet, being some of those found in almost half of individual's diet (e.g., *Cyperaceae* and seed #11). This shows that the consumption of seeding fruits by giant armadillos is more common among individuals than previously known.

Sedges (*Cyperaceae*) have very small seeds and may be found growing in almost all environments, with many species being associated with wetlands. Hence, the high frequency of occurrence of Cyperaceae in the samples indicates that giant armadillos are also feeding in wetlands. This corroborates previous stable isotope analysis performed with this population that indicated that individuals consumed resources from both open and closed vegetation areas (Magioli et al. 2023). Nevertheless, due to their reduced size, the consumption of this seed could be given incidentally while feeding on other food sources. Many of the other seed morphotypes found in the feces of giant armadillos were only found in samples from a restricted period of the year, most likely during the peak fruiting season of the plant. For example, *Annona* sp., which has its peak fruiting season from November to February, was only found in fecal samples collected in the months of December and January (Supplementary Material 3). This suggests that fruit consumption is not incidental and that individuals explore this type of resource opportunistically. Given giant armadillo's large body mass and the low caloric value of their main prey, the opportunistic consumption of seasonal fruits could optimize energy intake during their short period of above ground foraging activity (~ 5 h/day of which 77% is dedicated to foraging; Desbiez et al. 2021; Magioli et al. 2023; Cullen et al. 2023). Finally, due to their high movement rates (Desbiez et al. 2020a) and potential to carry seeds over long distances, the role of the large-sized giant armadillo as seed dispersers should be further explored.

The in-depth comprehension of the giant armadillo's natural history, including its dietary habits, can yield crucial insights into its role in ecosystem functioning. Armadillos stand out for providing an unparalleled array of ecosystem services amongst Brazilian mammals (Vale et al. 2023). Their presence can provide diverse benefits to humans, encompassing ecosystem engineering, bioturbation, nutrient cycling, disease sentinelling, pest and disease controlling, carrion control, nutrient transporting, and seed dispersal (Desbiez and Kluyber 2013; Rodrigues et al. 2020; Vale et al. 2023). Notably, giant armadillos can provide almost all these ecosystem services, perhaps except for carrion control. Nevertheless, despite the ecological significance of this naturally rare species, giant armadillos face numerous threats, and their population is experiencing a decline, warranting a Vulnerable classification by the IUCN. Here we showed that giant armadillos have established trophic interactions with a diverse array of invertebrates and plants. Hence, the loss of one of South America's largest specialist insectivore poses a risk to key interactions and ecosystem services, emphasizing the potential ramifications of the declining giant armadillo population in South America.

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Data availability The datasets generated and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval This study was performed in line with the guidelines of the American Society of Mammalogists (ASM) concerning the use of wildlife in research (Sikes et al. 2016) and was conducted under license #53798-10 granted by Chico Mendes Institute for Biodiversity Conservation (ICMBio).

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