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ORIGINAL ARTICLE

Uncovering the vertebrate scavenger guild composition and functioning in the *Cerrado* biodiversity hotspot

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Abstract

Scavenging is widespread among vertebrates, being very important for maintaining certain ecosystem functions. Despite this, the scavenger communities remain poorly known in some biomes, especially in the Neotropics. Our main objective was to describe for the first time the scavenger community and identify the factors affecting scavenging efficiency in the Brazilian *Cerrado*. We analyzed the effects of vegetation cover, time of carcass placement and carcass weight, on scavenger species richness, individual abundances, carcass detection and consumption times, and carcass consumption rate. We monitored 11 large and 45 small carcasses using automatic cameras. We documented a total of 19 vertebrate scavenging species, four species of vultures and 15 facultative scavengers. We found that carcass size was the most important factor affecting the scavenger assemblage and consumption patterns. Large carcasses were dominated by vultures, whereas small carcasses were consumed mainly by facultative scavengers. We also found differences between large and small carcasses in all carcass consumption variables except for detection time. However, we did not find an effect of vegetation cover or time of carcass placement on scavenging patterns. The negligible role of mammals and non-raptor birds in large carcasses is also noteworthy, probably due to the consumption and foraging efficiency of the vultures, and the more frugivorous habits of the mesocarnivores. Our results show a highly diverse and efficient scavenging vertebrate community in the Brazilian *Cerrado*, and the need to preserve them in the face of the significant habitat transformations suffered by this biodiversity hotspot.

Abstract in Portuguese is available with online material.

KEYWORDS
biodiversity, camera trapping, carcass removal rate, carrion, Cathartidae, Neotropical vultures, tropical savanna

1 | INTRODUCTION

The role of scavenger communities (i.e., carrion-eaters) has been underestimated until recently in ecological studies, even though they regulate important ecological processes and ecosystem functions (e.g., accelerating nutrient cycle, structuring food webs) (Ogada et al., 2012; Sebastián-González et al., 2016) and therefore provide important ecosystem services (e.g., decreasing disease transmission and infection rates) (DeVault et al., 2016; Donázar et al., 2016; Ogada et al., 2012). Among terrestrial vertebrate scavengers, we can differentiate two major functional groups: obligate scavengers (i.e., vultures) and facultative scavengers. Vultures are totally dependent on carrion, while facultative scavengers include other resources besides carrion in their diet, having a gradient in the propensity to scavenge, with species that scavenge very frequently to others that only scavenge occasionally (Allen et al., 2014; Ruxton & Houston, 2004). Thus, not all scavengers have the same role within the scavenger guild. Vultures and large mammalian carnivores have a great influence on the structure of scavenger communities through competition and facilitation processes (Allen et al., 2015; Sebastián-González et al., 2016). Consequently, scavenger communities are organized on a non-random basis (Selva & Fortuna, 2007), being governed by complex factors, such as the presence of key species, the differential predictability of the carcass, and environmental conditions (Moleón et al., 2015; Sebastián-González et al., 2016, 2020).

Carrion consumption by vertebrate scavengers is influenced by several factors. Some are intrinsic to the carcass, such as carcass origin (cause of death) or the species to which it belongs (Arrondo et al., 2019; Selva et al., 2005). Also, large carcasses allow for a greater richness of scavengers, in addition to influencing carcass consumption rate (Moleón et al., 2015; Olson et al., 2016; Sebastián-González et al., 2013). Other factors that influence scavenging patterns are directly related to the presence of specific scavenger species (Gutiérrez-Cánovas et al., 2020). Scavenging birds have some adaptations that often make them more efficient than mammals at locating carrion (Houston, 1979; Ruxton & Houston, 2004; Selva et al., 2005). In addition, within avian scavengers, vultures consume larger amounts of carrion biomass and at higher rates than facultative scavengers due to their adaptations for a scavenging lifestyle (e.g., soaring flights and high visual acuity), so communities in which vultures are present have a high scavenging efficiency (Hill et al., 2018; Morales-Reyes et al., 2017). It is also important to highlight the role of large carnivores since they can limit the access and availability of carrion to other scavengers by playing the role of dominant scavengers in the community, eating large amounts of carrion at very high rates. However, large predators can also provide carrion by killing prey and leaving remains available to other scavengers and by facilitating access to the interior of the carcass by opening it (Allen et al., 2014; Hunter et al., 2007; Selva et al., 2005).

There are also external factors that affect the use of carcasses by scavengers, such as alternative resource availability, seasonality in carrion supply, or habitat structure (Inagaki et al., 2020; Moleón et al., 2015; Ruzicka & Conover, 2012). However, the role of vegetation cover in carcass consumption patterns has been little studied (but see Pardo-Barquín et al., 2019; Stiegler et al., 2020). Dense vegetation cover may influence those scavengers who rely exclusively on visual cues to find carrion, like most avian scavengers, making them unable to locate and access carcasses (Bamford et al., 2009; Ogada, Torchin, et al., 2012). Conversely, non-avian scavengers might be able to find carcasses even in areas with high vegetation cover because they can rely on both visual and olfactory cues (Arrondo et al., 2019; Moleón et al., 2019).

The *Cerrado* biome, also called Brazilian savanna, is one of the largest biodiversity hotspots on the planet (Myers et al., 2000). It is the largest extension of savanna in South America, being the second largest biome in Brazil after the Amazon and the world's richest savanna, with more than 7000 species of vascular plants, around 200 species of mammals and more than 800 species of birds (Klink & Machado, 2005; Myers et al., 2000). In recent decades, it has undergone severe transformations and many of the habitats found in this ecoregion have been converted to pastures and agricultural areas (Strassburg et al., 2017).

Despite the enormous biodiversity hosted in the Brazilian *Cerrado* and the great impact it is currently suffering due to habitat destruction, the role of certain guilds in this area, such as scavengers, is still unknown. In the *Cerrado*, there are five of the seven species of the New World vultures (Cathartidae): turkey (*Cathartes aura*), lesser yellow-headed (*C. burrovianus*), greater yellow-headed (*C. melambrotus*), American black (*Coragyps atratus*), and king (*Sarcoramphus papa*) vultures. A characteristic feature of some of these vulture species is their developed sense of smell, as they have highly developed olfactory bulbs, which is not found in any of the Old World vulture species (Potier et al., 2019). This ability, together with the potential to fly great distances with little energy expenditure (Duriez et al., 2014), means that New World vultures are especially efficient at locating carrion even when vegetation is dense. Thus, they may be the main scavengers in some areas of the Neotropics, although this has yet to be investigated (Houston, 1985, 1988; Mallon et al., 2013). In addition to vultures, this biome holds many potential facultative scavengers such as jaguars (*Panthera onca*) and pumas (*Puma concolor*), which might also supply the scavenger community with carrion by killing their prey. Furthermore, the *Cerrado* also has many potential scavengers such as medium-sized mammals (e.g., ocelots, *Leopardus pardalis*, and hoary foxes, *Lycalopex vetulus*) and many raptor species (e.g., southern caracaras, *Caracara plancus*, and roadside hawks, *Rupornis magnirostris*) (Dénes et al., 2017; Lima, 2009).

The main goal of this study is to characterize the vertebrate scavenger community and scavenging patterns at carrion resources in the Brazilian *Cerrado*, as well as to determine the main factors influencing them. Our general hypothesis is that resource size and its spatiotemporal distribution influences the structure of the scavenger guild and the consumption patterns. First, we predict that community composition will vary among carcasses with different sizes, resulting in richer communities in larger carcasses and we expect higher consumption rate and lower detection time for larger carcasses (Travis L. DeVault et al., 2004; Moleón et al., 2015; Olson et al., 2016). Second, we test whether vegetation cover influences scavenging patterns, predicting that carcass detection time will be longer in areas with greater vegetation cover. Third, we assess the effect of time of day (morning vs afternoon) of carcass placement. We predict that carcasses deployed during the daytime will be detected and consumed faster because avian scavengers are diurnal and have high scavenging efficiency (Butler & du Toit, 2002; Olson et al., 2016; Selva et al., 2005). We discuss the importance of this scavenger community in the context of conservation, focusing on the transformation that this biome is undergoing and the potential threats to its scavenger species.

2 | METHODS

2.1 | Study area

The study was conducted in the surroundings of the *Nascentes do Rio Parnaíba* National Park, located in the state of Piauí (Brazil), in the north-eastern Brazilian *Cerrado* (Figure 1). The *Cerrado* biome is composed of woodlands, savannas, grasslands, and gallery and dry forests (Klink & Machado, 2005). The study area hosts a complex and diverse vegetation, with up to 5 different vegetation configurations: *cerrado sensu stricto*, floodplains, *cerradão*, gallery forest, and *carrasco* (Ribeiro & Walter, 1998). There is a great plant diversity in the area, from herbaceous species to fruiting tree species like *burití* (*Mauritia flexuosa*) or *puçá* (*Mouriri pusa*). In the last two decades, native vegetation cover in the park and surrounding areas has decreased due to increased anthropogenic activities—largely as a result of family farming and land conversion to monoculture and pasture. Fires (both anthropogenic and natural) are also an increasing threat to the native vegetation (Klink & Machado, 2005). In our study area, the main activity is extensive livestock farming (mainly cattle and goats). There are no paved roads in this area and within the park, only a few dirt roads generally with private access.

2.2 | Study design and data sampling

We studied carcass consumption patterns by the community of vertebrate scavengers during November 2018. We placed two types of fresh carcasses differing categorically in size: (1) large, goat carcasses weighing between 20 and 40 kg (n = 11)and (2) small, entire chickens or chicken parts weighting between 0.075 and 2 kg (n = 45). All

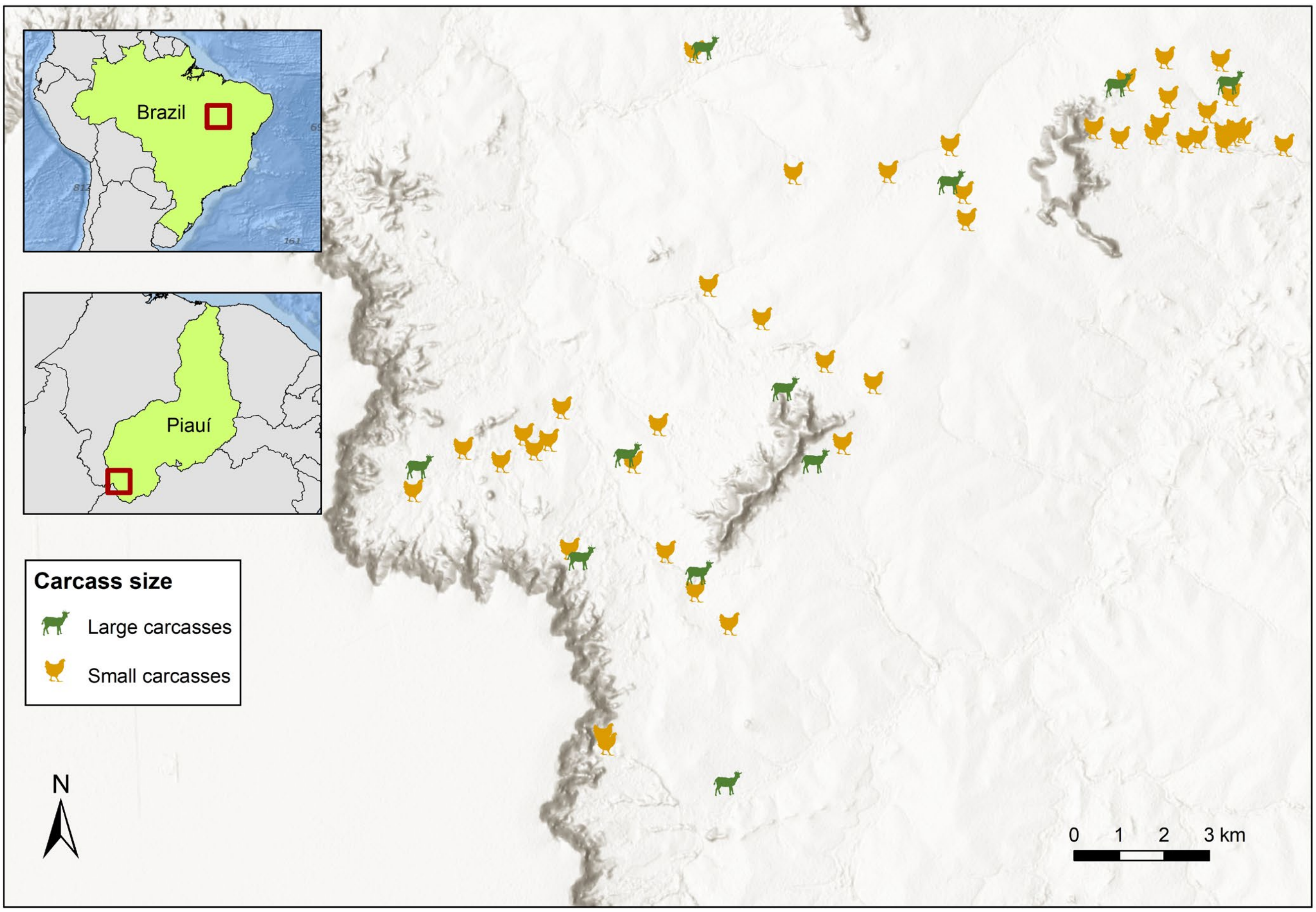

FIGURE 1 Map of the study area in the Brazilian *Cerrado*, in the state of Piauí (Brazil). We show the locations of 56 monitored carcasses (11 large and 45 small)

carcasses were weighted prior to placement, and carcass weight was also included as a continuous variable in all analyses (more details below and in the statistical analysis section). Carcasses were placed randomly within our study area. Large carcasses were placed at least 1.5 km apart to maximize independence between samples (Morales-Reyes et al., 2017). The minimum distance between small carcasses was 150 m; thus, we analyzed whether there was spatial autocorrelation among samples for all response variables subsequently used in the analyses: richness, abundance, consumption time, consumption rate, and detection time, and for the residuals of the models, using the *Moran.I* function in the *ape* package (Paradis et al., 2015), and we confirmed their spatial independence (for more details, see Table S1). Also, we constructed the species accumulation curves for large and small carcasses using *accumresult* function in the *BiodiversityR* package (Kindt, 2016), which showed us that the sampling effort had been sufficient to identify all vertebrate scavenger species (Figure S1). Carcasses were fixed to the ground by placing pickets or by tying them with ropes to trees or shrubs to prevent the scavengers from displacing them from the camera focus.

Carcasses were monitored using automatic cameras (Browning Strike Force pro HD) activated by movement. We placed cameras 5–10 meters from carcasses. Two cameras were placed in front of each carcass. One camera was programmed to take two pictures every 30 seconds and the other to record a video of one-minute length every two minutes in case there was movement. Cameras were programmed to work 24 hr a day and were maintained until carcasses were completely consumed. A carcass was judged totally consumed when only the skin and skeleton were left (Blázquez et al., 2009; Moleón et al., 2015; Sebastián-González et al., 2016). Only one of the small carcasses was not completely consumed (80% consumed), while one of the large carcasses was not monitored until the end of its consumption due to camera failure. Because of this, these two carcasses were excluded from the consumption time and consumption rate analyses. A species was considered a scavenger when they were clearly detected eating carrion in at least one camera. First, we checked the photographs to identify all the consumers in each of the carcasses. Second, we visualized the videos to avoid possible failures in species detection or identification. All vulture species were considered obligate scavengers. Facultative scavengers were classified into four categories: other raptors, other birds, mammals, and reptiles (see Table S2). The amount of biomass consumed by invertebrate scavengers and decomposers was insignificant as no activity was observed even in carcasses that took longer to be consumed, probably due to the high temperatures that dried carrion, so it was not considered in the analyses.

We first calculated two variables to describe the scavenging patterns by species and taxonomic groups: "percentage of visited carcasses" (i.e., proportion of carcasses that were consumed by each species) and "feeding time" (i.e., time that each scavenger species spent eating carrion at each monitored carcass). To determine the "feeding time" by species, we calculated the time elapsed between one image in which the species appeared and the next in which it was also present. If the time between these images was less than two minutes, it was assumed that the species had been feeding all that time between photographs, so duration of different feeding occasions was summed. If the time between pictures was more than two minutes, it was assumed that the species had stopped feeding and feeding time was not added as we considered that they were separate feeding events.

Then, we calculated five more variables describing the scavenger community and the scavenging efficiency that were used as response variables in our models. We used two response variables related to the scavenger community: (i) "richness" (i.e., number of scavenger species detected consuming carrion in each carcass) and (ii) "abundance" (i.e., maximum number of unequivocally different individuals of all scavenger species, by identifying the highest number of individuals appearing simultaneously on an image). We also measured three more response variables related to scavenging efficiency: (iii) "detection time" (i.e., time elapsed since carcass was placed until the first consumer was recorded); (iv) "consumption time" (i.e., time elapsed since carcass was available until it was fully consumed); and (v) "consumption rate" (i.e., kilograms of carrion consumed per hour by dividing the carrion biomass divided by consumption time).

We considered predictor variables concerned with carcasses that could influence consumption patterns: (i) "carcass weight," measured weight in kg of the carcass placed (i.e., 0.075–40 kg); (ii) "time of carcass placement," classified in "morning" (from sunrise to 12:00 hr) and "afternoon" (from 12:00 hr until sunset); and (iii) "vegetation cover," determined by the approximate percentage of surface area covered by trees and shrubs within a 5 m radius around the site where the carcass was placed, indicating how visible the carcass was from the sky (i.e., for avian scavengers). We also considered one more explanatory variable related to the scavengers: (iv) "detector group," which refers to the olfactory ability of the species that detected the carcass. Due to the difficulty of comparing the sense of smell of the different taxa, we established the following groups: birds with high olfactory capacity, birds with low olfactory capacity, mammals, and reptiles (see Table S2 for details at species level) (Gilbert & Chansocheat, 2006; Halpern, 1992; Moulton, 1967).

2.3 | Statistical analyses

We tested whether there were differences in variables related to the scavenger community and scavenging efficiency between large and small carcasses. To do so, we used univariate generalized linear models (GLMs) to analyze the influence of carcass type on (1) scavenger richness, with a Poisson distribution (log link function), and (2) abundance, (3) detection time, (4) consumption time, and (5) consumption rate, the four of them rounded to achieve a better fit of the residues and fitted to a negative binomial distribution (log link function).

Because the consumption patterns differed between the two carcass types (see Results), we performed one-predictor GLMs for large carcasses and multivariate GLMs for small carcasses separately to address our last two hypotheses on the influence of "vegetation cover" and "time of carcass placement" on consumption patterns. Thus, we used as response variables: (1) "richness," (2) "abundance," (3) "detection time," (4) "consumption time," and (5) "consumption rate" using the same distributions and link functions as in the initial univariate GLMs. For these models, we used as explanatory variables: "carcass weight," "time of carcass placement," and "vegetation cover." Furthermore, because the olfactory capacity of the species is important for detecting the carcass for the first time, when our response variable was "detection time," we also included the "detector group" as an explanatory variable. No interactions were included in any model. For GLMs, we used the *glm* function in the *lme4* package (Bates et al., 2007). The selection of models was based on Akaike's information criteria for small sample sizes (AICc). We explored all alternative models using the function *dredge* in the *MuMIn* package (Bartoń, 2019). Only models with an ΔAICc <2 (i.e., top-ranking models) were considered (Burnham & Anderson, 2002). We calculate the deviance explained (D^2) by the top-ranking models with an ΔAICc <2 using the formula D^2 = (null deviance − residual deviance)/null deviance × 100 (Burnham & Anderson, 2002). For multivariate GLMs (i.e., small carcasses models), when we got more than one candidate model, we calculated model-averaged coefficients using the *model.avg* function in the *MuMIn* package (Bartoń, 2019). We considered that a predictor variable had statistical support in a model when its confidence interval did not contain the value 0. All analyses were run in R 3.3.3 (R Core Team, 2013).

3 | RESULTS

3.1 | Scavenger community

Overall, we detected 19 vertebrate scavenger species (Figures 2 and 3; Table S2). We identified four species of obligate scavengers (turkey, lesser yellow-headed, American black, and king vultures) and 15 facultative species, including five species of other raptors, five species of mammals, three species of reptiles, and two species of other birds. All species within the vertebrate scavenger guild are listed as Least Concern except the maned wolf (*Chrysocyon brachyurus*), listed as Near Threatened. We also detected some species whose current population trend is decreasing at the global scale, including vultures, other raptors, and mammals (Table S2).

3.2 | Carcass consumption patterns

Most of the carcasses (98.2%) were totally consumed by vertebrates. Considering all carcasses together, the most frequent scavenger species were turkey vultures (48.2% of visited carcasses), followed by the southern caracara (46.4%) and the king vulture (33.9%; Figure 3). Vultures were the first detectors in 41% of carcasses, followed by other raptors (19.6%). Turkey vultures were the most common first detector species (30.4% of carcasses), followed by the southern caracara (10.7%) (Figure S2).

Large carcasses (i.e., goats) were consumed by six species, all of them raptors. We recorded at least three of the four vulture species

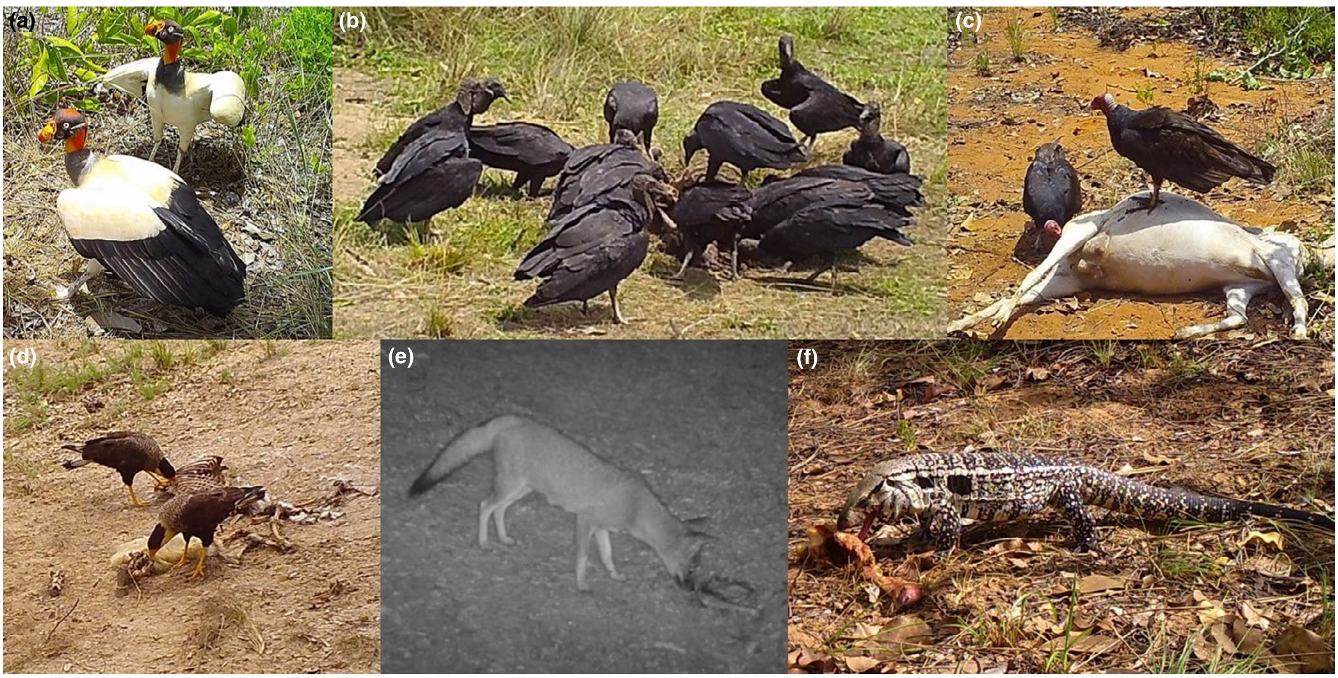

FIGURE 2 Images of some of the most frequent scavenger species obtained during this study with camera traps. (a) King vultures (*Sarcoramphus papa*), (b) American black vultures (*Coragyps atratus*), (c) turkey vultures (*Cathartes aura*), (d) southern caracaras (*Caracara plancus*), (e) hoary fox (*Lycalopex vetulus*), and (f) black-and-white tegu (*Salvator merianae*)

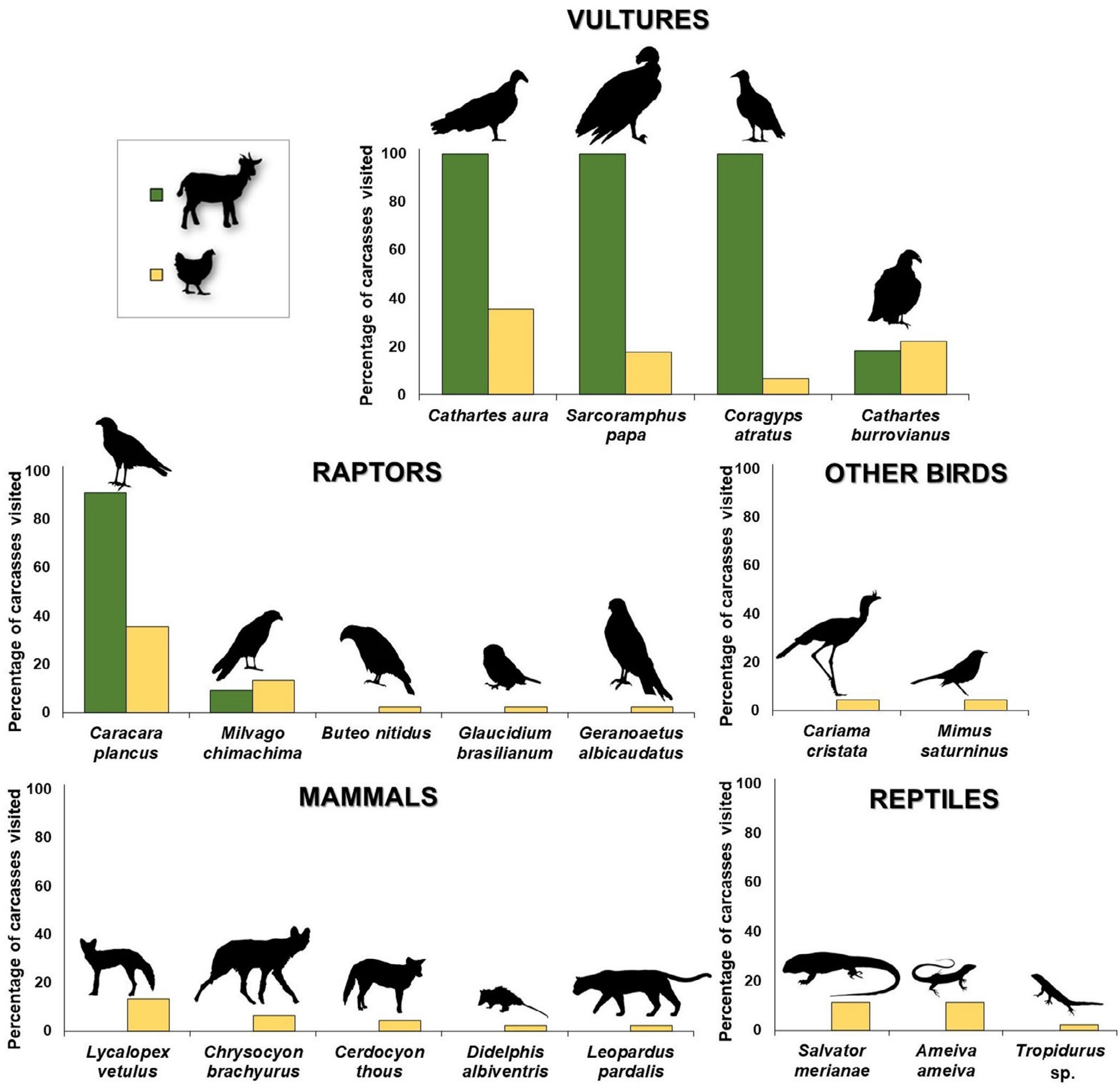

FIGURE 3 Percentage of large and small carcasses in which each scavenger species was detected eating. Small carcasses were consumed by 19 scavenger species, while large carcasses fed exclusively four vultures and two other raptor species

at all the large carcasses, as well as other raptors at 90% of them. Small carcasses (i.e., chickens) were consumed by the entire scavenger community. Raptors (excluding vultures) were recorded at 51.1% of small carcasses, followed by obligate scavengers (35.6%), mammals (28.9%), reptiles (22.2%), and other birds (6.7%; Figure 4).

We recorded a total feeding time on carcasses of 235.8 hr, of which 222.2 hr corresponded to the consumption of large carcasses and 13.6 hr to the consumption of small carcasses. Vultures were the species that spent more time scavenging at all carcasses considered together (208.1 hr in total, 88.26% of the total time), followed by other raptors (26.7 hr, 11.31%) (Figure 4). Of all the species registered, the king vulture spent the highest number of hours feeding on carcasses (77.9 hr, 33.06%), followed by the American black vulture (77.1 hr, 32.70%) and the turkey vulture (49.2 hr, 20.90%).

The American black vulture spent 76.9 hr (34.6% of total time) foraging in large carcasses, followed by the king vulture (76.7 hr, 34.52%). In small carcasses, the turkey vulture (5.7 hr, 41.83%) and the southern caracara (2.6 hr, 18.99%; Figure S3) spent more time than the other species.

Carcass size was an important factor affecting the scavenger community. GLM analyses showed that both scavenger richness and abundance were greater in large carcasses than in the small

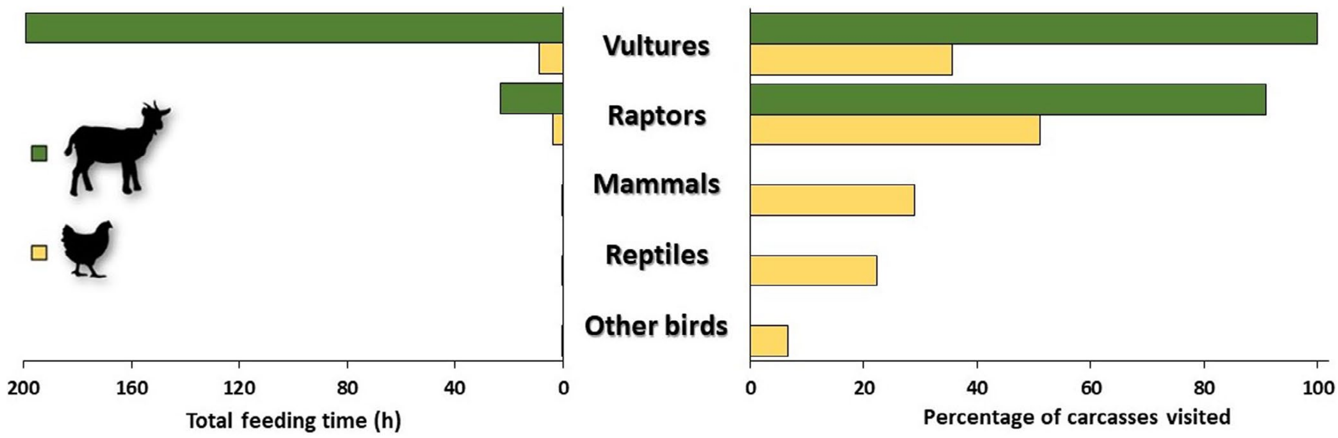

FIGURE 4 Feeding time (in hours) that each taxonomic group spent eating carrion (left panel) and percentage of carcasses visited by each group (right panel). The results are represented separately for small (yellow) and large (green) carcasses

ones (Table 1). The size of the carcass also affected the carcass consumption patterns, as consumption time and consumption rate were nearly four times higher in large carcasses (Table 1). We found no difference in detection time between large and small carcasses. When analyzing chicken and goat carcasses separately, we found that carcass weight, time of carcass placement, and vegetation cover had different effects depending on carcass size (Tables 2 and 3). For large carcasses, richness was not influenced by any factor, as the null model was the only top-ranking model obtained (Table S3). We also found that the null model was one of the top-ranking models for detection time and consumption time for large carcasses. For small carcasses, null model was a top-ranking model for scavenger richness and consumption time.

Carcass weight influenced the scavenger community (Tables 2 and 3, Tables S3 and S4). In large carcasses, weight increased the scavenger abundance. Carcass weight strongly affected consumption patterns, since it was also included in the top-ranking models as a predictor of detection time and consumption rate (Table 2). In small carcasses, weight also influenced the scavenger community and consumption patterns, having a positive effect on richness, abundance, and consumption rate. Detection time was negatively affected by weight, although in this model the weight had no statistical support (Table 3).

Vegetation cover had a positive effect on the consumption time for large carcasses (Table 2). In contrast, vegetation cover had no effect on any of the variables for small carcasses, although it was included in some of the top-ranking models (Table 3, Table S4).

Time of carcass placement did not affect the scavenger community and consumption patterns. This variable did not appear in any of the top-ranking models for large carcasses (i.e., goat carcasses), although it was included in some of the top-ranking models for small carcasses (i.e., chicken carcasses), but with no effect (Tables 2 and 3, Tables S3 and S4).

The detector group (i.e., olfactive capacity) did not influence detection times neither in large nor in small carcasses, since this variable was not included in any of the top-ranking models (Tables S3 and S4).

4 | DISCUSSION

Despite the increasing number of studies on vertebrate scavenging, little is known about the scavenger communities in the Neotropics. In fact, as far as we know, this paper is the first to describe the highly diverse and efficient scavenging vertebrate community in the Brazilian *Cerrado* biome. Carcass size was the main factor affecting consumption patterns, with different assemblages of consumers depending on whether the carcass was large or small (goat vs. chicken carcasses), as evidenced in previous studies (Travis L. DeVault et al., 2004; Moleón et al., 2015; Olson et al., 2016). However, we were unable to detect an effect of vegetation cover or time of carcass placement in the consumption patterns of both carcass sizes, maybe due to the high scavenging efficiency of the species in this community.

4.1 | The vertebrate scavenger assemblage at the *Cerrado* biome

The community of vertebrate scavengers in the north-eastern Brazilian *Cerrado* includes at least 19 vertebrate species. In fact, nearly 100% of carcasses were consumed by vertebrates, whereas invertebrates played a negligible role. We detected four species of New World vultures, as well as 15 facultative scavengers including raptors (5 species), other birds (2), mammals (5), and reptiles (3), showing that scavenging by vertebrates is widespread in this biome. This community is among the most diverse scavenger communities described worldwide, with 15 of the 19 of the species detected here being exclusive to the Neotropics (IUCN, 2020; Sebastián-González et al., 2019). We find few scavenging communities with higher species richness in the literature, like the Polish temperate forests, with

TABLE 1 Richness per carcass, abundance, detection and consumption times, and consumption rate for each carcass size (large or small)

	Large carcasses			Small carcasses			Comparison	
	Mean ±SD	Range	*n*	Mean ±SD	Range	*n*	Coefficient (small carcasses)	CI
Richness	4.18 ± 0.60	3–5	11	2 ± 1.17	1–6	45	−0.738	−1.087 to −0.375
Abundance	28.72 ± 8.22	19–43	11	3.42 ± 3.39	1–18	45	−2.128	−2.509 to −1.762
Detection time (h)	18.83 ± 9.22	1.5–27.33	11	21.45 ± 22.62	0.08–125.82	45	0.125	−0.601 to 0.771
Consumption time (h)	48.41 ± 14.41	46.55–98.97	10	13.55 ± 19.56	0.4–114.77	44	−0.712	−1.276 to −0.204
Consumption rate (kg/h)	0.46 ± 0.19	0.228–0.83	10	0.12 ± 0.34	0.002–1.54	44	−1.387	−2.563 to −0.440

Note: Values represent mean ± standard deviation (SD), range, and sample size (*n*). The differences between large and small carcasses are shown by the value of the coefficient referring in all cases to small carcasses. The estimate of the parameters and the 95% confidence interval (CI) are shown.

up to 36 species (Selva et al., 2005), or the Californian forests, with 29 species (Allen et al., 2014).

Despite the large number of potential scavenger species in this community (Dénes et al., 2017; Lima, 2009), our results highlight scavenging efficiency of vultures, over other taxonomic groups. In agreement with previous studies (Arrondo et al., 2019; Hill et al., 2018; Morales-Reyes et al., 2017; Ogada, Torchin, et al., 2012), vultures were the most efficient scavengers, being the main consumers in terms of both occurrence frequency and consumption time in all types of carcasses. Top predators such as pumas and jaguars that were detected in the area (through signs and camera traps) did not consume carrion, which contrasts with the important scavenging role of top predators in other ecosystems, such as African savannas (Moleón et al., 2015) or temperate forests (Selva et al., 2005). In our study area, other raptors also played an important role in terms of percentage of visited carcasses and feeding time, contrasting with other systems where carnivores are the main scavengers (Cunningham et al., 2018; Inagaki et al., 2020; Moleón et al., 2015). This may be related to the diet of the canid species that coexist in the Brazilian *Cerrado*, as they consume a great variety and quantity of fruits and insects (Juarez & Marinho-Filho, 2002) compared to other areas where mesocarnivores like red foxes (*Vulpes vulpes*) consume a greater proportion of animal prey (Padial et al., 2002). However, our results are only based on the wet season, when there is a greater availability of fruits than the dry season, so more studies would be necessary to determine whether the dependence of these species on carrion could be greater when there are fewer fruits available. These differences between communities could also be due to mesocarnivores being more abundant in those areas where there are no apex predators and also because of a weaker competition for the resource and a lower risk of predation at carcasses (Allen et al., 2015; Cunningham et al., 2018; Moleón & Sánchez-Zapata, 2021; O'Bryan et al., 2019).

4.2 | Factors affecting consumption patterns

In agreement with our first prediction, assemblages of scavenging species consuming large and small carcass were different. Vultures were the most efficient consumers of large carcasses, almost monopolizing them (Ruxton & Houston, 2004). In contrast, smaller carcasses were consumed mainly by facultative scavengers (i.e., medium-sized mammals, reptiles, and other raptors). In agreement with recent studies, the average richness of scavenger species per carcass was higher in large carcasses than in the small ones (Moleón et al., 2015; Sebastián-González et al., 2019; Turner et al., 2017). However, total species richness was higher in small carcasses. This may be because large carcasses were consumed mainly by obligate and dominant scavenger species (i.e., vultures and other raptors), whereas small carcasses might be quickly removed by other opportunistic facultative scavengers. Frequency of mesopredator occurrence (i.e., mammals and reptiles) and other birds was higher in small carcasses, a common pattern in other areas (DeVault et al., 2004;

TABLE 2 Model coefficients for large carcasses by means of one-predictor generalized lineal models (GLMs) showing the relation between scavenging efficiency (abundance, detection and consumption times, and consumption rate) and carcass weight, time of carcass placement, and vegetation cover

Response variable	Model	Estimate	CI
Abundance	(Intercept)	2.478	1.880–3.080
	weight	0.031	0.010–0.051
Detection time	(Intercept)	5.406	3.542–7.339
	weight	−0.091	−0.160–−0.023
Consumption time	(Intercept)	3.973	3.779–4.167
	vegetation cover	0.007	0.002–0.012
Consumption rate	(Intercept)	4.617	3.823–5.407
	weight	0.052	0.025–0.080

Note: Time of carcass placement was not retained in any model. The estimate of the parameters and the 95% confidence interval (CI) are shown. Coefficients are not presented for the model whose response variable is scavenger richness because the only top-ranking model was the null model.

TABLE 3 Model-averaged coefficients for small carcasses by means of generalized lineal models (GLMs) showing the relation between scavenging efficiency (richness, abundance, detection and consumption times, and consumption rate) and carcass weight, time of carcass placement, and vegetation cover

Response variable	Model	Estimate	CI
Richness	(Intercept)	0.456	0.023–0.888
	weight	0.273	0.002–0.68
	time: afternoon	0.094	−0.15–0.703
Abundance	(Intercept)	0.591	0.15–1.032
	time: afternoon	0.255	−0.023–0.852
	weight	0.671	0.312–1.029
Detection time	(Intercept)	3.018	2.216–3.82
	vegetation cover	0.006	−0.003–0.023
	weight	−0.587	−1.212–−0.089
	time: afternoon	0.237	−0.118–1.139
Consumption time	(Intercept)	3.444	2.99–3.896
	vegetation cover	0.002	−0.005–0.017
	weight	−0.042	−0.64–0.27
Consumption rate	(Intercept)	2.899	1.99–3.806
	weight	2.071	1.261–2.881
	vegetation cover	0.004	−0.008–0.031

Note: The estimate of the parameters and the 95% confidence interval (CI) are shown.

Moleón et al., 2015; Olson et al., 2016; Turner et al., 2017). The behavior of smaller carnivores (i.e., medium and small mammals and reptiles) at large carcasses might be influenced by the "landscape of fear" induced by predation risk (Cortés-Avizanda et al., 2009; Moleón & Sánchez-Zapata, 2021; Willems & Hill, 2009). In contrast, the number of individuals consuming a carcass diminished with decreasing carcass size. This is because small carcasses were often totally consumed by a single individual, while large carcasses usually persist longer in the environment, allowing more individuals to consume it (Sebastián-González et al., 2013; Turner et al., 2017).

Supporting our expectations, our results show differences between large and small carcasses in all consumption variables except for detection time. Carcass size did not affect detection time, which may be due to the high foraging efficiency of the vulture species in the community (Houston, 1985; Mallon et al., 2013), as is the case on the African savanna (Moleón et al., 2015). The species that first detected more carcasses was the turkey vulture, followed by the southern caracara. These two species are not only guided by the sense of sight and hearing, like most raptors, but also have a developed sense of smell (Houston, 1985; Potier et al., 2019). It has been hypothesized that these evolutionary differences between New and Old world vulture guilds (e.g., olfactory capacities of some species) are due to the type of habitat in which they have evolved; Old World vultures are distributed in areas of open habitat, while most New World species (except the two condor species) are mainly distributed in Neotropical forests (Houston, 1985). This clearly differentiates the New World from the Old world bird guild, giving American vultures a clear advantage when locating carrion regardless of vegetation cover (Houston, 1988; Mallon et al., 2013). By contrast, consumption time and consumption rate were significantly higher in large carcasses, coinciding with the results obtained in other scavenger communities (Moleón et al., 2015). If we compare our results with five other studies conducted using chickens or similar carcasses, we observe that all of them obtained lower consumption rates than ours (reviewed in Sebastián-González et al., 2020). In contrast, for large carcasses, compared to six other studies in which they also used goat or sheep carcasses, our observed consumption rate was average (reviewed in Sebastián-González et al., 2020). This suggests that the rich vertebrate scavenger guild in the *Cerrado* is very efficient in removing carcasses, especially those of small sizes.

Contrary to our prediction that vegetation cover influences scavenging patterns, we did not find a significant influence of vegetation cover on the ability of scavengers to locate the carcasses. However, detection and consumption times were generally higher in areas of dense vegetation in all carcasses. Previous studies showed that dense vegetation may prevent carrion localization by vertebrates, promoting carrion consumption by invertebrates (Ruzicka & Conover, 2012), because high vegetation densities may leave insufficient space for the vultures to take off (Bamford et al., 2009), and carcasses in open habitats are detected and consumed faster (Arrondo et al., 2019). However, this factor does not seem to be relevant in our system, probably because of the olfactory capacity of the main scavenger species. Likewise, our prediction that time of carcass placement influences consumption patterns was not supported by the analyses. Existing research has shown that mammals are more active than raptors during the afternoon and are thus the first to find carrion when it is located in the late afternoon. This increases detection times, because mammals are less efficient at finding carrion than vultures and other raptors (Butler & du Toit, 2002; Ruxton & Houston, 2004). However, this does not occur in the *Cerrado* system because other species (i.e., mammals and other raptors) could be functionally replacing vultures for carcass detection during the afternoon.

This study has certain methodological limitations that are important to consider. Data collection was carried out in one month and exclusively during the wet season (that lasts from November to April). Although previous research has shown changes in carrion consumption patterns among seasons, these have been carried out in temperate zones with a strong seasonality and have highlighted that the factor that most influences carrion acquisition is temperature (DeVault et al., 2004; Selva et al., 2005). However, even though the Brazilian *Cerrado* has two distinct seasons (i.e., wet and dry), the average temperatures in this area are 18 and 28°C during the dry and wet seasons, respectively. This variation is unlikely to affect the scavenger patterns (Dias, 1992). It would be interesting to carry out the same field experiment in the dry season, to see whether there are any changes in the scavenging patterns. The sample size of large carcasses is not very large ($n = 11$). However, as shown by the species accumulation curves, we identified the same scavenger community in almost all large carcasses, so we can conclude that there is little variability in the species that use this type of carcass.

4.3 | Concluding remarks and conservation implications

This is the first time the *Cerrado* scavenging community is described, and our findings emphasize the importance of the functions and ecosystem services provided by the scavenger guild in this Neotropical region. Several factors have been shown to influence the composition of scavenger communities, such as habitat, topography, and climate (Mateo-Tomás et al., 2017; Sebastián-González et al., 2019, 2020; Turner et al., 2017). Nevertheless, it has been concluded that human disturbance is the factor that most affects the richness of scavengers (Sebastián-González et al., 2019) and also influences the way scavenger assemblages are structured and their efficiency at the global scale (Sebastián-González et al., 2020). In the last decades, habitat loss rate in the Brazilian *Cerrado* has been very high due to the transformation of the territory for human use (Klink & Machado, 2005; Strassburg et al., 2017). This may be negatively affecting populations of species restricted to this biome and their ecological functions, although the population sizes of many species are not well known (e.g., king vultures) (IUCN, 2020).

Research on wildlife is scarce in this region and has focused mainly on protected areas and key species, but more studies at the functional group level are needed to understand the functioning and dynamics of communities and thus the importance of conserving them (Klink & Machado, 2005; Strassburg et al., 2017). Our results highlight the diversity and functionality of the vertebrate scavenger community at the *Cerrado*, which adds to the need to conserve this global biodiversity hotspot.

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AUTHORS' CONTRIBUTIONS

LNA, ZMR, ESG, and JASZ designed the research. All authors participated in data collection. LNA performed the analyses and led the writing. All authors read and revised the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.6wwpzgn01 (Naves-Alegre et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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