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ARTICLE

Circadian activity patterns and temporal overlap among cracids (Aves: Cracidae) within a vegetation mosaic in the Pantanal of Rio Negro, Brazil

Mauro Celso Rodrigues dos Santos[1,2,4]; Leandro Silveira[3,5]; Anah Tereza de Almeida Jácomo[3,6]; Giselle Bastos Alves[3,7] & Flávio Kulaif Ubaid[1,2,8]

[1] Universidade Estadual do Maranhão (UEMA), Centro de Estudos Superiores de Caxias (CESC), Departamento de Química e Biologia (DQB), Laboratório de Ornitologia. Caxias, MA, Brasil.
[2] Universidade Estadual do Maranhão (UEMA), Centro de Estudos Superiores de Caxias (CESC), Programa de Pós-Graduação em Biodiversidade, Meio Ambiente e Saúde. Caxias, MA, Brasil.
[3] Instituto Onça-Pintada (IOP). Mineiros, GO, Brasil.
[4] ORCID: https://orcid.org/0000-0002-1352-5311. E-mail: maurocelso.bio@gmail.com
[5] ORCID: https://orcid.org/0000-0003-3298-4457. E-mail: l.silveira@jaguar.org.br
[6] ORCID: https://orcid.org/0000-0002-5906-2981. E-mail: a.jacomo@jaguar.org.br
[7] ORCID: https://orcid.org/0000-0002-4760-1917. E-mail: gbastosalves@yahoo.com.br
[8] ORCID: https://orcid.org/0000-0001-8604-1206. E-mail: flavioubaid@gmail.com

Abstract. Vertebrates, overall, present a daily activity pattern when managing their needs, such as foraging, resting or searching for sexual partners. Most of the available information regarding the circadian rhythm in birds comes from controlled laboratory conditions, and little is known about these patterns in the wild. In this study we used camera traps to describe the daily activity patterns of three cracid species in the Pantanal of Rio Negro, Brazil. We had a sampling effort of 9,617 camera trap-days along 231 days (5,544 hours) from September 2013 to May 2014. This resulted in 4,833 independent records of cracids from a total of 7,713 individuals. *Crax fasciolata* was the species with the most records ($n_{rec} = 3{,}792$) and individuals ($n_{ind} = 5{,}781$), followed by *Ortalis canicollis* ($n_{rec} = 934$; $n_{ind} = 1{,}758$) and *Aburria grayi* ($n_{rec} = 107$; $n_{ind} = 174$). None of the species was uniformly distributed throughout the day, thus evidencing a periodization of their activities. The mean vectors of the activity patterns of *C. fasciolata, O. canicollis* and *A. grayi* were, respectively, $m\mu = 10{:}36 \pm 04{:}26$ (SD), $m\mu = 11{:}42 \pm 03{:}57$ and $m\mu = 11{:}44 \pm 03{:}47$. We observed a temporal overlap between *A. grayi* and *O. canicollis,* whereas *C. fasciolata* significantly differed from them. Because of their large home ranges, cracids are important indicators of environmental quality, and, as frugivores, they play key roles in the ecological dynamics of forests. In this sense, and given that cracids are notably more susceptible to extinction, the knowledge on their circadian activity patterns may be useful when establishing effective management and conservation strategies.

Keywords. Conservation; Cracidae; *Crax; Ortalis; Aburria.*

INTRODUCTION

The daily activity period, or circadian cycle, corresponds to the 24-hour span which establishes the biological cycles of nearly all living species. Such patterns have existed throughout the history of life on Earth, and virtually every life form has had its rhythm adapted to it (Beale *et al.,* 2016). Activity patterns may be influenced by abiotic factors, such as photoperiod, lunar cycle, temperature, precipitation, tides, and latitude, as well as by biotic factors, like food availability, reproduction, and interactions with predators and humans (Kronfeld-Schor & Dayan, 2003; Pita *et al.,* 2011; Ross *et al.,* 2013; Bennie *et al.,* 2014; Sassi *et al.,* 2015; Díaz-Ruiz *et al.,* 2016; Gaynor *et al.,* 2018). Knowing how species explore their habitats and spotting the basic resources and conditions for their occupation, survival and reproduction is essential for stakeholders when determining potential threats and planning efficient management programs (Willems & Hill, 2009; Morrison *et al.,* 2006).

Animals perform a number of activities within their circadian cycle (*e.g.,* foraging, resting or searching for reproductive partners) that may

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concentrate in specific times of the day or night. The activity pattern refers to the continuous period in which an individual concentrates its daily actions (Maffei *et al.,* 2002; Monroy-Vilchis *et al.,* 2011). The circadian cycle is involved in the regulation of several daily functions, including the patterns of greater activity (Pittendrigh, 1981; Laposky *et al.,* 2008; Cassone, 2014). Therefore, as ecosystems grow in complexity, organisms go on to explore not only their physical dimensions but also their temporal niches (Hut *et al.,* 2012). As a consequence, all life forms share physiological and behavioral processes for specific times of the day (West & Bechtold, 2015). Behavioral plasticity, although limited in some species, becomes evident in others from observations of intraspecific variation in foraging patterns (Ashby, 1972; Hertel *et al.,* 2016) that may lead to changes in the temporal niche (Fenn & MacDonald, 1995; Ensing *et al.,* 2014).

The circadian rhythm also allows animals to expect and prepare for predictable alterations in their environments (Stelzer *et al.,* 2010; Kumar *et al.,* 2010; Bloch *et al.,* 2013). Daily variations in animal physiology or behavior also present a strong endogenous (circadian) component (Reebs, 2002; Kronfeld-Schor & Dayan, 2003; Lazzari & Insausti, 2008). Facing this, information about animal movement, domestic environment, territoriality, and activity patterns greatly contribute to wildlife conservation and management (Rodríguez-Flores & Arizmendi, 2020).

Monitoring rare cryptic species is not a feasible task for researchers. Camera traps have been used to overcome this and successfully record, monitor and estimate the density of enigmatic taxa (Heilbrun *et al.,* 2006; Kelly & Holub, 2008). This tool is highly flexible and has been used for fauna inventories (*e.g.,* Jiménez *et al.,* 2010), relative abundance indexes (Monroy-Vilchis *et al.,* 2011), and to describe activity patterns (Hernández-SaintMartín *et al.,* 2013; Lafleur *et al.,* 2014) and land and habitat use (Michalski *et al.,* 2015; Blake *et al.,* 2017; Pardo *et al.,* 2017; Pérez-Irineo & Santos-Moreno, 2018). In birds, most of the available information regarding the circadian rhythm comes from controlled laboratory conditions, while data from the wild remains poorly reported. Studies from the last decade have shown the efficacy of camera traps for studying large birds in the wild in Brazil, especially in the Atlantic Forest (Srbek-Araújo *et al.,* 2009, 2012; Kuhnen *et al.,* 2013), and in other countries (Negret *et al.,* 2015).

The Cracidae is one of the most threatened families of large birds (curassows, guans and chachalacas) inhabiting the Neotropical woodlands (Brooks, 2006). Out of the 54 known cracid species (Winkler *et al.,* 2020), 26 are under some global degree of threat while one is extinct in nature, the Alagoas Curassow *Pauxi mitu* (ICMBio, 2018). The elevated risk of extinction faced by cracids – 50% of the species classified as threatened – derives basically from hunting and habitat modification (Brooks & Fuller, 2006; Benítez-López *et al.,* 2017). The Pantanal wetlands are home to six species of cracids: Chaco chachalaca (*Ortalis canicollis*), bare-faced curassow (*Crax fasciolata*), both broadly distributed in the Upper Paraguay Basin, rusty-margined guan (*Penelope superciliaris*), chestnut-bellied guan (*Penelope ochrogaster*), more abundant in the northern region, white-throated piping-guan (*Aburria grayi*), endemic to the Mato-Grosso do Sul state, and the red-throated piping-guan (*Aburria cujubi*), commonly found in northern Brazil and reaching northern Pantanal (del Hoyo & Kirwan, 2020).

In this study we deployed camera traps in the Pantanal of Rio Negro to describe the daily activity patterns of three cracid species (*A. grayi, O. canicollis* and *C. fasciolata*) and to check whether or not they overlap in time.

MATERIAL AND METHODS

Study area

The study was performed in a 26,500 ha area in the Pantanal wetlands of Rio Negro, in Aquidauana, Mato Grosso do Sul state, Brazil (Silva & Abdon, 1998). Most of the surveyed area (22,300 ha) was within the Barranco Alto ranch (19°33′35″S, 56°09′22″W, 100-120 m a.s.l.). The remaining sampling sites were located in a contiguous section of the Diacuí and Vera Lúcia ranches. The landscape is characterized by several bays and salt lakes, intertwined with open savannas, dense shrublands, fields and gallery forests. Non-flooded forests compose the most elevated areas. Secondary savannas and planted pastures occur in areas of greater anthropic influence (Silva *et al.,* 2011). The climate in the region is classified as tropical wet (Aw) in the Köppen-Geiger’s system (Kottek *et al.,* 2006), with rainy summers (June to September) and dry winters (December to March). The mean minimum and maximum annual temperatures range from 21° to 33°C, respectively (Soriano & Alves, 2005), while the mean annual precipitation is approximately 1,350 mm (Bergier *et al.,* 2018).

Sampling design and data collection

The birds were recorded by camera traps (Bushnell Trophy Cam HD E3). This method is recognized for its versatility and efficacy in obtaining ecological data, mainly when detecting rare species and determining their activity periods, as it provides a big volumes of information simultaneously (Hernández-SaintMartín *et al.,* 2013; Lafleur *et al.,* 2014; Pardo *et al.,* 2017). Data was collected over nine months, from September 2013 to May 2014. The traps were spread over a grid of 90 sampling stations (Fig. 1). All sites were at least 500 m apart from each other to avoid sampling gaps. The cameras possess infra-red sensors activated by heat and movement and were placed approximately 40 cm above the ground so that the targeted animal could be recorded 2-3 m away (Tobler *et al.,* 2008). The traps were set to work 24 h/day and make 60-second videos for every record, with 30-second intervals between successive records. The sites were checked every 30 days for battery and memory card replacement.

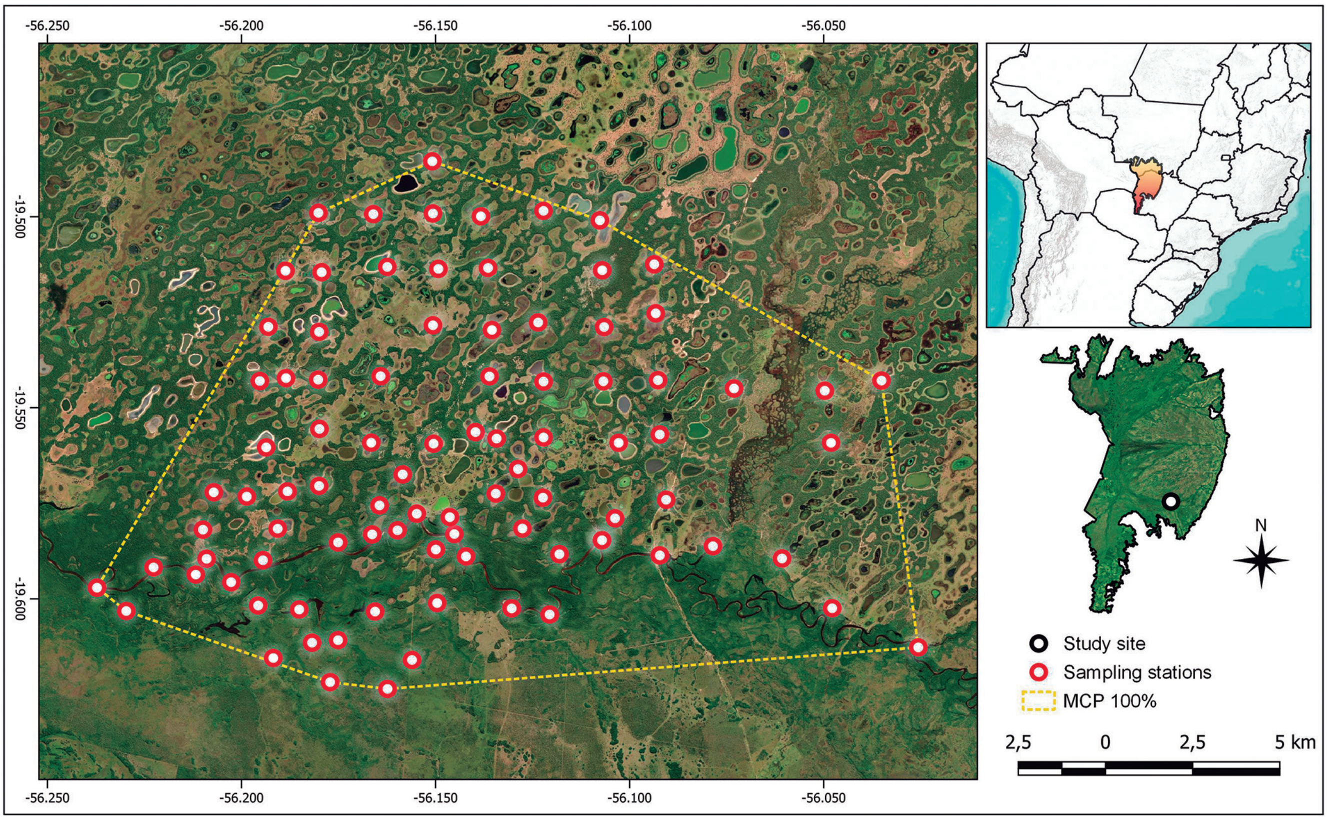

Figure 1. Study area and location of the 90 camera trap stations in the Pantanal of Rio Negro, Aquidauana, Mato Grosso do Sul, Brazil.

Data analyses

All registered animals were identified to species level. When the species could not be determined, the records were classified at the smallest scale within the following: 1) genus; 2) family; 3) order; 4) class; 5) not identified. Every video made for the sampled species was considered a record. They were subdivided in: 1) total, which are all records obtained, and; 2) independent, excluding repeated records of the same species at the same sampling site in intervals ≤ 20 min (Tobler *et al.,* 2008). Every record informed the recorded species, the number of individuals, date, and time of day. Videos depicting more than one species were considered independent records for each of them.

The sampling effort was calculated by multiplying the number of stations by the number of sampled days (1 day = 24 hours), and the catch rate by dividing the number of records by the sampling effort (Srbek-Araújo & Chiarello, 2005). The area covered by the camera traps was measured by the minimum convex polygon method (MCP) using all of the sampling stations. We performed a Shapiro-Wilk test for inspecting the normality of abundance distributions throughout the day.

We used circular statistics through the Rayleigh uniformity test (Z-test) to determine the circadian preferences of each species (Jammalamadaka & SenGupta, 2001). This test is employed to observe whether the records are uniformly distributed along a day. Our null hypothesis was a uniform circular distribution of the data, while our alternative hypothesis was a non-uniform distribution, with peaks of activity along the day. For this, the 24 hours of the day were distributed along 360°, with 1 h = 15° or 1 min = 0.25°. The mean vector (mμ), generated in degrees, was then converted into hours and corresponded to the mean hour of greater activity. We performed a nonparametric Mardia's two-sample test (Watson's U^2) to check for overlap between the mean active hours of the species (Mardia, 1967; Batschelet, 1981; Zar, 2010). The null hypothesis acknowledges that all samples come from a single population, whereas the alternative hypothesis considers that populations differ in their mean active hours and present time partitioning. All these analyses were performed on R 3.5.1 (R Development Core Team, 2011) with the packages vegan 2.5-5 (Oksanen *et al.,* 2020), circular 0.4-93 (Agostinelli & Lund, 2017) and plotly 4.9.2.1 (Sievert, 2020). We adopted significance at $p < 0.05$.

RESULTS

We had a sampling effort of 9,617 camera trap-days along 231 days (5,544 hours). The cameras covered an area of 23,391 ha in a 60.3 km perimeter, according to the MCP. We found a total of 26,559 records of vertebrates, 4,833 (18.2%) of which were independent records of the three studied cracids, *C. fasciolata, O. canicollis* and *A. grayi,* with 7,713 individuals detected. *Crax fasciolata* was the most registered (N_{rec} = 3,792) and abundant species (N_{ind} = 5,781), followed by *O. canicollis* (N_{rec} = 934; N_{ind} = 1,758) and *A. grayi* (N_{rec} = 107; N_{ind} = 174). The varia-

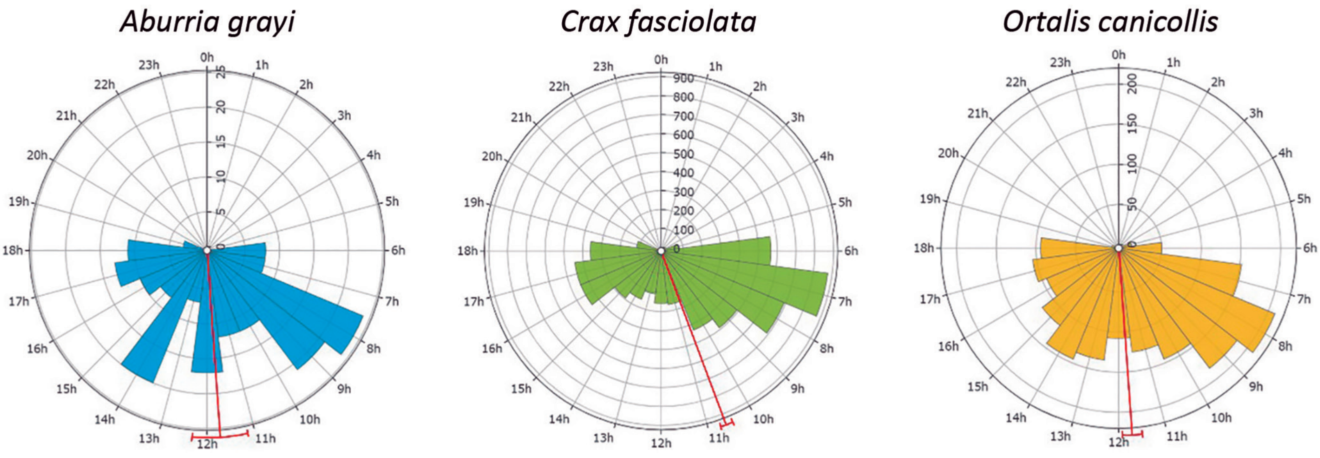

Figure 2. Circadian activity patterns of three cracid species in the Pantanal of Rio Negro, Aquidauana, Mato Grosso do Sul. The red line represents the mean circular vector (mµ) with CI95% of the distributions.

Table 1. Preferred activity period of three cracid species in the Rio Negro Pantanal, Aquidauana, Mato Grosso do Sul. N = number of records; mµ = mean vector; SD = standard deviation; r = length of the mean vector.

Species	N	mµ ± DP	r	Rayleigh (Z)	p-value
Aburria grayi	174	11:44 ± 03:47	0,612	65,104	< 0,05
Crax fasciolata	5.781	10:36 ± 04:26	0,508	1.490,208	< 0,05
Ortalis canicollis	1.758	11:42 ± 03:57	0,584	599,842	< 0,05

Table 2. Pairwise Watson's U^2 test of temporal overlap between cracid species in the Pantanal of Rio Negro, Aquidauana, Mato Grosso do Sul.

Species paired test	U^2	p-value	df
Aburria grayi & *Crax fasciolata*	0.818	< 0.001	174
Aburria grayi & *Ortalis canicollis*	0.059	> 0.5	174
Crax fasciolata & *Ortalis canicollis*	4.573	< 0.001	1758

tion in their abundances throughout the day had a non-normal distribution (Shapiro-Wilk normality test for all species, p-values < 0.05).

The distribution of the active time of the three species was non-uniform along the 24 hours, which evidences a periodization of their activities (Table 1). The mean vectors of the activity patterns of *C. fasciolata, O. canicollis* and *A. grayi* were, respectively, mµ = 10:36 ± 04:26 (SD), mµ = 11:42 ± 03:57 and mµ = 11:44 ± 03:47.

Aburria grayi presented two peaks of activity, one in the morning, between 07:30-09:30, and another in the afternoon, between 01:30-02:30. *Crax fasciolata* was active the most between 06:30-09:30 a.m. The peak of *O. canicollis* was between 07:30-09:30 a.m., although it was more evenly distributed along the day if compared to the other species (Fig. 2).

Watson's U^2 test showed a temporal overlap between *A. grayi* and *O. canicollis,* while their peak of activity differed significantly from *C. fasciolata* (Table 2).

DISCUSSION

Our results reveal that the three studied species (*C. fasciolata, A. grayi* and *O. canicollis*) share the activity patterns of other cracids. For instance, the red-billed curassow (*Crax blumenbachii*) has a peak of activity in the early morning that gradually decreases until midday, restarts in the afternoon and peaks again before dusk (Srbek-Araújo *et al.,* 2012; Hernández-SaintMartín *et al.,* 2013; Fernández-Duque *et al.,* 2013; Schaaf *et al.,* 2014; Pérez-Irineo & Santos-Moreno, 2018). Some other species, however, show distinct temporal patterns. The Sira Curassow (*Pauxi koepckeae*), in the Peruvian Andes, stays active between 10:00 a.m. and 06:00 p.m. (Beirne *et al.,* 2017). The razor-billed curassow (*Pauxi tuberosa*) is active mostly in the morning, whereas the Spix's guan (*Penelope jacquacu*), in the Xeruã river, Amazonas, peaks at midday (Sæbø, 2016). The incompatibility with the bimodal activity pattern in such species may be a result of the environments they inhabit, *i.e.,* mountain and tropical forests, with scarce solar radiation on the ground vegetation that allows animals to forage longer along the day (Sæbø, 2016; Beirne *et al.,* 2017).

Even though the activity periods of some cracids have been previously documented (*e.g., Crax* and *Penelope*), studies focused on *A. grayi* are deficient. The semi-arboreous habits of this bird may be responsible for the low number of records in our study. This species feeds primarily on leaves, seeds and fruits, which are collected in the canopy, and eventually forages on the ground (Schubart *et al.,* 1965; Sick, 1997). In Trinidad and Tobago, the congeneric Trinidad piping-guan *A. pipile* occupies canopies above 5 m (Hayes *et al.,* 2009). In that same study, *A. pipile* was registered more frequently in the morning and late afternoon, similarly to *A. grayi* in the Pantanal.

Contrary to *Aburria,* species in the *Crax* genus primarily inhabit the forest floor (Delacour & Amadon, 1973) in areas that either are or are not prone to seasonal floodings (Michalski *et al.,* 2015; Costa *et al.,* 2018). Seasonally floodable areas like the Pantanal present remarking differences in the density and richness of animal species between distinct seasons, which is driven by the effects of the flooding cycles on fruit production and habitat use by the animals (Haugaasen & Peres, 2007, 2008; Alvarenga *et al.,* 2018). Behavioral adaptations arise under environmental pressure, while changes in temporal distribution may also occur according to the heterogeneity of the site (Presley *et al.,* 2009; Reyes-Arriagada *et al.,* 2014). In our study, *C. fasciolata* was more active in the morning, with a gradual decrease in activity along the day. This pattern had already been observed for an Argentinean population in another camera-trap study (Fernández-Duque *et al.,* 2013). In the Vale Natural Reserve in the Espírito Santo state, Brazil, activities of *C. blumenbachii* peaked between 06:00-07:00 a.m. (Srbek-Araújo *et al.,* 2012), a similar pattern to what we observed for *C. fasciolata* in the Pantanal. Camera-trap assessments in Central America and other parts of South America revealed bimodal diurnal activity patterns for plain chachalaca *O. vetula,* great curassow *C. rubra,* and *C. fasciolata,* with activities beginning between 06:00-07:00 a.m., reaching a first peak still in the morning and another less evident one in the afternoon (Hernández-SaintMartín *et al.,* 2013; Fernández-Duque *et al.,* 2013). The peak in activity for *O. canicollis* also happened in the morning, between 07:30-09:30. Nevertheless, this species presented a more homogeneous pattern throughout the day compared to the two other cracids.

Camera-trap samplings have shown that temporal segregation is an important strategy for the coexistence of ecologically similar species (*e.g.,* Di Bitetti *et al.,* 2010; Monterroso *et al.,* 2014; Sunarto *et al.,* 2015). In the present study, the overlap in activity was prominent between *A. grayi* and *O. canicollis* but differed significantly for *C. fasciolata.* When resources are abundant, species tend to vastly overlap their use (Pianka, 1981). Estevo *et al.* (2017) observed a great overlap in time of activity between two sympatric land birds, brown tinamou *Crypturellus obsoletus* and tataupa tinamou *C. tataupa.* A study on the coast of the Argentinean Patagonia showed a high isotopic niche overlap among 14 seabird species during mating season that was maintained by a super-abundance of food (Forero *et al.,* 2004). Moreover, similar patterns of co-occurrence between species sharing the same food resources at the same times of the day have also been widely observed for mammalian carnivores (Davis *et al.,* 2018). Therefore, resource availability could be acting as a limiting agent to the co-occurrence of cracids in the Pantanal.

Cracids are important indicators of environmental quality, as they occupy large territories. They are frugivorous animals with a fundamental role in forest dynamics (Sedaghatkish, 1996; Jordano *et al.,* 2006; Muñoz & Kattan, 2007; Bueno *et al.,* 2013; Galetti *et al.,* 2013, 2016). Studies on activity patterns and interspecific co-occurrence present a straightforward application in the conservation strategies for protected areas, as they incorporate a zonal approach aiming at habitat protection for the cracids and also for other codependent species (Leite *et al.,* 2018). Continuous multiannual camera-trap studies would allow a better comprehension of how local alterations and anthropic disturbance affect the distribution and activity of species in this taxon.

This study presents the first data on the activity patterns of cracid birds in the Pantanal of Rio Negro obtained through camera-trapping, a reliable tool for the evaluation of activity rhythm in vertebrates (Ridout & Linkie, 2009; Monterroso *et al.,* 2013; Torretta *et al.,* 2017; Mori *et al.,* 2020). The presented data contribute substantially to fill the information gaps concerning our target species and their activity patterns, particularly in the Pantanal of Rio Negro.

The activity patterns described here suggest a clear niche partitioning within their circadian cycles. Furthermore, these patterns are similar to results previously found for other cracids. Given the environmental heterogeneity of the Pantanal, differences in behavior along the day may as well be guided by the capacities of each species, as the high habitat and resource availability allows these animals to occupy a wide variety of niches. Therefore, investigating how organisms occupy a landscape along time may provide support for researchers to better understand the patterns in community structure and interspecific coexistence.

From a conservationist viewpoint, cracids are particularly relevant as they have highly specific ecological requirements and significantly different daily activity patterns allowing species to coexist. Because they are seed predators and dispersers and perform essential services for the dynamics of vegetal communities, understanding their life history is of great conservation interest.

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