



Original investigation

Behavioural ecology in a predator–prey system

Douglas de Matos Dias^{a,*}, Claudia Bueno de Campos^b,
Flávio Henrique Guimarães Rodrigues^a^a Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, Departamento de Biologia Geral, Universidade Federal de Minas Gerais, Avenida Antônio Carlos 6627, Belo Horizonte, MG, CEP: 31270-901, Brazil^b Instituto para a Conservação dos Carnívoros Neotropicais, Pró-Carnívoros, Rua Horácio Neto, 1030, Atibaia, SP, CEP: 12945-010, Brazil

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ABSTRACT

Predator–prey systems are regulated by a behavioral response race, in which the predator develops adaptations that enhance its hunting success and its prey adopt anti-predator strategies. In the present study, we analyzed the activity patterns, the influence of moonlight, and the habitat use of *Leopardus pardalis* and *Puma concolor* in comparison with their potential prey, *Dasyurus novemcinctus*, *Mazama gouazoubira*, *Pecari tajacu*, *Sapajus libidinosus*, *Kerodon rupestris*, *Cuniculus paca* and *Dasyprocta prymnolopha*, in the Serra das Almas Nature Reserve in northeastern Brazil. *Leopardus pardalis* was predominantly nocturnal, while *P. concolor* presented a cathemeral pattern, however, the overlap coefficient between these species was high. The activity of *L. pardalis* overlapped strongly with three typical nocturnal prey (*D. novemcinctus*, *K. rupestris* and *C. paca*). While *P. concolor* had considerable temporal overlap with all prey. Both predators were habitat generalists, in contrast, most prey species exhibited a significant association with a specific type of habitat. The phases of the moon did not influence the activity patterns of the different species, except for *K. rupestris*, which was more active on moonlit nights. Our findings indicate that the predators maximize the efficiency of their foraging behavior by using habitats and the circadian cycle in a more generalist manner.

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Introduction

The co-evolution of predators and prey results in the development of a range of hunting techniques and anti-predator strategies, including behavioral adaptations, such as social organization, habitats preferences, and temporal segregation (Berger, 2010). Activity patterns are behavioral adaptations of the species and can be modified in response to various abiotic and/or biotic factors (Daan, 1981). Temporal adaptations play an important role in the structuring of communities and influence the predator–prey relationship (Daan, 1981). Predators, for instance, tend to synchronize their daily activity patterns with the activity of their main prey as a way to increase hunting success (Jenny and Zuberbuhler, 2005). In the northern hemisphere, some studies have shown that wolves, *Canis lupus* Linnaeus, 1758, adjust their activity patterns to those of their prey during different periods of the year (Theuerkauf et al., 2003; Eriksen et al., 2011). Widely-distributed, opportunistic predators

typically exploit a wide variety of prey, they thus tend to present more variation in activity patterns according to the principle prey species found at different sites (Harmsen et al., 2011; Foster et al., 2013). Mesopredators, those which occupy intermediary trophic levels (Prugh et al., 2009), can also shape their behavior according to the availability of prey. However, these medium-sized carnivores also have to deal with the strong influence of top predators (Oliveira and Pereira, 2014). In this scenario, mesopredators tend to avoid extreme interactions like interference competition and intraguild predation with superior carnivores segregating temporally (Di Bitetti et al., 2010). Temporal partitioning, however, is not always the main mechanism capable of reducing competition or the risk of predation; animals can segregate into other niche axes such as habitat use, for example (Schoener, 1974).

The selection of habitats by the predator, for example, may generally be accounted for by the success of hunting experienced in different types of environment (Gorini et al., 2012). However, spatial heterogeneity, that is, the variation of environments in a landscape, may affect prey vulnerability, and thus influence the behavioral responses induced by the relationship with their predators (Luttbeg et al., 2003; Gorini et al., 2012). In this case, prey species may respond to the presence of predators by avoiding

* Corresponding author.

E-mail addresses: douglasmd@ufmg.br (D. de Matos Dias), cbcampos@procarnivoros.org.br (C.B. de Campos), rodrigues@icb.ufmg.br (F.H. Guimarães Rodrigues).

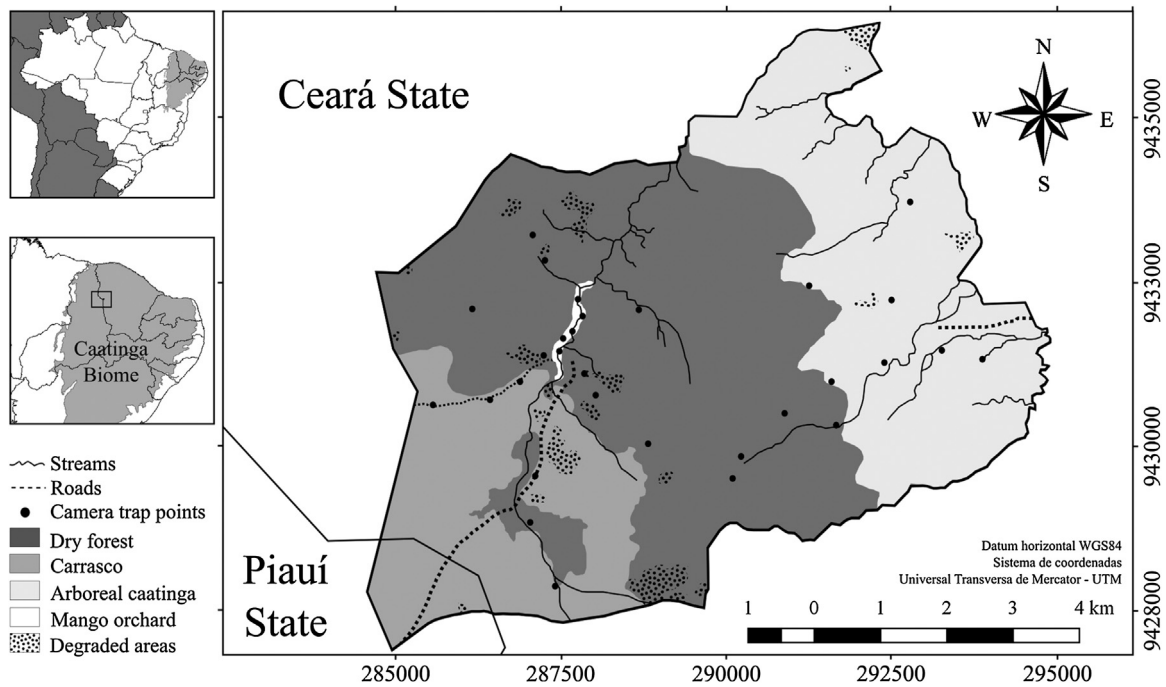


Fig. 1. Location of the Serra das Almas Nature Reserve, in the municipalities of Buriti dos Montes, Piauí state, and Crateús, in Ceará state, Brazil, showing the sampling stations used during the present study.

patches of habitat in which they are more abundant or where a greater risk of predation is perceived (Lima and Dill, 1990). This is the basis of Sih's (1984) model, which proposes that predators and their prey are involved in a behavioral response races, determined by the differential risk of predation in distinct habitat types.

The foraging success of predators and their prey, as well as the risk of predation, may also be affected profoundly by the lunar cycle, which may have a considerable influence on the behavior and ecology of nocturnal species (Prugh and Golden, 2014). These predictions have contributed to the development of the hypothesis of visual acuity, which predicts that the increase in nocturnal luminosity derived from the moonlight will allow visually-oriented prey species to increase the efficiency of their foraging behavior and their capacity for predator detection (Prugh and Golden, 2014). Among nocturnal mammals, species can respond in different ways to the effect of the moonlight. Some primates, for example, are more active on bright nights, since they are dependent on sight to detect predators and find food (Fernández-Duque, 2003; Gursky, 2003; Schwitzer et al., 2007). In contrast, some studies report that on full moon nights, nocturnal rodents and lagomorphs tend to reduce their activity levels in response to the risk of predation (Daly et al., 1992; Griffin et al., 2005). In the tropical forests of Central America, the activity of *P. concolor* and *Leopardus pardalis* (Linnaeus, 1758) was not affected by lunar phases, even with the change in the availability of some prey (Harmsen et al., 2011). For predators, however, little is known about their behavioral responses to the lunar cycle (Sábato et al., 2006).

In this sense, studies involving predator-prey systems are important for a better understanding of interspecific relations, especially in the Brazilian semi-arid biome, where studies on this topic are still incipient (Penido et al., 2017; Marinho et al., 2018). Thus, we describe the pattern of daily activity of two predators and their potential prey in a natural reserve located in the seasonally dry forest of northeastern Brazil (Caatinga biome). We also investigated the degree of temporal overlap between the two predators and later, between each predator and its potential prey. Additionally, we tested habitat use by species through their frequency of

occurrence in each phytophysiognomy of the reserve. Finally, we evaluated the effect of moonlight on species activity.

Material and methods

Study area

The present study was conducted in the Serra das Almas Nature Reserve (SANR), a private natural heritage reserve, which UNESCO has classified as an advanced outpost of the Caatinga Biosphere Reserve. This reserve is located in northeastern Brazil, divided between the states of Ceará and Piauí (Fig. 1).

The reserve covers a total area of 6126 ha of the Caatinga biome, with vegetation in different stages of succession. The annual rains are highly irregular, which is typical of the Brazilian semi-arid zone, with a long dry season, punctuated by short periods of rainfall. During the study, the rainy season was concentrated between February and April, with an average of 409 mm. Due to the topography of the study area, and its location within the ecotone between the Ibiapaba Plateau, which rises to an elevation of 700 m, and the peripheral depression of Crateús, at 300 m, the SANR is characterized by considerable variation in climate, with relatively cooler temperatures and higher precipitation levels at the highest altitudes of the plateau in comparison with the lower elevations of the reserve (Caatinga, 2012).

Three principal phytophysiognomies are found within the SANR – carrasco (dense seasonal scrub), arboreal caatinga (seasonal thorn forest), and dry forest (seasonal montane deciduous forest). The carrasco forms a narrow strip adjacent to the dry forest (Araújo et al., 1999). While there is some disagreement on its phytogeographic classification, Araújo and Martins (1999) define the carrasco as a distinct type of vegetation, with a dense and unstratified canopy, crowns entangled with lianas, scarce emergents, and an extremely dense understory. The arboreal caatinga, located in the peripheral depression, is dominated by trees with a mean height of 8 m. There is also an abundance of cacti and bromeliads, and most trees are deciduous (Caatinga, 2012). This phytophysiognomy can be distinguished from the carrasco vegetation by its greater strat-

ification, the thicker stems of its woody plants and its more open structure (Araújo and Martins, 1999).

The dry forest is seasonally deciduous, with most of the vegetation losing its leaves during the dry season. In the SANR, this habitat is dominated by trees and shrubs, which form a stratified canopy of between 8 m and 12 m in height (Lima et al., 2009). This dry forest can be distinguished from the arboreal caatinga by its greater tree density and, while it is physiognomically distinct from the carrasco, these two habitats share a large number of plant species (Lima et al., 2007, 2009). An abandoned mango orchard (*Mangifera indica* L.) is located in the middle of the dry forest, next to the Melancia stream, a perennial watercourse. The mango orchard extends along a valley bordered by rocky outcrops in many places, and has a grassy herbaceous stratum. During the dry season, this evergreen orchard stands out in the more arid landscape of the Caatinga. This environment is important not only because of the presence of a perennial body of water, but also the availability of fruit, especially during the part of the year when the Caatinga loses most of its foliage. The availability of fruit, water, and shade makes the mango orchard an attractive environment for many animals.

Sampling design

Camera traps were placed at 30 sampling stations, each equipped with one trap to record the presence of the target species over a total of 26 months, including the periods between February and December 2013 (except for April and July), January–October 2014 (except May), and January–August 2015. The camera traps were installed along trails and in the proximity of watering holes (springs, streams, and artificial troughs). The traps covered a total area of 25 km², and the stations active simultaneously were separated by distances of 0.5–1.0 km. The traps were set to record the time and date of each record. Activity patterns were obtained from the camera trap records of the puma, *P. concolor*, and the ocelot, *Leopardus pardalis* (Linnaeus, 1758), together with their potential prey, including gray brocket deer, *Mazama gouazoubira* (G. Fischer, 1814), collared peccary, *Pecari tajacu* (Linnaeus, 1758), paca, *Cuniculus paca* (Linnaeus, 1766), rock cavy, *Kerodon rupestris* (Wied-Neuwied, 1820), nine-banded armadillo, *Dasyurus novemcinctus* Linnaeus, 1758, agouti, *Dasyprocta prymnolopha* Wagler, 1831, and the capuchin monkey, *Sapajus libidinosus* (Spix, 1823). Considering that *L. pardalis* generally hunts small and medium-sized species (Murray and Gardner, 1997; Moreno et al., 2006), we do not consider *M. gouazoubira* and *P. tajacu* as potential preys of this feline in our study. We considered photographs of species taken at a camera site to be independent if images were obtained > 1 h apart.

For the analysis of activity patterns, the nycthemeral cycle was divided into diurnal (06:00–17:59h) and nocturnal (18:00–05:59h) periods (Dias and Bocchiglieri, 2016). We defined that one animal was predominantly nocturnal or predominantly diurnal when the proportion of detections was $\geq 70\%$ in the respective circadian period. When the proportion of records in a given period was less than 70%, we consider that the activity was cathemeral. Strictly diurnal or strictly nocturnal species were those whose records were obtained only during daytime or night time, respectively. The lunar phase was defined for each day of the study period using Quickfase Pro 3.3 (moonconnection.com). As the phase change of the moon, from new to full varies in length (13–16 days), the cycle was standardized according to the phases of the Moon on a scale of 15 levels, ranging from 0 for the new Moon to 14 for the full moon, with the first and last quarters being attributed a score of 7 (see Harmsen et al., 2011).

Data analysis

Through the time records, the general activity pattern of the mammals in the SANR was determined. The nycthemeral distribu-

tion of the camera trap records of each species was tested using a circular statistic, which tests whether the set of angles (that is, the records per hour of the day) is independent and uniformly distributed (Zar, 2010). The uniformity of the circular distribution of the records collected during the study period was verified using Rayleigh's test (Z) and the frequencies were plotted in circular histograms in Oriana 4.01 (Kovach Computing Services, Anglesey, UK).

Through Overlap package (Meredith and Ridout, 2014) we estimate Overlap coefficients between the daily activity patterns of both predator and potential prey. We opted for the estimator of overlapping Δ_1 , recommended for samples <50 records and data were bootstrapped (10,000 samples) to extract 95% confidence intervals (CI) from the overlap coefficients (Ridout and Linkie, 2009; Meredith and Ridout, 2014). Overlap coefficients range from 0 (no overlap), if species have no common active period, to 1 if the activity densities of two species would have complete overlap (Schmid and Schmidt, 2006). To complement the overlap coefficient information concerning predator–prey daily activity a Mardia–Watson–Wheeler (W) test was conducted to compare the 24 h-distribution of records of species according to Monterroso et al. (2014). Could not perform the temporal overlap analysis by habitat due to restrictions on the size of the samples. Thus, we grouped the daily activity records of the species to test the temporal overlap considering the entire reserve area. We classified the force of temporal overlap as low ($\Delta_1 < 0.5$), moderate ($0.5 \leq \Delta_1 < 0.7$) and high ($\Delta_1 \geq 0.7$) (adapted from Monterroso et al., 2014).

The capture success was calculated by dividing the number of detections (photographic records) of each species by the sampling effort in each site and multiplied by 100. This is provided an index of the frequency of occurrence of each species in each habitat sampled in the SANR. As data were not normally distributed (Crawley, 2013), we use generalized linear models (GLMs), corrected with quasi-Poisson error structure, to test the relationship between frequency of occurrence of the species and the habitats sampled. The capture success of predators and prey were calculated for all species for each phase of the lunar cycle, considering only the nocturnal records of the species. These data were then analyzed by Spearman Correlations (r_s) to verify the possible relationship between detection rates and the lunar phase. Statistics analyses were conducted on R-software (R Core Team, 2017).

Results

A total of 499 records of the target species were obtained in the SANR, 39 in the carrasco, 85 in the arboreal caatinga, 254 in the orchard and 121 in the dry forest. The dry forest was the only environment where we recorded all species, while in the arboreal caatinga we recorded only the predators and two preys (*M. gouazoubira* and *P. tajacu*). *Leopardus pardalis* presented a non-uniform activity pattern, and was predominantly nocturnal (Table 1).

While the species was registered during the day, 74.5% of the camera trap records were obtained during the nocturnal cycle (Fig. 2). This contrasts absolutely with the pattern observed in *D. prymnolopha* and *S. libidinosus*, which were strictly diurnal (Fig. 2). *Puma concolor* did not present a preference for any given time of day, i.e., a cathemeral pattern was recorded, and its records were distributed evenly over the circadian cycle (Table 1), with exactly half of the records being obtained during each half of the cycle (Fig. 2). In the case of the ungulates, *P. tajacu* was cathemeral, while *M. gouazoubira* tended to be more diurnal, with activity peaking between 06:00 h and 11:00 h (Fig. 2). Of the other prey species, *D. novemcinctus* and *K. rupestris* were predominantly nocturnal (Table 1), while *C. paca* was strictly nocturnal (Fig. 2).

The temporal overlap coefficient between the two predators was high ($\Delta_1 = 0.73$), but the W test indicated a difference between their

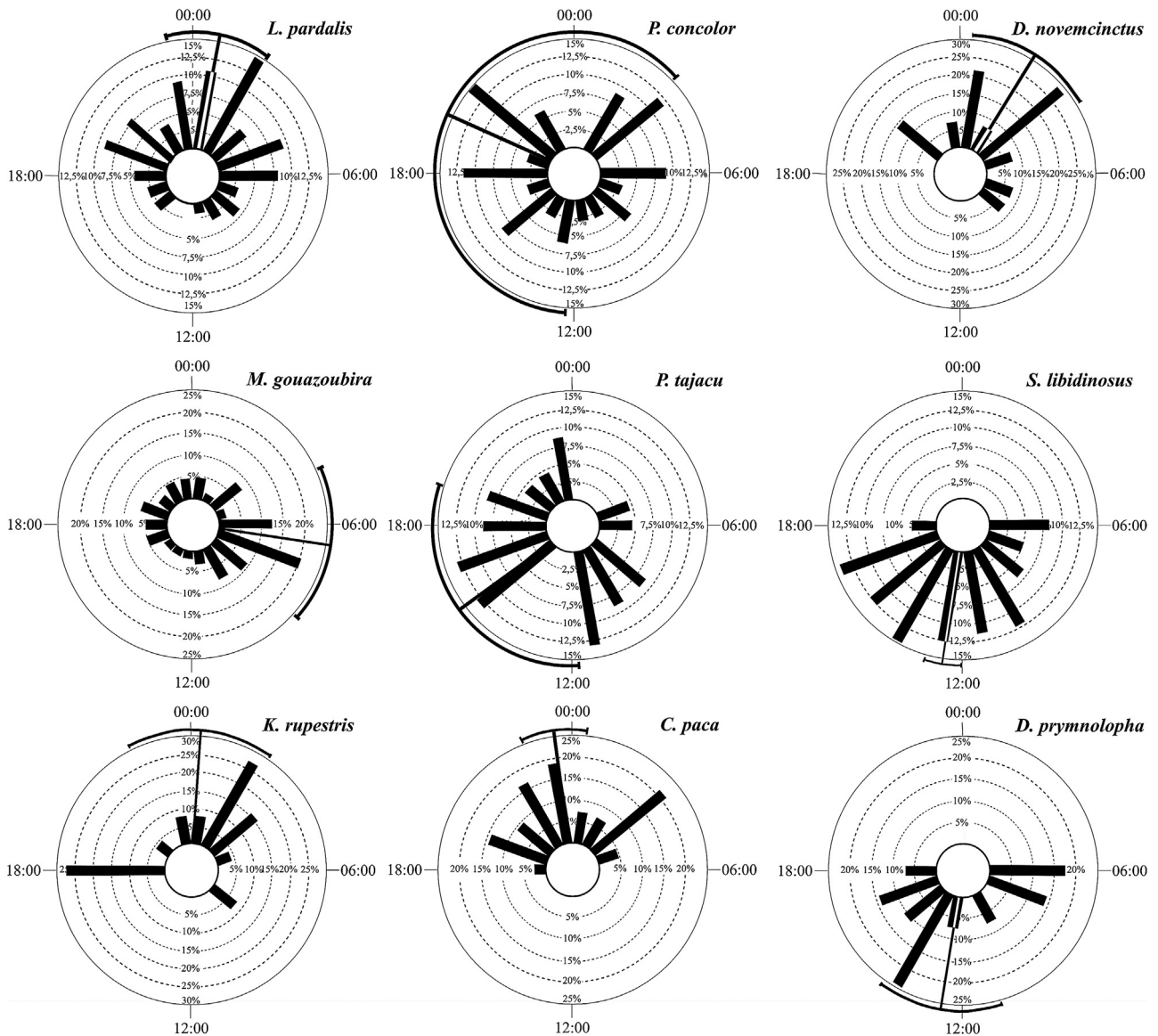


Fig. 2. Circular histograms of the timing of the activity of *Leopardus pardalis* and *Puma concolor*, and their potential prey in the Serra das Almas Nature Reserve in the municipalities of Buriti dos Montes (Piauí) and Crateús (Ceará), Brazil. The columns represent the number of records collected for each species at the corresponding hour of the circadian cycle, while the external line indicates the standard error of the mean.

Table 1
Results of Rayleigh’s uniformity test (Z) for the frequency of records; value of Z for the test of uniformity ($Z_{critical}$), based on the number of independent records (N) collected for each species.

	Z	p	$Z_{critical}$	N	Activity
<i>Leopardus pardalis</i>	12.32	4.4×10^{-6}	2.99	75	Predominantly nocturnal
<i>Puma concolor</i>	0.51	0.606	2.97	34	Cathemeral
<i>Dasyurus novemcinctus</i>	6.45	7.6×10^{-4}	2.94	14	Predominantly nocturnal
<i>Mazama gouazoubira</i>	5.61	0.004	2.98	65	Predominantly diurnal
<i>Pecari tajacu</i>	2.06	0.127	2.96	23	Cathemeral
<i>Sapajus libidinosus</i>	79.42	1.0×10^{-12}	2.99	184	Diurnal
<i>Kerodon rupestris</i>	5.98	0.002	2.97	26	Predominantly nocturnal
<i>Cuniculus paca</i>	22.58	1.8×10^{-10}	2.98	43	Nocturnal
<i>Dasyprocta prymnolopha</i>	8.00	2.0×10^{-4}	2.97	29	Diurnal

daily activities (Table 2) probably due to the cathemeral activity of the puma. The *L. pardalis* activity pattern showed high overlap with *D. novemcinctus*, *K. rupestris* and *C. paca*, with differences in activity distributions only in relation to the latter (Table 2) for being strictly nocturnal. The temporal overlap between this felid and its other potential preys was low (Table 2). The overlap coefficient between *P. concolor* and the two larger prey of the SANR was high, with a difference in daily activity only in relation to *M. gouazoubira* (Table 2) which differently from the puma, was predominantly diurnal. The temporal overlap of this predator with the other preys was moderate.

The predators were recorded in all habitats sampled at the SANR. However, the capture success of *L. pardalis* ($F=0.84$, $p=0.48$) and *P. concolor* ($F=1.98$, $p=0.14$) did not differ between environments. Among the prey species, habitat type influenced the capture success of *M. gouazoubira* ($F=6.45$; $p=0.002$) which, although it occurred in all habitats, was 6.3 times more frequent in the caatinga as well as *P. tajacu*, which also occurred preferentially in this environment

Table 2
Overlap coefficient (Δ_1) between ocelots and their potential prey, 95% confidence intervals (95% CI) and Mardia–Watson–Wheeler test (W).

Species	Δ_1	Lower 95% IC	Upper 95% IC	W	p
<i>L. pardalis</i>					
<i>P. concolor</i>	0.73	0.63	0.89	6.72	0.04
<i>D. novemcinctus</i>	0.73	0.62	0.96	3.20	0.20
<i>S. libidinosus</i>	0.36	0.23	0.39	116.04	1.0×10^{-12}
<i>K. rupestris</i>	0.70	0.54	0.85	0.64	0.72
<i>C. paca</i>	0.75	0.63	0.84	9.02	0.01
<i>D. prymnolopha</i>	0.36	0.20	0.42	42.23	6.8×10^{-10}
<i>P. concolor</i>					
<i>D. novemcinctus</i>	0.56	0.39	0.78	8.63	0.01
<i>M. gouazoubira</i>	0.70	0.54	0.84	7.30	0.03
<i>P. tajacu</i>	0.73	0.59	0.91	1.80	0.41
<i>S. libidinosus</i>	0.55	0.39	0.67	27.15	1.3×10^{-6}
<i>K. rupestris</i>	0.58	0.38	0.71	6.42	0.04
<i>C. paca</i>	0.57	0.40	0.69	19.45	5.9×10^{-5}
<i>D. prymnolopha</i>	0.52	0.34	0.64	13.05	0.001

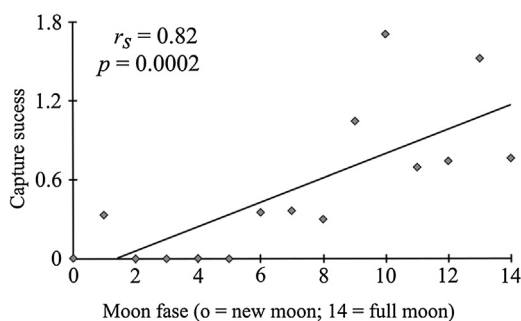


Fig. 3. Variation in the nocturnal capture success for *Kerodon rupestris* according to the phase of the lunar cycle in the Serra das Almas Nature Reserve in Ceará, Brazil.

($F = 10.13$; $p = 0.0001$). *Cuniculus paca* was recorded only in the dry forest and mango orchard, being significantly more frequent in the latter ($F = 4.37$, $p = 0.01$), while the capture success of *D. prymnolopha* was higher in the dry forest ($F = 10.21$; $p = 0.0001$). *Dasypros novemcinctus* occurred in all habitats, except in the caatinga, while *S. libidinosus* and *K. rupestris* were restricted to mango orchards and dry forest, but there was no difference in habitat use for these species ($p > 0.05$).

Kerodon rupestris was the only species in which the activity period varied significantly according to the phase of the moon, with activity increasing on more moonlit nights (Fig. 3).

Discussion

Surprisingly, we did not detect influence of *P. concolor* on the activity or habitat use by *L. pardalis*. Interference competition and intraguild predation are extreme ecological interactions, through which large carnivores can influence the distribution and behavior of subordinate species (Oliveira and Pereira, 2014). Studies have indicated that temporal and spatial segregation have been some of the strategies adopted by small felines as a way of avoiding competition and the risk of fatal encounters with large predators (Di Bitetti et al., 2010). In our study, however, we found a high temporal overlap between *L. pardalis* and *P. concolor*. Furthermore, both predators were common throughout SANR, without preference for a specific habitat, also indicating a spatial overlap. Our results suggest that coexistence between these predators in the SANR can be facilitated by segregation in other niche axes such as diet, for example. This is perfectly plausible, given the difference in body size between these species. In this sense, we believe that the pattern of activity and habitat use by *L. pardalis* and *P. concolor* in our area of study are more related to prey activities than avoidance of each other.

The predominantly nocturnal activity pattern of *L. pardalis* in the SANR is similar to that recorded in other regions (Di Bitetti et al., 2010; Penido et al., 2017). In our study, the activity this felid coincided with the periods during which three species potential prey—*D. novemcinctus*, *K. rupestris* and *C. paca*—were most active, with peaks of activity being recorded primarily during the second half of the nocturnal period. In addition, the three preys were restricted to the mango orchard and the dry forest. The exception was *D. novemcinctus*, which also occurred in the carrasco, environments frequently used by *L. pardalis*. However, only *C. paca* showed significantly higher frequency in mango orchard. The preference of *C. paca* for this habitat may be related to fruit availability, especially during the dry season in the Caatinga, besides the presence of the perennial stream. Notably, this rodent usually lives close to water courses, which use as an escape route in dangerous situations (Oliveira and Bonvicino, 2011). The high temporal overlap and similarities in habitat use suggest that this group of prey (*D. novemcinctus*, *K. rupestris* and *C. paca*) represents an important food base for *L. pardalis* in the SANR. Therefore, our findings corroborate previous studies on the diet of this carnivore, since in other Brazilian regions, both *D. novemcinctus* and *C. paca* are among the most important prey for *L. pardalis*, mainly in terms of biomass (Moreno et al., 2006; Bianchi and Mendes, 2007; Bianchi et al., 2010). *Kerodon rupestris*, in turn, is an endemic rodent of the Caatinga (Willig and Lacher et al., 1991) and although it is widely distributed in the biome, the predation of this species by *L. pardalis* has not yet been documented. This is due to the fact that studies on diet of carnivores in this region are rare (Olmos, 1993; Dias and Bocchiglieri, 2015). However, smaller rodents of the same size as *K. rupestris* make up a significant portion of the *L. pardalis* diet (Moreno et al., 2006; Bianchi et al., 2010; Dias and Bocchiglieri, 2015). That said, we consider this rodent as a potential prey of *L. pardalis* in the RNSA.

In general, *P. concolor* is predominantly nocturnal (Scognamillo et al., 2003; Harmsen et al., 2011), although in the SANR, this feline presented a cathemeral activity pattern, with equal proportions of records being obtained during the diurnal and nocturnal periods. A similar pattern was observed in the Gran Chaco of Bolivia (Maffei et al., 2002) and in tropical dry forest in Mexico (Hernández-Saintmartín et al., 2013), which, curiously, share many characteristics with the SANR, including a highly seasonal climate, accentuated variation in temperature, and a scarcity of perennial water sources. This pattern is surprising, since in extreme environments such as semi-arid ecosystems, carnivores tend to be more nocturnal, as a way to avoid intense heat during the day (Penido et al., 2017). In this sense, it is believed that the pattern of cathemeral activity observed in *P. concolor* in these localities is a reflection of the low level of anthropic disturbance (Hernández-Saintmartín et al., 2013). Indeed, the perimeter of the SANR is fenced off, and its trails and borders are monitored systematically, which minimizes the presence of human intruders and domestic animals within the area. This reduced risk of encounters with humans may allow *P. concolor* to be more active during the day within the limits of the reserve.

Alternatively, cathemeral activity increases the probability of encountering a more diverse prey basis (Scognamillo et al., 2003). Some authors (e.g., Núñez et al., 2000; Scognamillo et al., 2003; Harmsen et al., 2011) have suggested that the activity pattern of *P. concolor* is determined by that of its prey. In the Brazilian Pantanal wetlands, for example, *P. concolor* is more active during the day, which may reflect an association with the diurnal activity period of *H. hydrochaeris*, one of its principal prey species in this biome (Foster et al., 2013). In our study area, the pattern of *P. concolor* activity strongly overlapped with the daily activity of ungulates, which are the largest prey of the reserve. Both *M. gouazoubira* and *P. tajacu*, respectively, presented predominantly diurnal and cathemeral habits, moreover, occurred preferentially in the arboreal

caatinga. Peaks of activity in the daytime and preference for open habitats may be beneficial for these visually oriented species, since it facilitates the detection of the predator and consequently reduces the risk of predation (Prugh and Golden, 2014).

The predator-prey relationship in mammals has been considered to be a behaviorally sophisticated game of discretion and fear, in which a responsive prey attempts to avoid capture by a predator (Brown, 1999). As most environments are divided into patches of habitat, both predators and prey need to transit among these patches according to their biological needs. In this context, the prey seeks out patches that offer the best combination of feeding resources, refuge, and protection from predators, while the predators, in turn, search for patches that offer the best hunting opportunities (Laundré et al., 2010). *Mazama gouazoubira* are highly adaptable, and are generally associated with open areas, although they may typically seek refuge in patches of forest (Duarte et al., 2012). *Pecari tajacu* in turn is a gregarious species whose group cohesion facilitates the defense against predators (Tiepolo and Tomas, 2011). These ungulates are also highly adaptable and generalist in habitat use and occur frequently in open areas (Tiepolo and Tomas, 2011; Duarte et al., 2012). This allows for the detection of predators such as *P. concolor* that has a stealth mode of hunting and depends on structurally complex environments to surprise their prey (Elbroch and Wittmer, 2012).

It is notable the considerable temporal overlap between *P. concolor* and the other prey, both diurnal and nocturnal in the SANR. Added to this, its plasticity in habitat use makes it a generalist predator. The opportunistic behavior of *P. concolor* and its capacity to adapt to an enormous diversity of habitats and prey contribute to its status as one of the most successful carnivores of the Neotropics (Iriarte et al., 1990). The feeding behavior of this feline may vary considerably within its geographic range, influenced by a variety of factors, including sympatry with larger predators, such as *P. onca* (Iriarte et al., 1990; Moreno et al., 2006). As there is no competition from jaguar in the SANR, this probably favors a broadening of the spectrum of prey available to *P. concolor*, which may include prey of different sizes in your diet. This may explain the temporal synchronism of this predator with all prey evaluated.

Of the prey species studied in the SANR, only *K. rupestris* was significantly more active on moonlit nights. More illuminated nights facilitate the visualization of predators, making detection and avoidance mechanisms more effective (Prugh and Golden, 2014). These rodents are also gregarious (Oliveira et al., 2006), which reinforces the effectiveness of their vigilance during foraging, and are habitat specialists, living in cavities in rocks to protect themselves from predators. *Kerodon rupestris* also emits alarm vocalizations, which are used to alert the colony in situations of potential risk. When detecting the approach of predators from a distance, the cavies retreat to nearby rocks when the sentinels emit an alarm. This avoidance strategy is an adaptation to the rocky habitat occupied by this species, which limits its field of vision and detection of visually-oriented predators (White, 2009).

Activity in neither *L. pardalis* nor *P. concolor* varied with moonlight levels in the SANR, a pattern similar to that found in other studies (Maffei et al., 2005; Lucherini et al., 2009; Pratas-Santiago et al., 2016; Huck et al., 2017). The generalist behavior of these predators may reflect an adjustment to local conditions and the availability of prey. As observed in other areas, many prey species attempt to minimize the risk of predation by reducing their activity on more moonlit nights (Kotler et al., 2004; Harmsen et al., 2011; Marinho et al., 2018). Prey animals must cope with the conflicting demands of obtaining resources and avoiding predators, which invariably reduces the efficiency of their foraging behavior (Harmsen et al., 2011). In the SANR, however, moonlight did not influence behavior patterns, except in *K. rupestris*. The other prey species avoided encounters with predators through strategies

related to habitat selection and/or behavioral traits such as living in group.

Our results indicate that most prey species studied in the SANR are more selective in relation to habitat use and activity period, while *L. pardalis* and *P. concolor* occupy time and space in a more generalist way. The temporal synchronization of the activity pattern of *P. concolor* with those of most of its prey species thus suggests that this predator has access to a wide range of prey that are active over different periods of the circadian cycle, permitting the broadening of its trophic niche. This ecological release usually occurs where jaguars are absent (Moreno et al., 2006).

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