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Research Article

Population density, activity pattern and habitat use of the ocelot *Leopardus pardalis* in an Atlantic Forest protected area, Southeastern Brazil

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Abstract

The ocelot *Leopardus pardalis* (Linnaeus, 1758) is a nocturnal opportunistic felid that has a wide geographic distribution in almost every American continent. Although this species is classified as Least Concern, its populations have been declining as a direct consequence of the destruction of their habitats. Information on the density, occupancy and factors influencing habitat use of ocelots is of great importance for the establishment of action plans aimed for conservation. We studied ocelots in a protected area of the Atlantic Forest, Vale Natural Reserve, state of Espírito Santo, Brazil. We estimated density, characterized activity patterns, and evaluated how habitat use was influenced by six covariates. Estimated density (Mean±SE; 45.84±5.45 ocelots per 100 km^2) was higher than other areas studied within the Atlantic Forest. Ocelots were more active during twilight and night than other times of day (between 1330 and 2030 h and 2330 and 0400 h). The probability of occupancy was influenced by distance to the closest water resources (negatively), canopy cover, distance to the edge and number of prey (all three positively influenced), and the detectability was negatively influenced by distance from a water resource. Our data reinforce the importance of VNR as an important reservoir of the species. Therefore, the results presented herein can be a starting point to support future action plans for the species, making predictions regarding the ecosystem and management and conservation of the ocelot by using tools such as Population Viability Analysis. Furthermore, the results can be used as a surrogate for other regions in which the species occurs, because many locations may be affected by the same covariates used herein.

Introduction

Understanding how species use certain habitats allows us to better comprehend their ecology, making it possible to find patterns that explain variation in abundance and temporal and spatial distributions (Massara et al., 2018; Phillips et al., 2004). Characterizing these ecological aspects is crucial for management and conservation measures (Abrahms et al., 2016; Law and Dickman, 1998). Species are, in a way, selective, and have different associations with the structures that make up the habitat (Morris et al., 1987): for example, dense canopy cover, and presence of water resources may have positive effects on the abundance of some organisms (Ferreguetti et al., 2017; Crawshaw, 1991), while the proximity of habitat edges may be associated with a decrease of some organisms (Ferreguetti et al., 2016; Paviolo et al., 2009; Asquith and Mejía-Chang, 2005; Cullen et al., 2001).

As predators occupying the highest trophic levels, wild cats play a key role in ecosystems, which is especially important to their prey populations (Galetti et al., 2015; Terborgh et al., 1999; Wright et al., 1994). The absence or strong decrease of top species can lead to consequences as a hyper-increase of primary consumers, and may cause a great loss in the diversity of plants and animals through trophic cascades (Galetti et al., 2015; Terborgh et al., 2001) or may generate an increase in the density or distribution of mesopredators, in the called "mesopredators release" (Prugh et al., 2009).

The ocelot (*Leopardus pardalis*) is the largest mesofelid in Brazil, with an average weight of 11 kg and an average body length of 77.3 cm (Paviolo et al., 2015; Reis et al., 2006). It has a wide geographic distribution, extending from the south of the USA to South America, where it can be found in all countries except Chile (Paviolo et al., 2015). It inhabits all regions of Brazil, occurring in almost all biomes of the country (Amazon, Caatinga, Cerrado, Pantanal and Atlantic Forest) inhabiting forests, shrublands and savannas (Paviolo et al., 2015; Reis et al., 2006). Although nowadays its status is classified as "Least Concern", according to the IUCN Red list and Red list of the Brazilian Fauna (ICMBio., 2018; Paviolo et al., 2015), the present populations appear to be declining, mainly due to the habitat loss. Ocelots are typically nocturnal-crepuscular, with only moderate activity during daytime (Oliveira and Cassaro, 2005), which likely reflects its diet (Pérez-Irineo and Santos-Moreno, 2014) that consist primarily of nocturnal preys such as small mammals (rodents and marsupials) (Emmons, 1988), although larger animals such as armadillos, agoutis, pacas, primates, sloths, some birds and reptiles and fishes can also be a part of its diet (Giordano et al., 2018; Santos et al., 2014; Bianchi et al., 2010; Wang, 2002). Movements of ocelots also seem to be associated with forests of dense vegetation cover, avoiding open areas (Pérez-Irineo and Santos-Moreno, 2014; Di Bitetti et al., 2006).

We sought to provide additional data on ocelot ecology by using camera traps to estimate the density and to characterize activity patterns, and occupancy to evaluate habitat use. We evaluated whether occupancy would be higher in areas of denser vegetation, that were

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closer to water resources, and where prey was more common. Additionally, we expected the species to avoid near primary roads.

Methods

Study area

The study was conducted in the Vale Natural Reserve (VNR), located in the northern region of the state of Espírito Santo, between the municipalities of Linhares and Jaguaré (19°06'– 19°18' S and 39°45'– 40°19' W, Fig. 1).

The VNR was established gradually by a process of land acquisition that started in 1955, when Vale Company bought its first properties in the region. Currently, the VNR owns about 23,000 ha of forest, and together with the Sooretama Biological Reserve (24,000 ha) and two Private Reserves of Natural Heritage (RPPN), RPPN Recanto das Antas (2,212 ha) and RPPN Mutum Preto (379 ha) form a forest continuum of 50,000 ha. This large block is the largest forest remnant of Coastal Plain Forest in the entire Southeast region of Brazil (Ribeiro et al., 2009). The VNR is a mosaic dominated by four main vegetation types (Peixoto and Gentry, 1990): 1) coastal plain forest that covers almost 68% of the total area, 2) riparian forest associated with water bodies that covers about 4% and is characterized by sparse trees and a predominance of palm trees, 3) sandy soil forest that covers about 8% and is similar to initial or middle stages of regeneration, and 4) natural grassland that covers about 6% of the area that occurs in areas that were ponds in previous geological periods.

Camera trapping

We used a digital map to divide the reserve into several grids with a minimum size of 1 km^2 to increase the chances of independence between sampling points. We then selected 39 sampling sites using a systematic sampling design so that all four of the principal vegetation types were well represented (Fig. 1). Inside each of these grids, we established a random point where we installed one passive infrared Bushnell® camera trap in about 40 to 50 cm above the ground. We examined all stations every 20–25 days to change batteries, when necessary. Traps were programmed to operate for 24 h/day in picture function with three consecutive shoots, during the period between April 2013 to June 2014 (Ferreguetti et al., 2015).

Occupancy and detectability covariates

We used 6 covariates to model occupancy and detectability probability of ocelot: understory cover ("under", in %), distances to forest edge ("edge", in m), the closest water resource ("water", in m), and BR-101 Highway ("road", in m), canopy cover ("canopy", in %), and

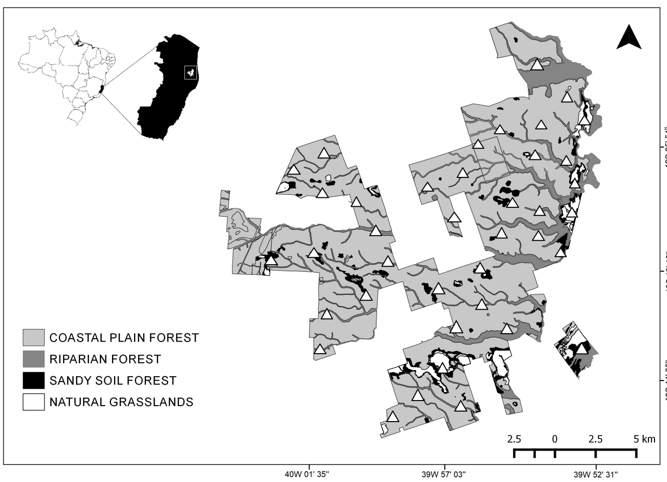

Figure 1 – Distribution of the camera traps (represented by triangles) within the habitat mosaic map inside the Vale Natural Reserve, Espírito Santo, Brazil.

Table 1 – 20 single-season occupancy and detectability models for ocelot (*Leopardus pardalis*) in the Vale Natural Reserve, Brazil, estimated by camera-trapping between May 2013 and June 2014, grouped in sampling intervals of 5 consecutive days. Covariates: distance to forest edge (in meters; edge); distance to road (in meters; road); distance to closest water resources (in meter; water); frequency of preys (total number of preys recorded; prey); canopy cover (in percent; canopy); and understory cover (in percent; under). Ψ=occupancy, p=detectability, AICw=Akaike weight, N=number of parameters.

Model	AIC	ΔAIC	AICw	N
Ψ(canopy;prey;water;edge);p(water)	602.12	0	0.486	7
Ψ(canopy;prey;water);p(water)	603.56	1.44	0.334	6
Ψ(prey;water);p(water)	605.89	3.77	0.091	5
Ψ(canopy;water);p(water)	606.98	4.86	0.062	5
Ψ(canopy;prey);p(water)	608.23	6.11	0.021	5
Ψ(prey);p(water)	608.78	6.66	<0.001	4
Ψ(water);p(water)	609.18	7.06	<0.001	4
Ψ(edge;water);p(water)	609.67	7.55	<0.001	5
Ψ(edge;prey;water);p(water)	609.98	7.86	<0.001	6
Ψ(.);p(water)	612.45	10.33	<0.001	3
Ψ(canopy;prey;water;road);p(water)	612.65	10.53	<0.001	7
Ψ(prey;water;road);p(water)	612.68	10.56	<0.001	6
Ψ(prey;water;edge;road);p(water)	613.08	10.96	<0.001	7
Ψ(canopy;water;edge);p(water)	613.54	11.42	<0.001	6
Ψ(prey;edge);p(water)	615.87	13.75	<0.001	5
Ψ(canopy;edge);p(water)	615.88	13.76	<0.001	5
Ψ(canopy;prey;water;edge;road);p(water)	615.92	13.8	<0.001	8
Ψ(canopy;prey;water;edge;under);p(water)	616.78	14.66	<0.001	8
Ψ(prey;water;under);p(water)	617.23	15.11	<0.001	6
Ψ(canopy;prey;water;under);p(water)	617.56	15.44	<0.001	7

frequency of prey species ("preys", in number of records per camera-trap).

At each sampling point, we established 4 plots (30×50 m) arranged by the cardinal compass points (north, south, east, and west). For all plots, canopy cover was estimated with a convex spherical densiometer and using digital camera images. Understory cover was measured along the central (longitudinal) line of each plot, considering 5 m on each side of the line (transect width of 10 m). Understory cover was measured every 10 m using a 2.0x0.5 m sighting frame (each 0.5 m^2 portion representing 25% visibility).

Frequency of prey was calculated by records of potential prey captured by camera traps, and included mammals, such as rodents (*Cuniculus paca* and *Dasyprocta leporina*) and armadillos (*Dasypus novemcinctus*), birds (*Tinamus solitarius*, *Crax blumenbachii* and *Penelope superciliaris*), and reptiles (*Salvator merianae*) (Bianchi et al., 2010).

Three spatial covariates—distance to forest edge, water resource, and main road—were quantified for each of the 39 sampling sites using ArcGIS software (ESRI*ArcMap 10.1, Redlands, California—ESRI 2011).

Data analysis

Density

We identified individual ocelots using their unique coat patterns to create individual-by-trap encounter histories, containing the number of records of an individual at a given camera-trap. We used only records from the left side of ocelots due to the more frequency of records as detailed in the Results section. We excluded records that we could not accurately identify at the individual level for this step. We considered only 105 sampling days (4 months, between April to August 2013) to generate the density estimate. We analyzed these data using closed, spatially explicit capture-recapture models (SECR). SECR models assume that animals have approximately circular and randomly distributed home ranges (Borchers and Efford, 2008; Efford, 2004). We implemented these models in the R software package `secr` (v. 2.9.5 and 2.10.4; Efford 2015, 2016) to estimate three parameters in separate analyses for the VNR: density (*D*), detection probability of an individual at its activity center (*g0*), and the spatial scale over which detection probability declines as the distance between an individual's activity center to the detection device increases (σ). We used a half-normal detection function for our observation model and a homogeneous Poisson distribution as our state model, which assumes latent activity centers are distributed evenly across the landscape (Efford et al., 2009). We assumed that parameters remained constant across all survey (105 sampling days). Spatially explicit capture–recapture also requires a habitat mask. We defined the habitat mask as the area of integration (i.e., area of interest that contains all possible latent activity center locations) that includes all animals observed during the study (Ivan et al., 2013). We generated the habitat mask by buffering outermost camera-trap stations by 3230 m. This corresponds to approximately 2xσ, which should be large enough to contain all potential home range centers of ocelots exposed to our sampling grid (Royle et al., 2014). To calculate ocelot trap success, we divided the number of ocelots captures by the total of trap nights multiplied by 100.

Occupancy and detectability models

To classify the data obtained using the camera traps and to model the probability of occupancy and detectability, sampling intervals of five days were marked as one occasion, forming a total of 40 occasions. The ocelot was then represented as: present (1), on occasions that it had been recorded, or non-detected (0), on unregistered occasions. A single-season model was used (MacKenzie et al., 2006), which considered that the occupancy status for each species was constant throughout the study, allowing the use of closed occupancy models to explore covariates.

We constructed a set of candidate models for the species, which were selected by a priori hypotheses based on two different approaches: (1) determining the 'best-fit' model for detection probability while holding occupancy constant; and (2) determining the 'best-fit' model for occupancy while modeling detection as determined by the 'best-fit' model in component 1, above. This allowed us to evaluate differences in occupancy as determined by a single covariate or using additive models with a set of covariates, which would contribute to an improvement in the model's performance. The occupancy models were fit in program PRESENCE version 12.7. We used Akaike Information Criterion adjusted for small samples (AICc; Akaike 1973) to compare candidate models, and considered models with ΔAICc<2 as equivalent. We also estimated the AICc weight (*wi*) for each model, which corresponds to how much each model influenced the occupancy.

Activity

We used the time that individuals were photographed in the camera–trap to evaluate the activity of ocelots in the VNR. A conditional circular kernel density function was applied to the time data to estimate the activity pattern, following Oliveira-Santos et al. (2013). This analysis was conducted in the `Circular` package in R. Circular summaries were used to determine the mean overall timing of the activity as recorded by camera traps (Lund and Agostinelli, 2007).

Results

Density

We obtained 165 independent records from the left side of the body of 42 individuals (25 males, 15 females and 2 unknown sex), the records of the right side of the ocelots' bodies (79 records) were discarded. We obtained 55 recaptures (of 12 males and 8 females). In total, 2 individuals were captured at more than one camera-trap station (2 males) and 12 individuals were recaptured multiple times at the same station (5 males and 7 females). Overall trap success was 5.25 ocelot captures per 100 trap nights. Estimated density was 45.84$\pm$5.45 [SE] ocelots per 100 km^2 (Mean$\pm$SE), the estimated movement parameter σ was 1.65$\pm$0.2 km, and the estimated baseline encounter rate λ^0 was 0.2$\pm$0.03 (Mean$\pm$SE).

Occupancy

Between May 2013 and June 2014, we obtained 382 photographs of ocelot. On these 40 occasions, 93 records (83%) were in the coastal plain forest, 17% in the sandy soil forest, and none in natural grasslands. Two of the 20 models we considered were approximately equivalent (Tab. 1). Occupancy varied with four covariates (Fig. 2): distance from forest edge had a positive effect on occupancy, distance to the closest water resource had a negative effect on occupancy, canopy cover had a positive effect, and the number of prey had a positive effect on the occupancy rate. Detectability varied with one covariate, distance to the water resource (Fig. 3), which showed a negative relationship reaching zero detectability before reaching 1 km.

Activity

Ocelot were most active in the twilight and at night, with two peaks of activity (Fig. 4). One peak was between 1730 and 2030 h and one was between 2330 and 0400 h. The species was not recorded between 1200 and 1330 hours.

Discussion

Density and population size

The ocelot's density that we estimated (45.8 individuals per 100 km^2) is the first from an Atlantic Forest area based on a spatially explicit capture-recapture model approach. Ocelot density studies in the Atlantic Forest reported estimates varying from 4 individuals per 100 km^2 in Caraguatá Reserve, Brazil (Goulart et al., 2009) up to 117 individuals per 100 km^2 in the Fazenda Macêdonia Reserve, Brazil (Massara et al., 2015). Fifteen studies in this biome found lower density estimations for the species than those in the present study and five found near or greater values (Tab. 2). However, all those previous studies in the Atlantic Forest were based on non-spatial capture-recapture models making comparisons between studies difficult (Rocha et al., 2016; Ivan et al., 2013).

Occupancy

The canopy cover variable presented a positive relationship with the occupancy rate, thus showing that the ocelot prefers denser forest environments. According to Harveson et al. (2004) the ocelot is considered a specialist habitat species, preferentially using heavily forested environments with a closed canopy cover (>95%), avoiding open areas (<75%). The ocelot showed a low occupancy in places near the forest edge, which infer a preference for the forest interior. This may be caused by the edge effect in the VNR, since the reserve has an irregular form which increases this effect. The matrix that surrounds the VNR is composed of large agricultural and urban properties and, according to Cruz et al. (2019), among all the smaller felids, the ocelot is the most sensitive to human disturbance, being strongly affected by land uses and the lack of forest.

The sites with the highest frequency of prey presented an increase in the occupancy rate of the ocelot. This response is justified because the population density of the ocelot is dependent on the quantity of prey in the environment (Connolly, 2009; Emmons, 1988), what is also seen with other felids (Carbone et al., 2011; Karanth et al., 2004; Polisar et al., 2003). The distance to the water resource was a key variable for the occupancy of the ocelot, the more distant the sampling site was from the source of water the less the presence of the species in the region, with a marked variation mainly in the first kilometer. Consequently, ocelot's detectability was also low in places far from water resources. In studies with other cats, as in the case of jaguars, the distance from the water source was a major response factor that caused a limitation in their distribution and allowed a possible explanation for their distribution patterns (Hatten et al., 2003). There is a gap in studies that used this covariate to determine the occupancy and factors influencing habitat use by ocelot and even within the studies that used this variable, the results were significantly different, presenting from neutral to negative

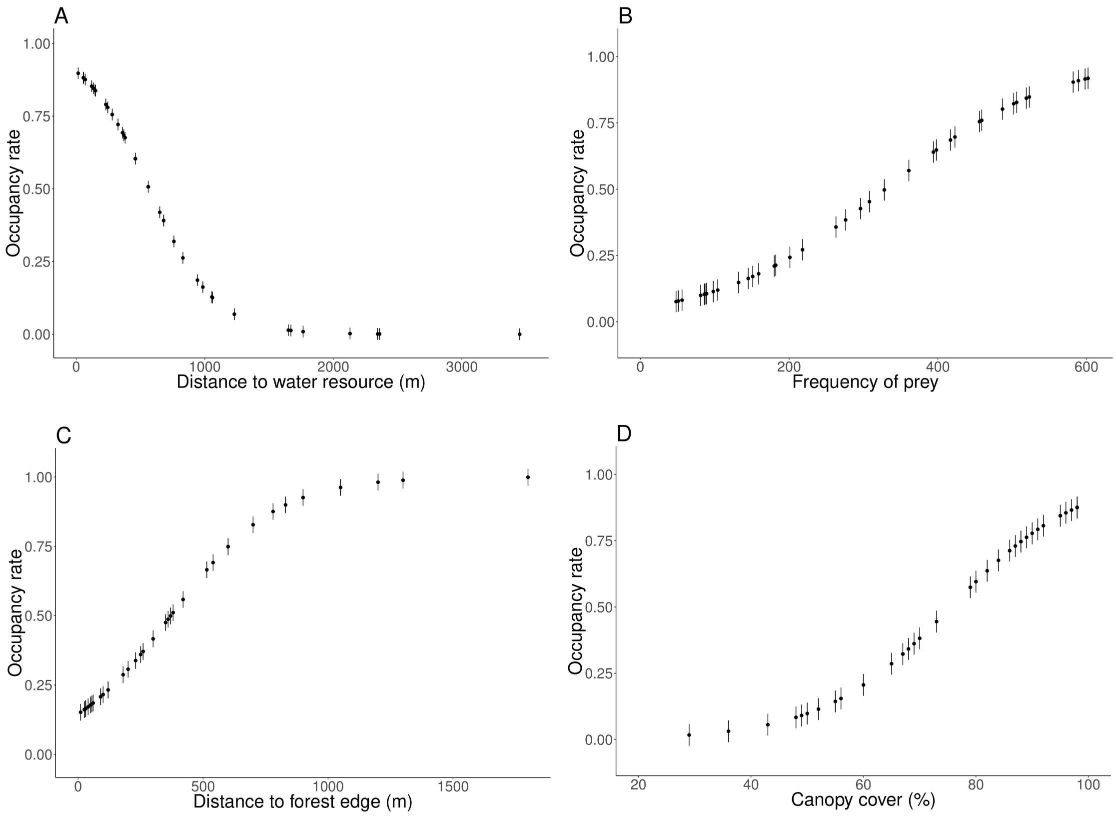

Figure 2 – Relationships between the occupancy rate of the ocelot (*Leopardus pardalis*) and A) distance to water resource; B) frequency of prey; C) distance to the edge; and D) canopy cover. Data was estimated by camera-trapping at the Vale Natural Reserve between May 2013 and June 2014, grouped in sampling intervals of 5 consecutive days.

effects in the presence of ocelots close to water resources (Vera, 2017; Pérez-Irineo and Santos-Moreno, 2014; Connolly, 2009).

The two variables that did not present significant responses were distance to the BR-101 road and understory cover. The lack of response to the BR-101 may be because just a small part of the highway crosses the VNR, in an area very close to the edge of the reserve which is already avoided by the ocelot. However, it is possible that a higher effect may be found in the Sooretama Biological Reserve (SBR) because the BR-101 road intercepts the SBR on a stretch of 5.7 km (Srbek-Araujo et al., 2015).

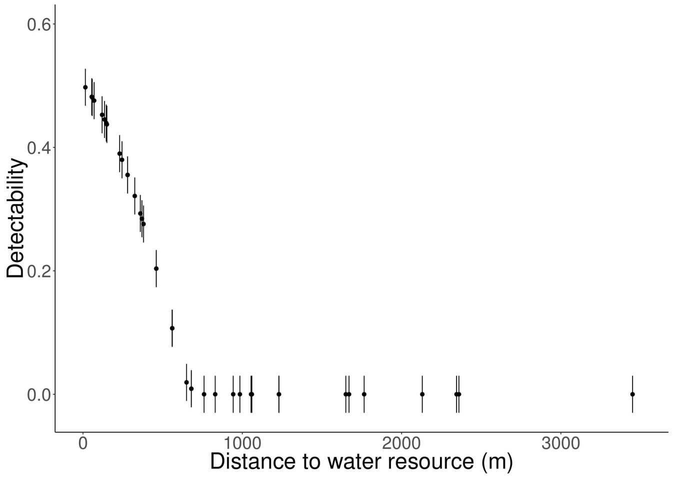

Figure 3 – Relationships between the detectability of ocelot (*Leopardus pardalis*) and distance to closest the water resource. Data was estimated by camera-trapping at the Vale Natural Reserve between May 2013 and June 2014, grouped in sampling intervals of 5 consecutive days.

Activity

Ocelots are mainly nocturnal and crepuscular in the VNR, presenting a significantly lower activity during the middle of the day (12:00 to 13:00). This nocturnal pattern has been previously reported in other studies (Salvador and Espinosa, 2016; Kolowski et al., 2010; Goulart et al., 2009), however the degree of activity of ocelot seems to vary from one region to another, presenting peaks even during the day (10:00 to 12:00 - De La Torre et al. (2016)). Nocturnal behavior of ocelot may reflect the activity patterns of their prey (Pratas-Santiago et al., 2016;

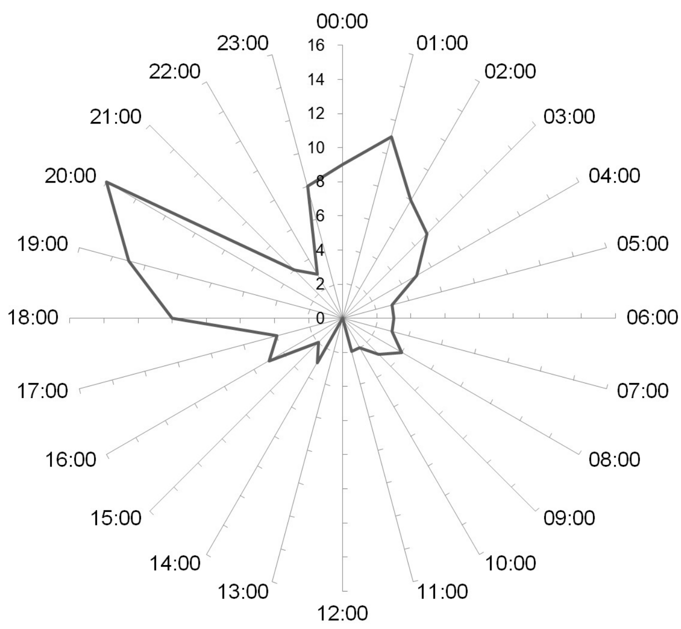

Figure 4 – Circadian activity pattern of *Leopardus pardalis* in the Atlantic Forest in the Vale Natural Reserve, Espírito Santo, Brazil, estimated by camera-trapping between May 2013 and June 2014.

Table 2 – Comparison of estimated ocelot densities for sites in the Atlantic Forest Biome where camera-trap surveys in combination with capture-recapture models (HMMDM— half the mean maximum distance moved— and SECR —spatially explicit capture–recapture—) were used to estimate ocelot density. Studies are listed chronologically, and the density values are reported in ocelots per 100 km^2 .

Country	Study site	Density	Method	Source
Brazil	Caraguatá Reserve	4	HMMDM	Goulart et al. (2009)
Brazil	Feliciano Miguel Abdala Reserve	5	HMMDM	Massara et al. (2015)
Brazil	Sete Salões State Park	6	HMMDM	Massara et al. (2015)
Argentina	Yabotí Biosphere Reserve	8.6	HMMDM	Di Bitetti et al. (2008)
Brazil	Serra do Brigadeiro State Park	9	HMMDM	Massara et al. (2015)
Brazil	Mata do Sossego Reserve	13	HMMDM	Massara et al. (2015)
Argentina	Urugua-í	13.3	HMMDM	Di Bitetti et al. (2006)
Brazil	Turvo State Park	14–26	HMMDM	Kasper et al. (2015)
Brazil/Argentina	Iguaçú/Iguazú National Parks and San Jorge Forest Reserve	16.8	HMMDM	Di Bitetti et al. (2008)
Brazil	Ponte Branca—ESEC MPL	17	HMMDM	Lima (2009)
Argentina	Iguazú National Park	19.9	HMMDM	Di Bitetti et al. (2006)
Brazil	Ilha do Cardoso	21	HMMDM	Fusco-Costa et al. (2010)
Brazil	Rio Doce State Park	24	HMMDM	Massara et al. (2015)
Brazil	Seis R	25	HMMDM	Lima (2009)Lima, 2009
Brazil	Morro do Diabo State Park	31.3	HMMDM	Jacob (2002)
Brazil	Ilha do Cardoso State Park	40	HMMDM	Costa (2007)
Brazil	**Vale Natural Reserve**	**45.8**	**SECR**	**Current study**
Brazil	Feliciano Miguel Abdala Reserve	52.1	HMMDM	Paschoal (2008)
Brazil	Santa Mônica	62	HMMDM	Lima (2009)
Brazil	Fazenda Macedônia Reserve	117	HMMDM	Massara et al. (2015)

Salvador and Espinosa, 2016), because their primary choice of prey is small mammals (rodents), which are mostly nocturnal (Emmons, 1987). Human impact is also a factor that may increase the nocturnal activity of ocelots, with the occurrence of temporal shifts to increase its avoidance (Cruz et al., 2018).

We concluded that the density of ocelots in VNR is one of the highest in comparison to other protected areas; however, given the difference in the methodology applied in other studies, an additional data is necessary to be gathered for a more reliable comparison. Also, we found that there is a strong link between ocelot and the water sources inside the VNR, which raises a new need to investigate the influence of the long-lasting drought that occurs in the northern state of Espírito Santo. Furthermore, we suggest that future studies should investigate how these covariates may affect other regions or biomes in which the species occurs, because many locations may be affected by the same covariates used herein.

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