Forced neighbours: Coexistence between jaguars and pumas in a harsh environment

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ABSTRACT

Carnivores face conflicts with humans, which has reduced their numbers and distribution. Carnivores compete in intraguild predation systems, Subordinate predators usually avoid top predators through spatial or temporal separation. Coexistence requires a complex combination of resources and environmental conditions. In this study, we assessed the occupancy and temporal activity during night time of the jaguar (*Panthera onca*) and puma (*Puma concolor*) in the Serra da Capivara National Park (SCNP), located in the semi-arid Caatinga biome of Brazil. Felines face biological limitations in hot environments. We used camera-traps, occupancy models and temporal analysis to evaluate their patterns of habitat use, activity and interactions in SCNP between 2009 and 2011. We considered jaguar as dominant predator and puma as subordinate, and expected to find spatial and temporal avoidance between them. We found evidence of spatial and temporal coexistence. This coexistence could be a result of a restriction of niche separation between both species, influenced by the harsh conditions in the Caatinga, represented by a combination of extreme temperatures, scarcity of refuges to thermoregulate, an environment around SCNP with a high level of human disturbance and an apparent increase in prey due conservation policies.

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1. Introduction

Sharing the top of the trophic chain with humans, carnivores face increasing conflict for space and prey. Those conflicts can lead to dramatic changes such as population decline or local extinction (Woodroffe and Ginsberg, 1998). This might be more severe for larger and competitively dominant species that are seen as a threat to humans (Ray et al., 2005).

When a carnivore guild preys on a similar suit of species, their members face intraguild predation, a form of interference competition in which the species that compete for a shared set of resources also kill each other. According to theory (Holt and Polis, 1987; Verdy and Amarasekare, 2010), an intraguild predation system is regulated by the availability of resources, in which both carnivore species, the intraguild predator and intraguild prey, face three possible scenarios: First, under resource scarcity, the system tends towards exclusion of the intraguild predator and prevalence of the intraguild prey. In the second case, when resources are abundant, predation overtakes the system and results in the exclusion of the intraguild prey and prevalence of the intraguild predator. The third case considers intermediate resource levels and the possibility of coexistence between predators; in this scenario the intraguild prey persists despite mortality induced by the intraguild predator. All those models make the assumption that the intraguild prey is a superior competitor for the resource than the intraguild predator, since it has also the disadvantage of being itself the victim of predation (Verdy and Amarasekare, 2010).

In order to survive in an intraguild predation system, intraguild prey species must obtain sufficient food but also avoid to be killed by larger predators. Theory predicts that while the dominant

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predator should be distributed according to food availability and habitat selection, the occurrence of the subordinate predator should reflect trade-offs between prey availability and the risk of potential predation (Heithaus, 2001). The strategies adopted by intraguild prey may vary depending on guild, environment and/or availability of resources. In heavily poached reserves in Thailand, interspecific differences in use of habitat, space and time of subordinate predators (leopard and dhole) compared to larger predators (tiger) have been recorded (Steinmetz et al., 2013); in a game reserve in South Africa intraguild prey (leopard, cheetah and wild dog) show spatial avoidance of larger predators (lion) in energetically rewarding areas with large prey (Vanak et al., 2013); in large and unfenced reserves in different countries in Africa subordinate predators (wild dog and cheetah) have been observed to employ a temporal partitioning system facilitating coexistence by minimizing interference competition with larger predators (lion and hyena) (Hayward and Slotow, 2009); other recent studies in large areas in Botswana suggest extensive temporal overlap, with activity pattern of subdominant species (cheetah and wild dog) constrained by environmental conditions rather than by the activity of the dominant predator (hyena and lion) (Cozzi et al., 2012).

The semi-arid Caatinga (a seasonally dry tropical forest biome) covers an area of almost 750.000 km^2 in northeastern Brazil (MMA, 2005). Its conservation has received little attention, reflected by the scarcity of protected areas in the Caatinga, covering only 1.21% of its total area (Capobianco, 2002). Considering that there is relatively low mammalian endemism in the Caatinga and that mammals seemingly do not have physiological adaptations to arid conditions (Mares et al., 1985), the identification of landscape features associated with the occurrence of mammals in the Caatinga and how these species interact with each other become important questions for conservation.

The Caatinga is home to two large predators, the jaguar (*Panthera onca*) and puma (*Puma concolor*). The jaguar originally occurred from the southern USA to northern Argentina, but in the last century the species has been extirpated from more than half of its historical range (Sanderson et al., 2002; Ferraz et al., 2012), mostly due to conflicts with humans. Jaguars occur sympatrically with the puma, whose distribution is wider and includes habitats that jaguars do not occupy (Iriarte et al., 1990; Sanderson et al., 2002). Pumas also persist in areas where jaguars have been eradicated (Sunquist and Sunquist, 2002). Where both species occur together, jaguars tend to feed on larger prey species, while pumas explore a wider base of prey consisting of smaller animals (Scognamillo et al., 2003).

In this study we assessed the spatial and temporal relationships between these two predators in a protected area of the semi-arid Caatinga, subject to poaching, between two consecutive surveys in 2009 and 2010. We aimed at understanding the environmental and biological variables that might influence the species' habitat use by applying multi-species single-season occupancy models (MacKenzie et al., 2006) to two years of camera-trapping data to evaluate their occupancy and the interactions. Due to its larger size, we considered the jaguar as the dominant predator and the puma as the subordinate predator (Schaller and Crawshaw, 1980; Crawshaw and Quigley, 1991). We expected to find evidence of avoidance between predators (Sollmann et al., 2012) and that the puma, being a superior competitor, makes more efficient use of areas or habitats that could be marginal to the jaguar.

2. Materials and methods

2.1. Study area

Located in northeastern Brazil, in Piauí State, the Serra da Capivara National Park is one of the largest protected areas in the Caatinga biome (MMA, 2005) comprising an area of 1291.40 km^2, surrounded by human settlements. The temperature in SCNP ranges from 12 °C at night up to 50 °C at day, the rainy season lasts from October to April (FUMDHAM, 1998; Figueiredo and Puccioni, 2006), and the mean annual precipitation is 689 mm (FUMDHAM, 1998). There are eight habitat types found in SCNP ranging from open to dense arboreal vegetation, dominated by thorny shrub vegetation with areas of tall trees reaching 6–8 m in size (SMAPR, 1994). The altitude varies between 280 and 600 m, and the topography consists of a main plateau bounded by 50–200 m cliffs cut by canyons and valleys (SMAPR, 1994). SCNP has no natural perennial water bodies and as part of the park management a series of permanent artificial waterholes have been installed since 1994 (FUMDHAM, 1998). SCNP has been declared a World Heritage site by UNESCO due to its archeological legacy. In order to facilitate access and research the Park has an extensive network of dirt roads and trails. The study in SCNP was authorized by the Brazilian environmental agency ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade).

2.2. Camera traps

We sampled SCNP with camera traps between July 2009 and January 2010 and between July 2010 and January 2011. We deployed 58 georeferenced camera trap stations along roads and trails of the Park, spaced on average 3.22 km from each other (Fig. 1). Cameras were placed along roads, in order to increase detection probability of target species (Sollmann et al., 2013). Each sampling station consisted of two cameras facing each other. We used CamTrakker (Camtrack South Inc., Watkinsville, USA) and LeafRiver (Leaf River Outdoor Products, Tailorsville, MS, USA) passive infrared remote cameras, activated by heat and motion. Cameras were set to photograph with a 5-min delay between photos. They were checked every month for film and battery replacement. All cameras were programmed to work only at night, because previous studies showed that in SCNP jaguars (Astete et al., 2008) and pumas (Astete, 2008) were almost exclusively nocturnal. This setting also prevented malfunction of equipment due to extremely high temperatures during daytime. Camera traps were operational
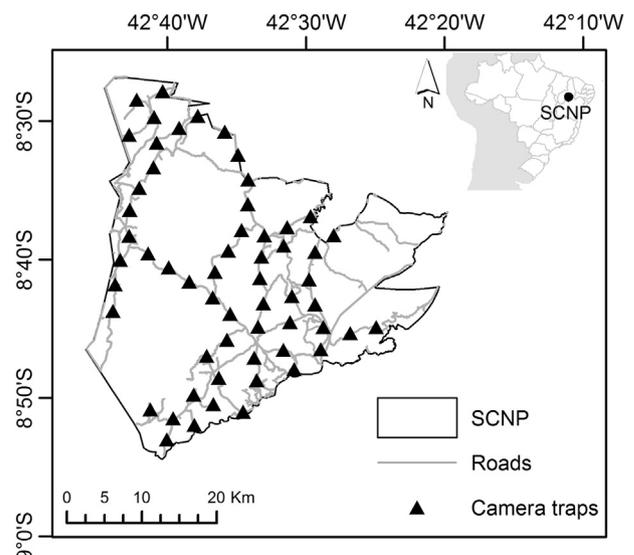

Fig. 1. Location of the Serra da Capivara National Park (SCNP) in Brazil and distribution of the camera-traps in the study between 2009 and 2011.

for a total of 15,205 trap nights.

We divided the data into 42 7-day occasions (21 in 2009 and 21 in 2010). Data were too sparse to fit a multi-season occupancy model where transition probabilities (extinction/recolonization rate) are estimated. Instead, we treated the 2 years as independent surveys. Because we do not expect relationships between species occurrence and environmental covariates to change over the time frame of our study, we built models so that parameters were shared between years (e.g., the relationship between occupancy and habitat covariates remained the same in 2009 and 2010; for details of candidate models see below). If a jaguar or puma was photographed at a site on one or more days during a 7-day occasion, this was considered as a single detection. The intervals were used to create detection histories for each species at each site. Because individuals did not have to be continually present at a site for it to be classified as occupied, occupancy in our study was interpreted as the probability of habitat use (MacKenzie et al., 2006).

2.3. Occupancy and covariates

Occupancy models estimate the probability of a species occupying a site, while correcting for imperfect detection (MacKenzie et al., 2006). The simplest models, called single-species single-season models, estimate probability of detection (p) and a unique probability of occupancy (Ψ) (MacKenzie et al., 2006). Multi-species single-season models can be used to model the interaction between two species (MacKenzie et al., 2006) and include the concept of conditional occupancy and conditional detection, i.e., a species being present/detected conditional on the presence of the other species (See Table 1).

We assessed the influence of habitat covariates on jaguar and puma occupancy and detection probabilities. To model occupancy we used covariates which remain constant throughout a survey (MacKenzie et al., 2006) such as altitude, distance to waterholes and distance to human settlements. These covariates were obtained from 30-m resolution maps created from Landsat TM images. To model detection we used covariates that may vary between sampling occasions (MacKenzie et al., 2006). Considering that seasonality is pronounced in the Caatinga and other semi-arid systems, we created the covariate "season" by dividing each annual survey into a dry and a rainy season, using the observed start of rains for each year. In 2009, the first nine 7-day intervals were classified as dry and the twelve remaining were classified as rainy season. In 2010, the first eight intervals were classified as dry and the thirteen remaining were classified as rainy season. Finally, we were interested in how prey influenced occupancy and detection of jaguars and pumas. Because data for several potential prey species were too sparse for occupancy modeling, we opted instead for the use of the relative photographic rate (number of photographs at a camera-trap station divided by total number of photographs) of all potential prey species as a covariate on occupancy and detection. Whereas this measure cannot be interpreted as an index of abundance, we consider it an index of prey activity at each

camera-trap station and divided it in two classes: Big prey (>15 kg) and small prey (<15 kg). We used the index of activity to model detection probability and to model occupancy. We allowed detection probabilities to vary between years, but held occupancy probability constant across years because preliminary data analysis suggested negligible variation in occupancy between the two surveys.

2.4. Model building and hypothesis

Multi-species single-season occupancy models describe the relationship of a dominant ("A") and a subordinate species ("B") with covariates, as well as and the interaction between these two species, which results into various conditional occupancy and detection parameters (MacKenzie et al., 2006) (Table 1).

Due to the many possible combinations of parameters, the set of candidate models can become impractically large. Therefore, we used a two-step modeling approach (Doherty et al., 2012) to reduce the set of candidate models to a reasonable number. We first built multi-species single-season models to identify in them the best detection covariates for each species, while occupancy remained constant. We used Akaike's Information Criterion (AIC, Burnham and Anderson, 2002) to rank candidate detection models. We retained detection covariates from those model that had a ΔAIC<2 relative to the top model (with the lowest AIC). In the second step, these retained detection covariates were used in a set of multi-species single-season models that included occupancy covariates for each species. Those covariates were added in multiple combinations. Again, we used AIC to rank this second set of models. Because several models in this second set received similar AIC support (see Results for details), we applied Model Averaging (Burnham and Anderson, 2002). Model Averaging is suggested if no model is clearly superior to some of the others in the set, and computes an average parameter estimates which are weighted by the Akaike weights of the selected models (Burnham and Anderson, 2002). The Standard Error of parameter estimates derived from Model Averaging is called Unconditional Standard Error. Finally, we used the results of these top models to test the following *a priori* hypotheses:

1) That, being the subordinate predator, puma occupancy is lower at sites where jaguars also occur ($\psi^{BA} < \psi^{Ba}$), and detection is lower where jaguars are also detected ($r^{BA} < p^{B}$).
2) Pumas are assumed to be more ecologically flexible, and thus we expect covariates to have a stronger effect on the occurrence of jaguars.

We also tested for the equality of both conditional occupancies ($\psi^{A} = \psi^{BA}$ and $\psi^{BA} = \psi^{Ba}$). If $\psi^{BA} = \psi^{Ba}$, then the occupancy of the dominant predator has no influence on the subordinate one. If $\psi^{A} = \psi^{BA}$, then the occupancy of the dominant predator is not influenced by the subordinate one.

We were interested in determining whether both species co-

Table 1
Description of the parameters in the multispecies single-season conditional occupancy model, where "A" is the dominant and "B" the subordinate species.

ψ^{A}	Probability of occupancy for species A, regardless of occupancy status of species Bs
ψ^{BA}	Probability of occupancy for species B, given that species A is present
ψ^{Ba}	Probability of occupancy for species B, given that species A is absent
p^{A}	Probability of detecting species A, if only species A is present
p^{B}	Probability of detecting species B, if only species B is present
r^{A}	Probability of detecting species A, given both species are present.
r^{BA}	Probability of detecting species B, given that both species are present and species A is detected.
r^{Ba}	Probability of detecting species B, given that both species are present and species A is not detected.

occur more or less often than expected, assuming that their distributions are independent. To do so, we calculated the species interaction factor (SIF) (Richmond et al., 2010), which is defined as:

$$SIF = \frac{\psi A \psi BA}{\psi A(\psi A \psi BA + (1 - \psi A)\psi Ba)}$$

An SIF = 1 indicates that both species occur independently. An SIF >1 indicates that both species co-occur more than expected by chance, and an SIF<1 indicates spatial avoidance, i.e., that species B is less likely to co-occur with species A than would be expected under independence.

We implemented our analyses in program PRESENCE 6.4 (Hines, 2006), which performs parameter estimation in the Maximum Likelihood framework.

2.5. Analysis of activity patterns

Our analysis of activity patterns is restricted to nocturnal activity, but previous studies have shown that jaguars and pumas are almost exclusively active at night in SCNP (Astete, 2008; Astete et al., 2008). Thus, this analysis covers the most significant period of the day during which jaguars and pumas could show temporal avoidance. Each record of each species was considered a random sample from a underlying continuous distribution (Ridout and Linkie, 2009). This procedure produces a curve of activity for both species. Then we applied an estimate of the coefficient of overlap (Δ), as described by Ridout and Linkie (2009), to quantify temporal overlap between the nocturnal activity patterns of both carnivores. This coefficient ranges from 1 (complete overlap) to 0 (no overlap). We chose the estimator Δ_1 (Ridout and Linkie, 2009), since this estimator showed less bias in small samples. We conducted this analysis in software R 3.0.0 (R Core Team, 2013) using the packages "boot" (Canty and Ripley, 2013) and "circular" (Agostinelli and Lund, 2011).

3. Results

Pumas were recorded in 182 occasions and jaguars in 299. Jaguars were registered at 49 cameras (84% of the total set) and pumas at 51 cameras (87%). Both species were recorded at 47 cameras, with pumas being almost always detected at sites where jaguars also occurred (96%). In the first step (modeling variation in detection probability), the best ranked models according to AIC were those two that included the covariate "seasonality" in the jaguar's detection probability with puma present (r^A), the other detection parameters remained constant (Table 2). Because those two models differed in less than two AIC units, both of them were considered for the second step of the analysis. In the second model set (modeling variation in occupancy probability), after the inclusion of covariates we found that the first and second-ranked models had substantial empirical support (Delta AIC < 2). We therefore proceeded to apply Model Averaging to those two top models, which had a combined AIC Weight of 80.08% (the complete set of candidate models can be found in Supplementary Materials). When we considered the relative importance of the occupancy covariates of the new set of candidate models, we found that Altitude was the most important covariate, present in both models followed by "Distance to human settlements" (See Table 3).

Site-specific estimates for jaguar occupancy probability (ψ^A) and the probability of jaguars and pumas both occupying a site (ψ^{BA}) both varied between 0.559 and 0.989, with a mean value of 0.912 (See Fig. 2). The model was unable to estimate the probability of the puma occupying a site with the jaguar absent (ψ^{Ba}); this result repeated for any model which included equality between (ψ^A) and

(ψ^{BA}). Puma detection probability without jaguars (p^B) was 0.031 SE = 0.013. Puma detection probability with both species present and jaguar detected during the sampling interval ($r^{BA} = 0.522$ SE = 0.029) was considerably higher than when the jaguar was not detected during the sampling interval ($r^{Ba} = 0.043$ SE = 0.005). Jaguar detection probability with puma present or not was higher in the dry season ($r^A = 0.165$ SE = 0.012) than in the rainy season ($r^A = 0.131$ SE = 0.010). The program was unable to estimate jaguar detection without presence of puma (p^A). The SIF value varied between 1.011 and 1.787, with a mean value of 1.115, suggesting coexistence between jaguars and pumas during 2009 and 2011. The model estimates did not support our first hypothesis; we could not calculate a value for ψ^{Ba}, and puma detection was higher where jaguars are also detected ($r^{BA} > p^B$).

We noted that the occupancy values for both predators increased with Altitude (Fig. 2). We found the same when we plotted the occupancy result of the competing models against the predictors (Altitude and Distance to human settlements): there was a positive relationship between the predictors and occupancy (Fig. 3). Our second hypothesis had also no support, as covariate had the same effect in the jaguar and puma.

Jaguar activity presented two peaks near 03:00 and 20:00, while puma had only one peak near 00:00 (Fig. 4). Overlap in the activities of these species was very high ($\Delta_1 = 0.84$; CI = 0.76−0.88) without a clear indication of segregation in nocturnal activity.

4. Discussion

The positive relationship between occupancy and altitude (Fig. 2) corroborates the pattern described in the habitat suitability study for jaguars in the Caatinga by Morato et al. (2014), which found that elevation was the variable that most influenced the species presence in this biome. The region of higher occupancy by both species (the central and southern region) in the Park coincides with a concentration of geographic features and refuges such as cliffs, canyons and caves, located in the highest areas of the Park.

The extremely high temperatures of the Caatinga (we recorded 45 °C on some days of the dry season of 2009), represent a constraint for felids which have limited ability to thermo-regulate (West, 2005). The species may be forced to concentrate activity in higher altitudes and rest in more shaded areas during daylight. A study of how pre-historic humans used natural cavities in rocky formations of SCNP as refuges, showed that during the dry season, when the temperature in the hottest time of the day could reach up to 50 °C outside the refuges, it remained under 30 °C inside (Figueiredo and Puccioni, 2006). Other big felines use such heat refuges in similar situations. Where available, African leopards make use of caves as an important survival strategy to escape high daytime temperatures in hot climates, and to reduce water loss; some caves in the Namib Desert may be used for many years by successive generations of leopards (Bothma, 1998). Similar behavior seems to occur in SCNP. In 2009, during the installation of camera traps in a high altitude region, we observed a jaguar around midday in a rocky, shady location (Samuel Astete, personal observation).

We expected that within the park, both predators would exhibit space partitioning. The results of our SIF value did not support this hypothesis, suggesting that jaguars and pumas co-occurred more frequently than expected under independent distributions. These findings were also contrary to the only other study of occupancy of jaguars and pumas from the Cerrado grasslands of Brazil, in Emas National Park (Sollmann et al., 2012). The SIF value of 0.73 found by the authors suggests spatial avoidance of the dominant jaguar by pumas. Emas National Park is a reserve located in the middle of a matrix of large-scale agriculture and cattle ranching. The park consists of a mosaic of watercourses with dense gallery forests, the

Table 2
Ranking of First Step of the Single-Season Multi-Species model selection; modeling the detection (p^A, p^B) and conditional detection (r^A, r^{BA}, r^{Ba}) probabilities with covariates for the jaguar (A) and puma (B) in the Serra da Capivara National Park between 2009 and 2011. ABig2009-2010 = Activity Index of the intraguild prey for years 2009–2010 and 2010–2011, ASmall2009-2010 = Activity Index of the small prey for years 2009–2010 and 2010–2011, dry-rain = variation along seasons.

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	no.Par.	=-2*LogLike
psiA = psiBA,psiBa,pA,pB,rA(dry-rain),rBA,rBa	2869.870	0.000	0.587	1.000	8	2853.870
psiA,psiBA,psiBa,pA,pB,rA(dry-rain),rBA,rBa	2871.760	1.890	0.228	0.389	9	2853.760
psiA = psiBA,psiBa,pA,pB,rA,rBA,rBa(dry-rain)	2872.840	2.970	0.133	0.227	8	2856.840
psiA,psiBA,psiBa,pA,pB,rA,rBA,rBa(dry-rain)	2874.730	4.860	0.052	0.088	9	2856.730
psiA,psiBA,psiBa,pA,pB,rA,rBA(ASmal2009-2010)	2896.010	26.140	0.000	0.000	9	2878.010
psiA,psiBA,psiBa,pA,pB,rA,rBA(ASmall2009-2010),rBa	2897.650	27.780	0.000	0.000	9	2879.650
psiA,psiBA,psiBa,pA,pB,rA,rBA,rBa	2898.570	28.700	0.000	0.000	8	2882.570
psiA,psiBA,psiBa,pA,pB,rA,rBA,rBa(ABig2009-2010)	2898.790	28.920	0.000	0.000	9	2880.790
psiA,psiBA,psiBa,pA,pB,rA(ASmall2009-2010),rBA,rBa	2899.160	29.290	0.000	0.000	9	2881.160
psiA,psiBA,psiBa,pA,pB(dry-rain),rA,rBA,rBa	2899.240	29.370	0.000	0.000	9	2881.240
psiA,psiBA,psiBa,pA,pB,rA,rBA(dry-rain),rBa	2900.090	30.220	0.000	0.000	9	2882.090
psiA,psiBA,psiBa,pA,pB,rA,rBA(ABig2009-2010),rBa	2900.440	30.570	0.000	0.000	9	2882.440
psiA,psiBA,psiBa,pA,pB,rA(ABig2009-2010),rBA,rBa	2900.510	30.640	0.000	0.000	9	2882.510
psiA,psiBA,psiBa,pA(ASmall2009-2010),pB,rA,rBA,rBa	2900.570	30.700	0.000	0.000	9	2882.570
psiA,psiBA,psiBa,pA,pB(ASmall2009-2010),rA,rBA,rBa	2900.570	30.700	0.000	0.000	9	2882.570
psiA,psiBA,psiBa,pA(dry-rain),pB,rA,rBA,rBa	2900.570	30.700	0.000	0.000	9	2882.570
psiA,psiBA,psiBa,pA(ABig2009-2010),pB,rA,rBA,rBa	2900.570	30.700	0.000	0.000	9	2882.570
psiA,psiBA,psiBa,pA,pB(ABig2009-2010),rA,rBA,rBa	2900.570	30.700	0.000	0.000	9	2882.570
psiA = psiBA,psiBa,pA,pB,rA,rBA,rBa(ASmall2009-2010)	2900.650	30.780	0.000	0.000	8	2884.650
psiA = psiBA,psiBa,pA,pB,rA,rBA(ASmall2009-2010),rBa	2902.320	32.450	0.000	0.000	8	2886.320
psiA = psiBA,psiBa,pA,pB,rA,rBA,rBa	2903.240	33.370	0.000	0.000	7	2889.240
psiA = psiBA,psiBa,pA,pB,rA,rBA,rBa(ABig2009-2010)	2903.460	33.590	0.000	0.000	8	2887.460
psiA = psiBA,psiBa,pA,pB,rA(ASmall2009-2010),rBA,rBa	2903.780	33.910	0.000	0.000	8	2887.780
psiA = psiBA,psiBa,pA,pB,rA,rBA(dry-rain),rBa	2904.760	34.890	0.000	0.000	8	2888.760
psiA = psiBA,psiBa,pA,pB,rA,rBA(ABig2009-2010),rBa	2905.110	35.240	0.000	0.000	8	2889.110
psiA = psiBA,psiBa,pA,pB,rA(ABig2009-2010),rBA,rBa	2905.180	35.310	0.000	0.000	8	2889.180
psiA = psiBA,psiBa,pA,pB(ABig2009-2010),rA,rBA,rBa	2905.240	35.370	0.000	0.000	8	2889.240
psiA = psiBA,psiBa,pA(ASmall2009-2010),pB,rA,rBA,rBa	2905.240	35.370	0.000	0.000	8	2889.240
psiA = psiBA,psiBa,pA,pB(ASmall2009-2010),rA,rBA,rBa	2905.240	35.370	0.000	0.000	8	2889.240
psiA = psiBA,psiBa,pA(dry-rain),pB,rA,rBA,rBa	2905.240	35.370	0.000	0.000	8	2889.240
psiA = psiBA,psiBa,pA,pB(dry-rain),rA,rBA,rBa	2905.240	35.370	0.000	0.000	8	2889.240
psiA = psiBA,psiBa,pA(ABig2009-2010),pB,rA,rBA,rBa	2905.240	35.370	0.000	0.000	8	2889.240
psiA,psiBA = psiBa,pA,pB,rA,rBA,rBa	2930.240	60.370	0.000	0.000	7	2916.240
psiA,psiBA,psiBa,pA,pB,rA,rBA = rBa	3318.250	448.380	0.000	0.000	7	3304.250

Table 3
Ranking of the best Single-Season Multi-Species candidate models (AIC Weight > 10%), modeling the probability of occupancy and detection probability with covariates for the jaguar (A) and puma (B) in the Serra da Capivara National Park between 2009 and 2011. Dist_town = Distance to human settlements, Alt = Altitude, dry-rain = variation along seasons.

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	no.Par.	=-2*LogLike
psiA(Alt + Dist_town) = psiBA(Alt + Dist_town),psiBa,pA,pB,rA(dry-rain),rBA,rBa	2860.890	0.000	0.737	1.000	10	2840.890
psiA(Alt) = psiBA(Alt),psiBa,pA,pB,rA(dry-rain),rBA,rBa	2862.950	2.060	0.263	0.357	9	2844.950

ideal type of habitat for jaguars, and abundant grasslands, which the puma, a generalist both in terms of food and space use habits (Iriarte et al., 1990), can explore, facilitating coexistence through a space partitioning strategy and active avoidance of the jaguar. A recent niche modeling study in SCNP (Astete et al., 2016) found that the habitat suitability for jaguars and pumas in the Park overlaps almost completely, with elevation (altitude) being the second most important ecogeographical variable, while distance to artificial waterholes was the most important. In SCNP, The need to escape high daytime temperatures may force both species into similar habitats.

Niche partitioning promotes diversity and structures the carnivore community (Schuette et al., 2013). One of its mechanisms, space partitioning, permits the coexistence of sympatric carnivores, reducing the frequency of potentially costly encounters between a subordinate carnivore and the apex predator (Palomares et al., 1996; Durant, 1998). Another mechanism of niche partitioning is food partitioning. Although dietary separation could be a strategy to permit coexistence, it seems not to be the best explanation for the coexistence between jaguar and pumas in SCNP. In

contrast to the neighboring biome of the Cerrado grasslands, where both species exploit preys of different sizes, with the jaguar consuming bigger species (Silveira, 2004), jaguars and pumas in the SCNP prey on the same species, and feed mostly on medium-sized mammals like armadillos (*Dasypus* sp.) and anteaters (*Tamandua tetradactyla*), all of them weighing less than 15 kg (Olmos, 1993; Wolff, 2001). This pattern in diet could be a consequence of both an abundance of medium prey species such as armadillos (for the jaguar's diet see Hayward et al., 2016) and the lack of bigger prey species such as peccaries or deer, probably due to poaching. Poaching is a common and lucrative activity in the region around SCNP. This activity could be a quite important income source in Brazil's historically poorest region. Considering that the rampant conflicts between humans and carnivores for land and prey can lead to drastic population declines and even local extinction of predators, and that the largest and competitively dominant species could pose a threat to humans (Woodroffe and Ginsberg, 1998; Ray et al., 2005), it is plausible to predict that jaguar and puma populations outside the protected SCNP — as well as their prey species— are scarce and that both cats could concentrate in the Park to escape
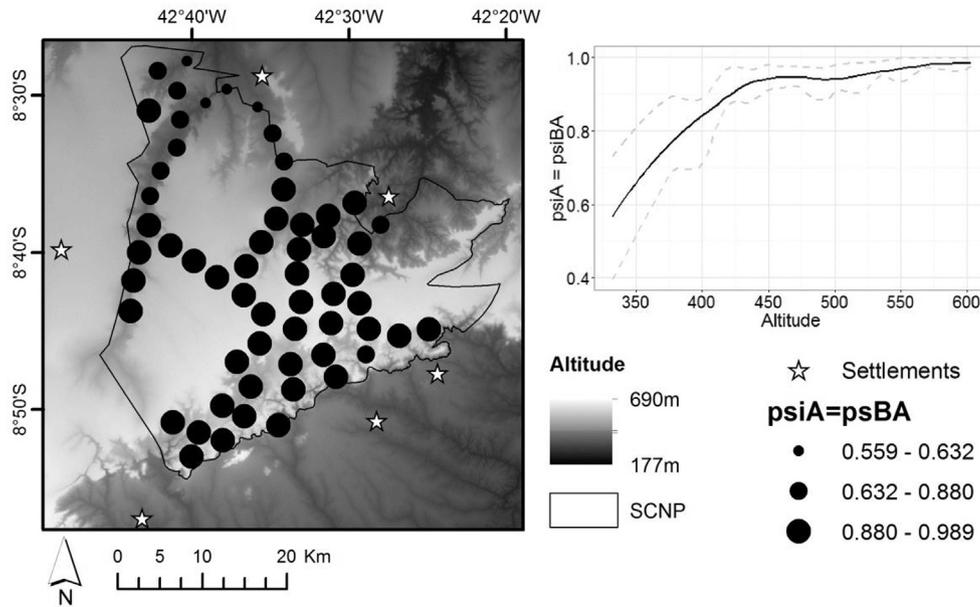
Fig. 2. Estimates of occupancy ($\psi^A = \psi^{BA}$) as a function of Altitude derived from Model Averaging for the jaguar (A) and puma (B) in the Serra da Capivara National Park (SCNP) between 2009 and 2011.
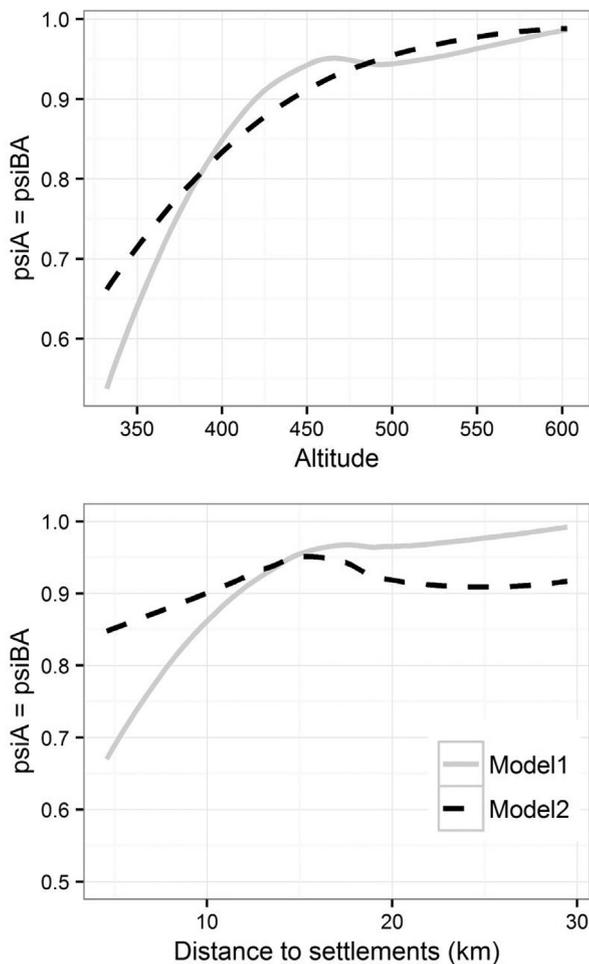

Fig. 3. Estimates of occupancy from the two competing models plotted against their predictors (Altitude and Distance to human settlements) for the jaguar and puma in the Serra da Capivara National Park (SCNP) between 2009 and 2011.

from the anthropogenic pressures outside. This idea is seemingly supported by the positive relationship between occupancy and the distance from human settlements.

In the harsh environment of the Caatinga, the available habitat for jaguars and pumas in SCNP could lack the so-called "competition refuges" (Durant, 1998), with both predators tending to use the very same landscape features. The high SIF value and the inability to estimate in any candidate model the probability of occupancy by pumas without jaguars (ψ^{Ba}) suggest that their coexistence in SCNP is not driven by space partitioning. Also, the inability to calculate the detection of the dominant jaguar without the presence of puma (p^A) and the low value of puma detection without the jaguar present (compared to the conditional detection of both predators ($p^B < r^{BA}$)) seems to reinforce the idea that both predators are more commonly detected together than alone. The equality included in the best candidate models ($\psi^A = \psi^{BA}$) means that the occupancy of both species is always the same, even when the dominant species is present. We also did not find any temporal partitioning, and the extensive temporal overlap between the species' nocturnal activity patterns in the Park seems to fit the system proposed by Cozzi et al. (2012), in which the subdominant species' activity is constrained by environmental conditions rather than by the activity of the dominant one.

The Caatinga is characterized by low availability of water, limiting primary productivity (Heisler-White et al., 2008), which, in turn, can limit the density of prey species (McNaughton et al., 1989), and consequently, the population of carnivores (Carbone and Gittleman, 2002). Considering the positive relationship between environmental suitability and abundance (VanDerWal et al., 2009), it is not surprising to observe that jaguar densities in the Caatinga are lower than in other habitats which could be more favorable for the species (Astete et al., 2008; Silveira et al., 2009). The response of a subordinate predator to the top predator depends on the relative density of both species and the extent of competition between them; consequently, if the top competitor is at sufficiently low density, there is no great need to adjust behavior to its presence (Durant, 1998). Considering this, the low density of jaguars in SCNP could facilitate the coexistence with pumas. The theory of
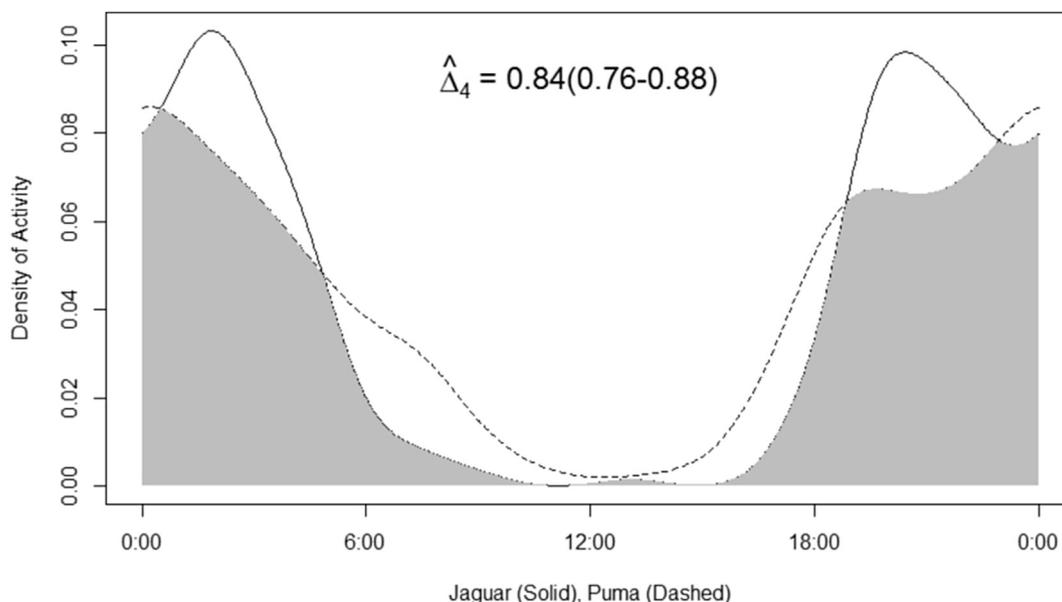
Fig. 4. Estimates of the nocturnal activity patterns of jaguars and pumas in Serra da Capivara National Park. Kernel-density estimates for Puma (dashed line) and jaguar (solid line) are based on individual photograph times. The overlap coefficient is the area under the minimum of the two density estimates (Ridout and Linkie, 2009), as indicated by the shaded area. Bootstrap confidence interval of 95% indicated in parentheses.

intraguild predation also considers that under a condition of intermediate resources coexistence is possible between carnivores, despite mortality induced by the intraguild predator (Verdy and Amarasekare, 2010).

The coexistence of jaguars and pumas in the Serra da Capivara National Park seems to be explained by a unique combination of environmental and anthropogenic factors. The extremely high temperatures and the concentration of natural refuges to thermoregulate in certain areas of the park, combined with a high human pressure around the Park could be forcing the two species to share the same habitat and activity period. As the anthropogenic transformation of the landscape continues, the situation of coexistence of both species could be repeating itself in other regions of the Caatinga. It is important to identify this situation and to continue evaluating other actions such as the implementation of artificial waterholes for future management actions in this harsh biome.

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2017.07.005.

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