Living in extreme environments: modeling habitat suitability for jaguars, pumas, and their prey in a semiarid habitat

Samuel Astete,* Jader Marinho-Filho, Ricardo B. Machado, Bárbara Zimbres, Anah T. A. Jácomo, Rahel Sollmann, Natália M. Tôrres, and Leandro Silveira

Programa de Pós-Graduação em Ecologia, Universidade de Brasília, Brasília 70910-900, Brazil (SA)
Departamento de Zoologia, Universidade de Brasília, Brasíllia 70910-900, Brazil (JMF, RBM)
Jaguar Conservation Fund/Instituto Onça-Pintada, Mineiros, Goiás 75830-000, Brazil (ATAJ, RS, NMT, LS)
Department of Wildlife, Fish, and Conservation Biology, University of California Davis, Davis, CA 95616, USA (RS)
Programa de Pós-Graduação em Zoologia, Universidade de Brasília, Brasília 70910-900, Brazil (BZ)
Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, MG 38400-902, Brazil (NMT)

* Correspondent: samastete@yahoo.com

Carnivores and their prey occurring at the extremes of their ecological niches face particular constraints in terms of habitat suitability (HS). We combined the use of camera traps and Ecological Niche Factor Analysis (ENFA) to calculate HS for jaguars (*Panthera onca*), pumas (*Puma concolor*), and 4 prey species (3-banded armadillos, *Tolypeutes tricinctus*; 9-banded armadillos, *Dasypus novemcinctus*; collared peccaries, *Pecari tajacu*; and gray brocket deer, *Mazama gouazoubira*) in Serra da Capivara National Park (SCNP), located in the semiarid Caatinga biome of Brazil. We also evaluated HS in relation to water management applied in the Park since 1994. Considering the physiological limitations of the Caatinga's species, we used an "edge of niche" habitat-suitability algorithm. For all species examined, distance to waterholes was the ecogeographical variable with the greatest contribution for the ENFA. Water management implemented in SCNP helps to ensure the persistence of predators and prey species, since the combination of topographic characteristics and location of waterholes explained most of HS for the analyzed species.

Os carnívoros e suas presas que ocorrem nos extremos dos seus nichos ecológicos enfrentam restrições particulares em termos de adequabilidade de habitat (AH). Neste estudo, combinamos o uso de armadilhas-fotográficas e a Análise Fatorial de Nicho Ecologico (ENFA- Ecological Niche Factor Analysis) para calcular a AH para a onça-pintada (*Panthera onca*), a onça-parda (*Puma concolor*) e 4 espécies presa (3 o tatu-bola, *Tolypeutes tricintus*; o tatu-galinha, *Dasypus novemcinctus*; o cateto, *Pecari tajacu*; e o veado-catingueiro, *Mazama gouazoubira*) no Parque Nacional Serra da Capivara (PNSC), localizado no bioma semiárido da Caatinga do Brasil. Também avaliamos os resultados da AH em termos de uma política de manejo de água aplicada no parque desde 1994. Considerando as limitações fisiológicas das espécies na Caatinga, utilizamos um algoritmo de AH de "beira de nicho". Para todas as espécies analisadas, a distância a poços de água foi a variavel eco-geográfica com a maior contribuição para o ENFA. A política de manejo de água aplicada no PNSC contribui a asegurar a persistência dos predadores e presas, uma vez que a combinação de características topográficas e poços de água explicaram a maior parte da AH para as espécies analisadas.

Key words: Caatinga, ENFA, gray brocket deer, jaguar, puma, water management

Acquiring reliable information about species distributions and building models that can explain and estimate species occurrences is a major concern for conservation efforts (Araújo and Williams 2000). Carnivores worldwide compete with humans for space and food and the alteration of habitats has led to escalated human–carnivore conflicts (Treves and Karanth 2003). As carnivores depend on their prey, reliable information on distribution and habitat suitability (HS) for

both predator and prey is crucial for carnivore conservation efforts.

HS models that predict the spatial distribution of species (Guisan and Zimmermann 2000; Pearce and Boyce 2006) based on their ecological requirements present a useful tool for conservation and management of endangered species (Palma et al. 1999; Rondinini et al. 2005). HS models relate a set of field records of the target species to a group of ecological variables that are presumed to reflect some key factors of the species' niche (Hirzel et al. 2001). Models based on presence-only or presence–pseudo-absence data are the most standard approach to habitat modeling (Hirzel et al. 2001; Segurado and Araujo 2004; Chefaoui and Lobo 2008).

The semiarid Caatinga biome (seasonal dry tropical forest) covers an area of almost 750,000 km^2 in northeastern Brazil (MMA 2005). Little attention has been given to its conservation (Silva et al. 2004) and fully protected areas cover only 1.21% of its territory (Capobianco 2002). The facts that there is low endemism and absence of physiological adaptations of mammals to the arid conditions in the Caatinga (Mares et al. 1985) raise important questions for conservation: how do mammals that also occur in other regions cope with the conditions in this severe biome, what landscape components do they select (e.g., topography, position of natural or anthropogenic ecosystems, etc.), and how do species interact with each other?

Semiarid habitats, such as the Caatinga, are particularly vulnerable to global climate change, because in such habitats changes in water availability and climate may have disproportionate effects on biodiversity (Millennium Ecosystem Assessment 2005). In Africa, to avoid these effects inside protected areas, water management has been applied as a way to recover herbivores (Pienaar 1985; Glaylard et al. 2003).

Using camera-trapping data in combination with Ecological Niche Factor Analysis (ENFA), a presence-only-based HS model (Hirzel et al. 2002), we investigated HS for jaguars (*Panthera onca*), pumas (*Puma concolor*), and 4 potential prey species—3-banded armadillos (*Tolypeutes tricinctus*), 9-banded armadillos (*Dasypus novemcinctus*), collared peccaries (*Pecari tajacu*), and gray brocket deer (*Mazama gouazoubira*)—in the Serra da Capivara National Park (SCNP), the 2nd largest protected area in the Caatinga. Due to its size, the SCNP is extremely important for the conservation of biodiversity in this biome, particularly of wide-ranging mammals. We used the so-called "edge of niche" algorithms, which are recommended for a species occurring at the margin of its distribution (Braunisch et al. 2008), as is the case for most of the species in this study. We expected that for most species, scarce resources, such as water or places to thermoregulate, would be the most important factors influencing suitability. As carnivores depend on their prey, and the prey are subject to the same climatic stressors, we also expected a high overlap between the HS models of jaguars and pumas and some of their prey species.

MATERIALS AND METHODS

Study area.—The SCNP is located in the state of Piauí, northeastern Brazil. With 1,291.4 km^2, it is one of the largest protected areas of the Caatinga biome (MMA 2005). Temperature can vary from 12°C to 50°C in the dry season, with a rainy season from October to mid-April (but it can begin later or end earlier—Emperaire 1984; Figueiredo and Puccioni 2006), and mean annual precipitation of 689 mm, with a maximum, over the past 70 years, of 1,269 mm and a minimum of 250 mm. Those values are, however, much lower than the 1,462.4 mm yearly potential evapotranspiration (FUMDHAM 1998). There are 8 habitat types recognized in SCNP (from open to dense arboreal Caatinga vegetation), the predominant habitat being tall, shrubby vegetation 6–10 m high (Emperaire 1984). The elevation varies between 280 and 600 m a.s.l. and the topography consists of a main plateau bounded by 50- to 200-m-high cliffs cut by canyons and valleys (Emperaire 1984). SCNP has no natural perennial water bodies, and a series of permanent artificial waterholes has been installed since 1994 as part of the park management (SMAPR 1994). SCNP has been declared a World Heritage Site by UNESCO due to its archeological legacy. To facilitate access and research, the park has an extensive network of dirt roads and trails. Our study in SCNP was authorized by the Brazilian environmental agency ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade).

Species data.—We created presence-only distribution maps of the target species based on records from 3 camera-trap surveys implemented in SCNP in 2007, 2009–2010, and 2010–2011, covering both the dry and rainy seasons in each survey with an equivalent effort in each season. Each camera-trap station was on average 3.1 km away from its nearest neighbor. We used 24 stations in 2007 and 70 stations from 2009 to 2011. The last 2 camera-trap surveys covered the entire park, with cameras placed proportionally in the types of vegetation present at SCNP. Cameras were placed along roads throughout the park (Fig. 1), because the dense vegetation impeded placing cameras far from roads. We defined a record as the register of a species by a camera trap.

Species maps were produced for 2 predators, jaguars and pumas, and for 4 potential prey species for which we had enough data: gray brocket deer, collared peccaries, 3-banded armadillos, and 9-banded armadillos.

Environmental variables.—In ENFA, ecogeographical variables (EGVs) are variables assumed to reflect some key factors of the species' niche. We created EGVs using the programs ArcGIS 9.31 (ESRI 2009) and Idrisi Taiga (Eastman 2009). We used 6 EGVs including proximity to artificial waterholes, a digital elevation model (DEM), slope, normalized difference vegetation index (NDVI) for each season, distance to paved roads, and distance to human settlements around SCNP. NDVI is derived from remote-sensing data on visible and near-infrared bands of the electromagnetic spectrum, varies from −1.0 to 1.0, and is positively related to cover by photosynthetic biomass. All maps excluding NDVI were provided by the Fundação Museu do Homem Americano (FUMDHAM), which administers the park. We considered these EGVs to summarize characteristics of the physical environment and vegetation, as well as human influence in SCNP. Because cameras were placed along dirt roads, we did not include a map of these roads as an EGV.
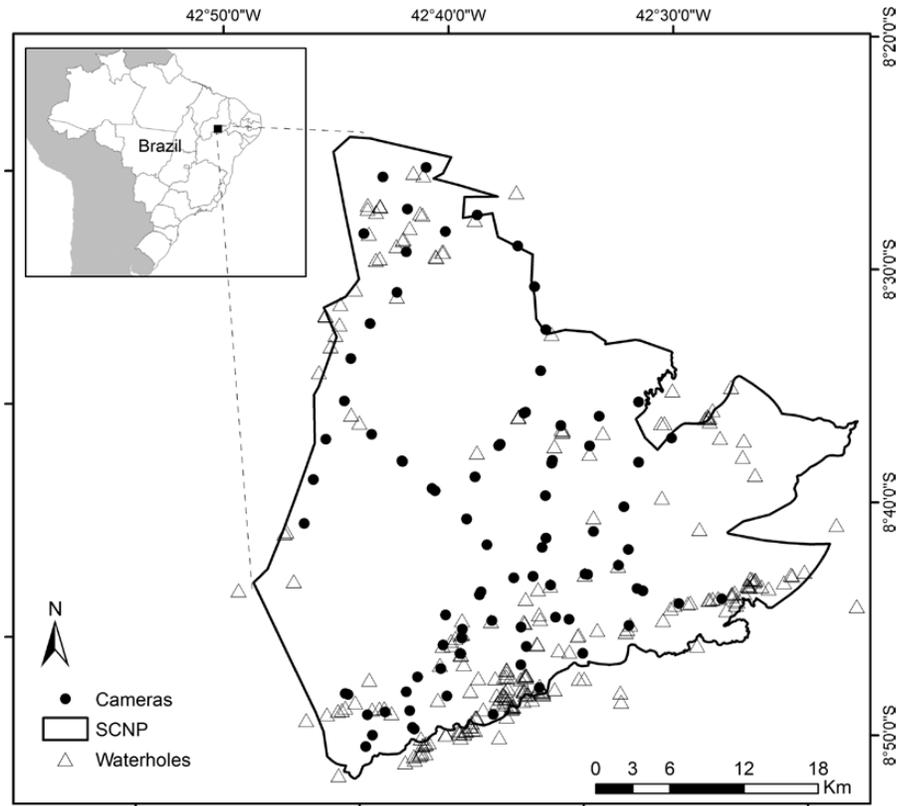
Fig. 1.—Location of the Serra da Capivara National Park (SCNP) in the Caatinga biome of Brazil (dashed area), and spatial distribution of artificial waterholes and camera traps in the park.

We tested for correlation among EGVs and since there were no significant associations (see Supplementary Data SD1), we used all of them in our analysis. The values of each EGV at each sampling point can be found in Supplementary Data SD2.

Since some of the EGV maps were derived from Landsat 5 TM images (such as NDVI), we produced all of them with 30-m spatial resolution, the same resolution as the DEM and slope maps (Valeriano 2008). The Landsat images were from 2010 and came from the INPE (www.inpe.br) database. We used Box-Cox or square-root transformations to normalize EGVs (Hirzel et al. 2002). As pointed out by Pettorelli et al. (2009), the coefficients computed by ENFA for each EGV should be interpreted with care in the case of distance maps (e.g., distance to waterholes, roads, and human settlements): a high positive value indicates species avoidance, whereas a high negative value indicates preference for the EGV considered.

ENFA analysis.—ENFA is an approach that uses presence-only data to create an HS model of a species, based on Hutchinson's niche concept (Hutchinson 1957), referred to here as an area in the ecogeographical space where a species has a reasonable chance to occur (Hirzel et al. 2002). ENFA uses a multivariate factor approach to aggregate information for the species, aiming to identify general patterns in habitat use based on 2 indices: marginality and specialization. Marginality, ranging from 0 to 1, maximizes the multivariate distance between the cells occupied by a species and the average global distribution of each variable. The aggregation of the remaining axes, called specialization, is the ratio of the variance of the global

distribution to that of the focal species' distribution. The inverse of specialization is defined as the species tolerance and represents a measurement of the focal species' selectiveness within the available conditions in the area determined by the variables. A global marginality factor close to 1 means that the species lives in a very particular habitat relative to the reference set, whereas a tolerance value < 1 indicates some degree of specialization (Hirzel et al. 2002). An advantage of ENFA is that its results allow a direct comparison between multiple species that inhabit the same region, by interpreting the parameters from the perspective of the ecological niche (i.e., marginality).

To estimate HS scores from ENFA factors (Hirzel et al. 2002), we used the software BIOMAPPER 4.0 (Hirzel et al. 2008). The program uses a set of algorithms which assume that the environmental conditions are optimal where the species is most frequently found. The default algorithm of BIOMAPPER is the median algorithm (M), which considers that the optimum condition is represented by the median of the species frequency distribution, assumed to be unimodal and asymmetrical. Considering that HS model results could be biased when environmental conditions in the study area represent a marginal part of the species' fundamental niche, and that this situation occurs mostly at the margins of a species geographic distribution, we chose an "edge of niche" algorithm, specifically the "area-adjusted median algorithm" (Ma), which considers the relative availability of habitat conditions, comparing habitat use to habitat availability to evaluate how species might select a habitat (Braunisch et al. 2008).

We ran 3 different models for each species, 1 considering only dry season records, 1 considering only wet season records, and 1 with the combined set of records. The maximum number of records for the models was the total number of camera-trap sites. We assumed that the dry season might be the limiting season in terms of resources and by splitting the data into seasonal records we tried to understand seasonal differences.

To evaluate the resulting HS models, we used a 10-fold jack-knife cross-validation, the default option in BIOMAPPER (Hirzel et al. 2006). We computed 2 presence-only evaluation measures: AVI (Absolute Validation Index) and the Continuous Boyce Index (CBI—Hirzel et al. 2006). AVI ranges from 0 to 1 and indicates how well the model discriminates high-suitability from low-suitability areas. The CBI, a threshold-independent modification of the Boyce Index (Boyce et al. 2002), is calculated as the Spearman correlation coefficient between the ratio of the predicted over expected frequency of evaluation points and the habitat suitability index (HSI). It varies from −1 to 1: −1 for an inverse model to 0 for a random model to 1 for a perfect model. In BIOMAPPER, the default option for the 10 k-fold model evaluation (predicted-to-expected ratio) in CBI is a sliding window size of 20 HSI units, thus discarding data sets resulting in less than 20 records. We established a CBI threshold of 0.200, and models with a CBI < 0.200 were considered having little support and therefore were discarded for further analysis (Pettorelli et al. 2009).

ENFA deals with spatial autocorrelation between sampling points with a 10-fold jack-knife cross-validation, where the data set is divided into 10 k-independent partitions, using $k − 1$ of them to calibrate the model, and computing the evaluator on the left-out partition (Hirzel et al. 2001). This procedure is repeated k times, each time leaving out another partition. This produces k estimations of the evaluator, allowing assessment of its central tendency and variance (Hirzel et al. 2001). Spatial autocorrelation may have a particularly bad effect in the cross-validation. If the data set is randomly 10-fold partitioned and the presence points are aggregated, then the assumedly independent partition that is being cross-validating will not be independent and will produce over-confidence in the model accuracy. In BIOMAPPER, the cross-validation partitioning is by default geographical: the data partitions for model validation are partitioned evenly but randomly (Hirzel and Arlettaz 2003; Sattler et al. 2007), so that they do not overlap geographically, minimizing the potential for spatial autocorrelation (Unger et al. 2008).

Species and model comparison.—We looked for interspecific differences in HS models through marginality and tolerance. We also examined differences among species and seasons between the resulting HS maps that passed the CBI threshold. Using Hawth's Tools (Beyer 2004) for ArcGIS, we created 500 random points inside our study area and extracted their HS values. Points with zero value for both HS maps being compared were discarded. For all remaining points, their values were compared with a paired Mann–Whitney test, using the statistical software R (R Development Core Team 2012). If the results showed nonsignificant differences, we considered both

HS maps as similar. We did the analyses considering HS maps derived from the total and seasonal records.

As jaguars and pumas are sympatric predators (Iriarte et al. 1990), we looked for information on niche breadth and potential overlap. Following the methodology of Sattler et al. (2007), we used BIOMAPPER Discriminant Analysis to estimate niche breadth and overlap indices (De Angelo et al. 2011), such as traditional niche breadth index (Levin's standardized index) and overlap indices (Pianka's overlap index and Lloyd's asymmetric overlap index—Colwell and Futuyama 1971; Hurlbert 1978). Lloyd's asymmetric overlap index is a measure of directional niche overlap: Z12 represents the density of species 2 encountered, on average, by species 1; Z21 is the reciprocal. The index is also called measure of interspecific crowding, so that the ratio of interspecific crowding values for 2 species is the reciprocal of the ratio of their abundances (Hurlbert 1978).

RESULTS

We accumulated a total effort of 19,938 camera-trap days: 3,833 during a 9-month sample in 2007 (February to October) and 16,105 in 2009–2011 (2 samples, from September to January each). The 2007 sampling included 3 months from the rainy season and 6 from the dry season. The samplings in 2009 and 2010 included 3 months of the rainy season and 2 months of the dry season every year. For all species, the EGV "Distance to Waterholes" had the greatest coefficient value (Table 1). For jaguars, pumas, and gray brocket deer, for all models considering total or seasonal records, altitude (DEM) was the 2nd strongest EGV. Of those 3 species, jaguars had the lowest tolerance value in all models. Considering models derived from total records, the marginality of jaguars was greater than that of pumas, and tolerance was lower. In seasonal models, tolerance of pumas was greater than that of jaguars, especially in the dry season, where marginality of pumas was also greater (Table 1).

The models of some species were classified by the AVI as consistent, although they were clearly classified as random or with little support by the CBI threshold (i.e., for 3-banded armadillos considering dry season records AVI = 0.533 and CBI = −0.040; Table 2). We obtained 9 models with a CBI value over the 0.200 threshold (Table 2).

Considering only CBI-approved models, we compared HS models derived from total records between species of predators, and between predators and potential prey. We also compared models derived from seasonal records within the same species between seasons (i.e., rainy versus dry seasons), between predators within seasons, and between predators and potential prey within seasons. We found significant differences between jaguars and pumas based on total records ($P < 0.0001$), and between seasons for jaguars ($P < 0.0001$). Differences between jaguars and pumas in the dry season were not significant ($P > 0.05$), meaning that HS maps were similar. Comparing HS maps between predators and prey, we found significant differences between pumas and 9-banded armadillos based on total records ($P < 0.005$), jaguars and gray brocket deer in the rainy season ($P < 0.0001$), and jaguars and 9-banded armadillos in

Table 1.—Coefficients of the ecogeographical variables under Ecological Niche Factor Analysis for the marginality factor for 6 mammalian species in the Serra da Capivara National Park, Caatinga, Brazil (jaguar = jaguar; puma = puma; graydeer = gray brocket deer; collared = white-collared peccary; threearm = 3-banded armadillo; ninearm = 9-banded armadillo), for habitat suitability models considering the total (tot) number of records, as well as records in the rainy (rai) and dry (dry) seasons. The number of records from which the models were created is denominated as "*n*." NDVI = normalized difference vegetation index.

Model name	Distance human settlements	Distance to paved roads	Slope	Distance to waterholes	Digital elevation model	NDVI rainy/ dry season	Marginality	Tolerance	n	Number of factors retained	% information explained	% explained by marginality	% explained by the 1st axis of specialization
jaguar_tot	−0.051	0.197	0.016	−0.712	0.556	0.376	0.705	0.514	81	5	0.987	0.589	0.200
puma_tot	−0.070	0.194	−0.032	−0.712	0.529	0.410	0.681	0.560	71	5	0.985	0.507	0.217
graydeer_tot	−0.037	0.197	0.090	−0.808	0.429	0.338	0.672	0.550	62	5	0.988	0.536	0.197
collared_tot	−0.092	0.151	−0.085	−0.770	0.445	0.413	0.664	0.525	30	5	0.992	0.543	0.219
threearm_tot	0.232	0.362	−0.119	−0.717	0.394	0.363	0.641	0.525	35	5	0.991	0.431	0.244
ninearm_tot	0.111	0.307	0.017	−0.751	0.401	0.411	0.610	0.577	48	5	0.988	0.441	0.238
jaguar_rai	−0.010	0.152	−0.075	−0.699	0.570	0.396	0.676	0.510	65	5	0.988	0.588	0.186
puma_rai	0.057	0.240	−0.104	−0.727	0.546	0.319	0.663	0.511	48	5	0.987	0.562	0.182
graydeer_rai	−0.007	0.191	0.084	−0.780	0.439	0.394	0.685	0.523	43	5	0.988	0.588	0.177
collared_rai	−0.167	0.065	0.005	−0.731	0.417	0.509	0.729	0.494	20	5	0.994	0.479	0.295
threearm_rai	−0.059	0.387	−0.141	−0.594	0.501	0.471	0.737	0.479	21	5	0.990	0.545	0.225
ninearm_rai	0.108	0.298	0.016	−0.729	0.390	0.464	0.627	0.543	48	5	0.990	0.530	0.189
jaguar_dry	0.016	0.233	−0.071	−0.691	0.539	0.417	0.709	0.481	64	5	0.990	0.619	0.165
puma_dry	−0.158	0.227	−0.077	−0.673	0.565	0.381	0.715	0.551	58	5	0.981	0.483	0.230
graydeer_dry	−0.033	0.223	0.069	−0.813	0.422	0.325	0.676	0.548	51	5	0.989	0.474	0.214
collared_dry	0.105	0.267	−0.137	−0.707	0.420	0.472	0.707	0.312	15	5	0.998	0.763	0.120
threearm_dry	0.337	0.380	−0.194	−0.669	0.390	0.324	0.625	0.453	21	5	0.994	0.569	0.162
ninearm_dry	−0.068	0.238	−0.006	−0.843	0.343	0.326	0.592	0.506	13	5	0.993	0.293	0.310

Table 2.—Ecological Niche Factor Analysis evaluation indices (AVI = Absolute Validation Index and CBI = Continuous Boyce Index) for habitat suitability models of 6 mammalian species (jaguar = jaguar; puma = puma; graydeer = gray brocket deer; collared = white-collared peccary; threearm = 3-banded armadillo; ninearm = 9-banded armadillo) in the Serra da Capivara National Park, Brazil. The models considered the total (tot) number of records, as well as records in the rainy (rai) and dry (dry) seasons. Results are from the Ma (area-adjusted median) algorithm. Models marked in bold were considered as approved by the CBI (i.e., CBI > 0.2).

Model name	AVI	CBI
jaguar_tot	0.486 ± 0.315	**0.468 ± 0.377**
puma_tot	0.498 ± 0.306	**0.417 ± 0.484**
graydeer_tot	0.502 ± 0.418	0.111 ± 0.544
collared_tot	0.467 ± 0.450	0.035 ± 0.585
threearm_tot	0.517 ± 0.285	0.152 ± 0.478
ninearm_tot	0.513 ± 0.274	**0.259 ± 0.446**
jaguar_rai	0.494 ± 0.326	**0.320 ± 0.464**
uma_rai	0.513 ± 0.346	0.195 ± 0.519
graydeer_rai	0.482 ± 0.300	**0.258 ± 0.542**
collared_rai	0.450 ± 0.438	−0.020 ± 0.581
threearm_rai	0.450 ± 0.438	−0.059 ± 0.587
ninearm_rai	0.487 ± 0.274	**0.244 ± 0.509**
jaguar_dry	0.512 ± 0.232	**0.448 ± 0.460**
puma_dry	0.508 ± 0.273	**0.344 ± 0.422**
graydeer_dry	0.470 ± 0.283	**0.205 ± 0.470**
collared_dry		
threearm_dry	0.533 ± 0.341	−0.040 ± 0.447
ninearm_dry		

the rainy season ($P < 0.0001$). We found similarities in HS maps between both jaguars and pumas and gray brocket deer in the dry season, and between jaguars and 9-banded armadillos based on total records (all $P > 0.05$). HS maps also did not differ significantly between seasons for gray brocket deer ($P > 0.05$). All HS maps for jaguars, pumas, and gray brocket deer showed a more defined core area in the central and southern region of the park (Figs. 2–4).

Considering Levins's standardized index based on the total set of records, jaguars had a narrower niche than pumas. For both species, the index was wider in the dry season than considering the total set of records (dry and rainy season; Table 3). Similarly, Lloyd's asymmetric overlap index showed higher values for both species in the dry season than considering the total set of records. Both comparisons registered greater overlap between the jaguar's niche and that of the puma than the reverse, as showed by the greater Z21 values (Table 3). Those values decreased for both species in the dry season, especially for jaguars, by almost one-half. According to Pianka's niche overlap index, both niches were close to complete overlap (1.0 indicates complete overlap) considering total records or records from the dry season (Table 3). We did not include models from the rainy season because the HS model for pumas in the rainy season was not approved by the CBI threshold. In the Discriminant Analysis, DEM was the EGV with the largest weight for the discriminant factor, which summarizes the resources used by both jaguars and pumas (see Supplementary Data SD3).
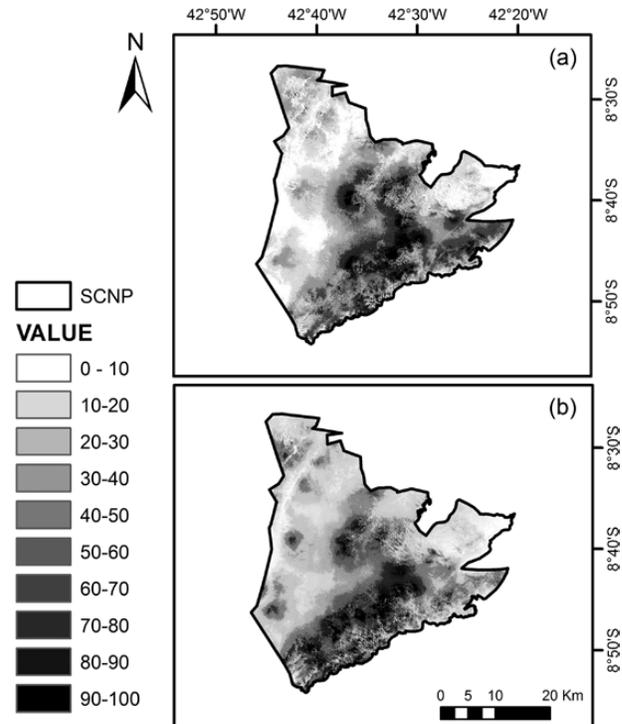

Fig. 2.—Habitat suitability maps from Ecological Niche Factor Analysis based on camera-trapping records for jaguars (*Panthera onca*) in the rainy (a) and dry season (b) in the Serra da Capivara National Park, Caatinga, Brazil, resulting from the area-adjusted median (Ma) algorithm. SCNP = Serra da Capivara National Park.
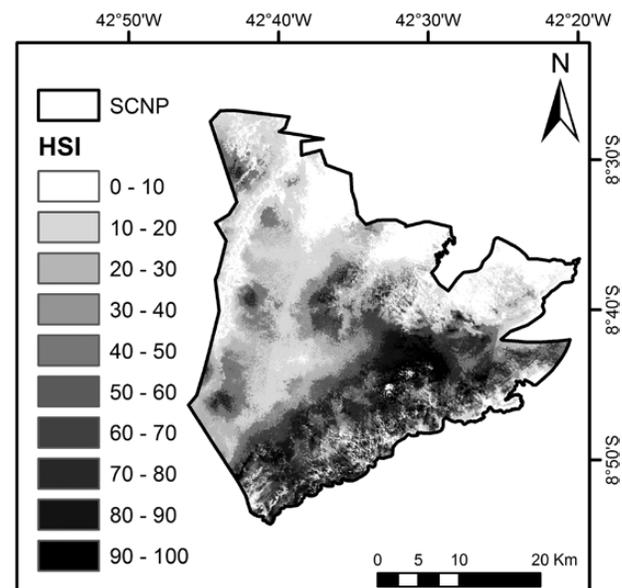

Fig. 3.—Habitat suitability maps from Ecological Niche Factor Analysis based on camera-trapping records for pumas (*Puma concolor*) in the dry season in the Serra da Capivara National Park, Caatinga, Brazil, resulting from the area-adjusted median (Ma) algorithm. HSI = habitat suitability index; SCNP = Serra da Capivara National Park.

DISCUSSION

One of the greatest advantages of ENFA is its ability to make an analysis of multiple species at the same time using the same

set of ecological factors. We found that the different species in this arid biome—where none of them are endemic—show preferences for the same resource: artificial waterholes. Three of the 6 (jaguars, pumas, gray brocket deer) also showed the same preference for a 2nd factor: elevation.

The fact that distance from artificial waterholes was the EGV with the highest coefficient for the marginality factor for some species was not surprising. In an ENFA modeling effort for jaguars across Mexico, Rodríguez-Soto et al. (2011) found that arid vegetation was characterized by low suitability values. In the present study, the park's southern region holds the highest suitability for both jaguars and pumas (see Figs. 2 and 3). This is SCNP's most elevated region, with the highest concentration of waterholes as well as canyons, rocky formations, and deep forested valleys, in contrast to the central plateau of the park. Those formations could be used by jaguars and pumas as refuges or resting places in the warmest hours of the day. Modeling

Fig. 4.—Habitat suitability maps from Ecological Niche Factor Analysis based on camera-trapping records for gray brocket deer (*Mazama gouazoubira*) in the rainy (a) and dry season (b) in the Serra da Capivara National Park, Caatinga, Brazil, resulting from the area-adjusted median (Ma) algorithm. HSI = habitat suitability index; SCNP = Serra da Capivara National Park.

HS for jaguars in the Caatinga, Morato et al. (2014) found that elevation was the variable that most influenced presence of jaguars in this biome. The authors suggested 2 explanations: first, that higher elevations are somewhat sheltered from human activity, and second, that the vegetation types in the elevated areas favor jaguar presence. We found that distance to human settlements was of little relevance to HS of these species. We offer an alternative explanation related to thermoregulation: in a study of natural formations of SCNP, such as caves used as refuges by prehistoric humans, Figueiredo and Puccioni (2006) found that during the dry season, while the temperature in the hottest moments of the day could reach up to 50°C outside the refuges, inside them it remained under 30°C. The extreme temperatures during the dry season could represent a constraint for felids such as jaguars and pumas, which, unlike canids, do not thermoregulate by panting and radiating heat from the skin (West 2005). In a typical Caatinga scenario with high temperatures and deciduous vegetation, those animals would most likely prefer places where they can thermoregulate during daytime, such as waterholes and refuges. In semiarid regions of Africa, waterholes are used by felids, and where available, leopards (*Panthera pardus*) make use of caves as a strategy to escape high daytime temperatures in hot climates and to reduce water loss (Bothma 1998). This is supported by the mostly nocturnal activity patterns of jaguars and pumas at SCNP (Astete et al. 2008; Foster et al. 2013).

In the rainy season, SCNP turns into a green landscape and rainwater stores in natural formations on the rocks (FUMDHAM 1998). Considering this seasonal change in vegetation and availability of water, we expected seasonal differences between the HS maps for all the species, but this trend was only shown by jaguars. However, when Levin's standardized index was compared between jaguars and pumas, for both species it was wider in the dry season than the combination of dry and rainy season, suggesting that both species had to explore a broader set of resources during the harsh dry season.

Food habits of jaguars and pumas are similar in the semiarid Chaco (Taber et al. 1997), a habitat similar to the Caatinga, and the high value of Pianka's overlap index for these species based on our data indicates the potential for competition. Those results coincide with the similarities of HS maps between those 2 species in the dry season. Competition between large predators and mesopredators has been widely reported (Ritchie and Johnson 2009), with the mesopredator restricting its habitat use and altering its foraging behavior to avoid the large predator. The higher asymmetric niche overlap index Z21 and its decrease for both species in the dry season (more notable for
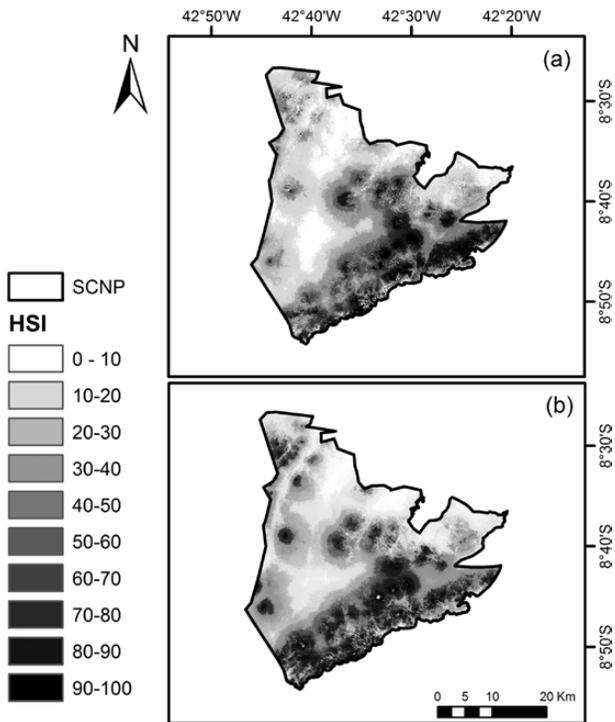
Table 3.—Results of the Discriminant Analysis and Niche Overlap between jaguars (*Panthera onca*) and pumas (*Puma concolor*) at Serra da Capivara National Park, Brazil, considering the total (tot) number of records, as well as records in the dry (dry) season. LSI = Levins' standardized index; Pianka's_O = Pianka's niche overlap index; Jaguar-Puma(Z12) and Puma-Jaguar(Z21) = Lloyd's asymmetric overlap index, a measure of directional niche overlap: Z12 represents the density of species 2 (puma) encountered, on average, by species 1 (jaguar), whereas Z21 is the reciprocal.

Model name	Jaguar_LSI	Puma_LSI	Pianka's_O	Jaguar-Puma(Z12)	Puma-Jaguar(Z21)
Jaguar_Puma_tot	0.163	0.180	0.922	6.963	7.944
Jaguar_Puma_dry	0.260	0.250	0.941	4.047	4.466

the jaguar) could suggest that: 1) both species try to avoid each other more actively during the harsh dry season, or 2) that jaguar presence decreases everywhere in the dry season due to its lower tolerance, concentrating in critical regions most suitable for the species, where it has a higher overlap with the puma's niche. This last supposition is also supported by the seasonal HS maps for jaguars and pumas.

Previous studies of jaguars in SCNP, which sampled mostly the southern area (Silveira et al. 2009; Sollmann et al. 2013), found that jaguars occur at a density of 1.57/100 km²—a value unexpectedly high considering the harsh habitat of the study area (Sollmann et al. 2013), but still one of the lowest compared to other habitats (Astete et al. 2008). The sampling area for those studies coincided with SCNP's region with the highest HS values for jaguars and other species, which, assuming a positive relationship between HS and abundance (VanDerWal et al. 2009), could explain the unexpected density value. It is therefore conceivable that future population surveys in SCNP covering the park's total area will result in lower density estimates.

Space use of solitary carnivores such as jaguars and pumas is not only influenced by the distribution of habitats but also by the distribution and abundance of their prey (Sandell 1989). SCNP's southern region combines the greatest concentration of waterholes and a topography that favors the ambush by predators, which seem to prefer prey availability more than prey vulnerability (Hopcraft et al. 2005). As expected, in the dry season, the models predicted significant similarities between HS maps of both felids and deer.

For gray brocket deer, as for jaguars and pumas, the distance to waterholes also had the highest EGV coefficient for marginality. Previous research in SCNP observed a correlation between the spatial distribution of deer and the presence of waterholes (Wolff 2001). A study on herbivores in an African semiarid reserve without permanent sources of water, but with artificial waterholes (Valeix et al. 2008), showed that when natural water abundance decreases, artificial waterholes become more crucial. In Kruger National Park, another protected area with water management, Smit et al. (2007) found that surface water availability is more important for water-dependent mixed feeders (grazer and browsers) than for less water-dependent browsers. Seemingly, gray brocket deer—a mixed feeder (Black-Décima et al. 2010)—is following the same water-dependent pattern. We suggest that the deer's preference for higher elevation could be explained because high-elevation areas in SCNP (especially the central and southern region) are covered by woody vegetation (Emperaire 1984; FUMDHAM 1998), which is seemingly preferred by the species (Serbent et al. 2011). For the deer, the EGV NDVI (vegetation) was also the 3rd most important factor.

Artificial waterholes are cited as preferred places for predators to stalk ungulate prey, something that could not only affect prey distribution (Valeix et al. 2009) but also the local community structure of the mammal assemblage (Owen-Smith and Mills 2006; De Boer et al. 2010). However, we do not think waterholes represent a menace for gray brocket deer in SCNP. The diet of jaguars and pumas in SCNP is well studied, and both species seem to share the same prey items, mostly feeding on medium-sized mammals like armadillos (*Dasypus* spp.) and anteaters (*Tamandua tetradactyla*), all of them weighing less than 15 kg, with birds, reptiles, and other species representing less than 10% of their diet (Olmos 1993; Wolff 2001). Another aspect favorable for gray brocket deer is that deer are predominantly diurnal (Astete 2008), whereas jaguars and pumas are predominantly nocturnal, so the chances to be depredated at waterholes are reduced.

Camera trapping has been effective for surveying medium- and large-sized mammals (Karanth 1995; O'Connell et al. 2011), providing reliable identification of target species. Our camera stations were designed to estimate abundance of jaguars (Silveira et al. 2009) and therefore to maximize the chance of detecting jaguars and mid- to large-sized animals. The camera stations were fixed in place during the sample period, so that over time their chances to detect target species were higher, but as a trade-off, the number of locations we could sample was limited.

We focused our discussion on only 3 of the 6 species because only they showed robust ENFA models, considering the total set of data and the seasonal separation of records. All cameras were placed on roads, which are thought to be used preferentially by felids and other mid- to large-sized mammals (Tobler et al. 2008; Harmsen et al. 2010). Small animals, such as armadillos, are more likely to pass in front of a camera without being photographed (Tobler et al. 2008) and other species, such as collared peccaries, may have a tendency for crossing trails more than following them (Harmsen et al. 2010), leading to sample sizes that are too small to build reliable ENFA models.

Like other ENFA studies focused on mid- to large-sized mammals (Pettorelli et al. 2009; Durant et al. 2010), we noted that the less conservative AVI classified the models as more robust than the CBI. The index values obtained in those studies are in most cases similar to ours, approving models with a CBI with values over 0.2 (Pettorelli et al. 2009). As the areas sampled by Pettorelli et al. (2009) included semiarid regions, we also decided to accept a CBI threshold of 0.2, indicating that the accuracy of our models was relatively low. This is a general feature with species having a widespread distribution (Segurado and Araujo 2004) and has been proposed to explain the low predictive power of their models for carnivores, a relatively generalist taxon with a broad ecological niche and less habitat specificity than other taxa (Durant et al. 2010). Similar to the carnivores, the prey species found in SCNP also have relatively wide geographic distributions, occupying different habitats throughout South America. The exception is the 3-banded armadillo, endemic to the semiarid Caatinga biome and adjacent Cerrado vegetation associations (Marinho-Filho et al. 1997).

Spatial autocorrelation is always problematic with the use of geographical space (Legendre 1993), although there are some options to solve the problem (Diniz-Filho and Telles 2002; Segurado et al. 2006). We do not believe this issue is relevant in our study because the applied method (ENFA) has a special way to deal with the problem. ENFA, a presence-only algorithm, is a kind of principal component analysis (PCA—Hirzel et al. 2001), where points of occurrence are crossed with environmental variables to produce different maps that correspond

to the factors in a PCA: the marginality and the specialization. As a PCA, the analysis extracts most of the data variance and allocates it into uncorrelated factors that contain ecological information (Hirzel et al. 2004). The marginality component would have a very low importance if the original data had a strong autocorrelation. Consequently, the CBI would classify the model as inadequate, which was not the case.

Due to our limitation to place cameras only in roads, there were areas of SCNP that were not surveyed. However, those areas did not have different conditions from those from which the models were derived, as cameras were placed proportionally in the different vegetation and landscape types in SCNP. Thus, our results were not biased by sampling the least favored areas less than other areas, which could lead to spatial autocorrelation.

The semiarid Caatinga does not seem to be the most suitable habitat for predators like jaguars and pumas, or for some of their prey, considering their physiological limitations. Using ENFA, we determined that the region with the combination of rocky areas and the highest abundance of artificial waterholes in SCNP explained most of HS for gray brocket deer, jaguars, and pumas, especially during the hot, dry season. To our knowledge, this is the 1st study to show the positive effects of water management policies in protected areas in Brazil or South America. This combination of characteristics has the potential to make SCNP a key area in the maintenance of jaguars, pumas, and gray brocket deer in the Caatinga.

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SUPPLEMENTARY DATA

Supplementary Data SD1.—Correlation matrix of the ecogeographical variables (EGVs) used in the Ecological Niche Factor Analysis.

Supplementary Data SD2.—Values for all ecogeographical variables at each camera-trap sampling point in the Serra da Capivara National Park, Caatinga, Brazil.

Supplementary Data SD3.—Weights of the ecogeographical variables (EGVs) in the discriminant factor, which summarizes the resources used by both jaguars and pumas in the different models, using the total (tot) set or records and the ones in the dry (dry) season.

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