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Original Investigation

Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil

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ABSTRACT

Coexistence of sympatric species is mediated by resource partitioning. Pumas occur sympatrically with jaguars throughout most of the jaguar's range but few studies have investigated space partitioning between both species. Here, camera trapping and occupancy models accounting for imperfect detection were employed in a Bayesian framework to investigate space partitioning between the jaguar and puma in Emas National Park (ENP), central Brazil. Jaguars were estimated to occupy 54.1% and pumas 39.3% of the sample sites. Jaguar occupancy was negatively correlated with distance to water and positively correlated with the amount of dense habitat surrounding the camera trap. Puma occupancy only showed a weak negative correlation with distance to water and with jaguar presence. Both species were less often present at the same site than expected under independent distributions. Jaguars had a significantly higher detection probability at cameras on roads than at off-road locations. For pumas, detection was similar on and off-road. Results indicate that both differences in habitat use and active avoidance shape space partitioning between jaguars and pumas in ENP. Considering its size, the jaguar is likely the competitively dominant of the two species. Owing to its habitat preferences, suitable jaguar habitat outside the park is probably sparse. Consequently, the jaguar population is likely largely confined to the park, while the puma population is known to extend into ENP's surroundings.

Introduction

Differences between sympatric species in the use of trophic, temporal and spatial resources are thought to promote species coexistence in ecological systems (Schoener, 1974). For sympatric carnivores with similar morphology and foraging strategies, variation in body mass, often correlated with prey body mass (Carbone and Gittleman, 2002), can reduce competition for trophic resources (Rosenzweig, 1966; Karanth and Sunquist, 1995). Partitioning of food resources also takes place between similar sized carnivores (e.g., Kruuk et al., 1994; Jácomo et al., 2004). For species with similar feeding habits, the partitioning of habitat (Jácomo et al., 2004) or, more generally, space (Creel and Creel, 1996; Palomares et al., 1996; Durant 1998), as well as differences in activity patterns (Karanth and Sunquist, 2000; Romero-Muñoz et al., 2010) can facilitate coexistence.

The jaguar Panthera onca (Linnaeus 1758) is the largest neotropical felid. Having experienced a range contraction of almost 50% over the last century (Zeller, 2007) the species is classified as Near Threatened with decreasing population trends (IUCN, 2010). Throughout most of its distribution, the species occurs sympatrically with the puma Puma concolor (Iriarte et al., 1990). Although listed as Least Concern, puma population trends are also decreasing (IUCN, 2010) and very little is known about the species in the neotropical part of its distribution (Kelly et al., 2008).

Owing to its larger size, the jaguar is thought to be competitively dominant over the puma (Schaller and Crawshaw, 1980; Crawshaw and Quigley, 1991). Several authors report avoidance between jaguars and pumas on a local scale in both spatial and temporal terms (Emmons, 1987; Scognamillo et al., 2003; Harmsen et al., 2009; Romero-Muñoz et al., 2010). In a larger spatial context, pumas seem to be rare at sites where jaguars are abundant (Rabinowitz and Nottingham, 1986; Azevedo and Murray, 2007) and vice versa (Noss et al., 2006; Kelly et al., 2008).

Partitioning in space can be achieved either through evolved differences in species-specific habitat preferences (Núñez et al., 2000), or by active avoidance of the actual presence of competitor individuals, for example by using olfactory cues. While aspects

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of spatial ecology and interaction among species and/or individuals are best studied using radio or GPS-based telemetry (Millspaugh and Marzluff, 2001), these methodologies are invasive and for elusive species like jaguars often have to rely on small sample size. In contrast, non-invasive methods such as camera traps can yield information on a larger part of the population under study (MacKay et al., 2008). Since camera detections can be geographically referenced, these data can also be used to gain insight in aspects of spatial ecology of elusive species (Kays and Slauson, 2008; Harmsen et al., 2009; Foster et al., 2010).

However, just as with other survey methods, our ability to detect a species present in an area with a camera trap is not perfect. Whether or not (or how often) we detect a given species will depend on how it moves through the area we sample and where and how we set up the camera trap. Therefore, the use of raw photographic data such as count statistics can be problematic. Analyses of space use can lead to biased results if they do not account for imperfect detection, which can further vary among species and in space (MacKenzie et al., 2006; Royle and Dorazio, 2008). An adequate approach to this problem is provided by hierarchical models, which explicitly describe the observation process–in this case detection by camera traps – separately from the underlying ecological process–here, the actual distribution of a species in space (Royle and Dorazio, 2008). In the present study we use camera trapping data and Royle and Dorazio's (2008) hierarchical formulation of the occupancy models developed by MacKenzie et al. (2006) as implemented in a Bayesian framework to investigate differences in habitat use and patterns of co-occurrence of the jaguar and the puma in Emas National Park (ENP), central Brazil. The park is one of the last refuges for both species in the central Brazilian Cerrado grasslands, one of the world's 25 ecological hot spots (Myers et al., 2000). In spite of a severe threat of large scale habitat loss, both species remain very little studied in this biome.

Material and methods

Study site

Emas National Park, listed as a Human Heritage Reserve by UNESCO, is located in south-western Goiás state (18°19′S, 52°45′W; Fig. 1) in the Cerrado grasslands of central Brazil. The park has a size of 1320 km^2 and protects large tracts of grassland plains, interspersed with small patches of shrub fields, marshes, and riparian forest. During the wet season (October–March), rainfall averages 1500 mm. There is very little precipitation during the rest of the year, when daytime temperatures can reach 40 °C and night temperatures may drop to −1.5 °C (IBDF/FBCN, 1981). ENP is situated in a highly productive agricultural area. Large-scale soybean, corn and sugar cane plantations dominate and fragment the regional landscape. This situation is typical of the Cerrado: Brazil's second largest biome covers 21% of the country's area but over the last 35 years more than half of it was transformed into cultivated land (Klink and Machado, 2005). Today, only 1.9% is strictly protected and 80% is considered degraded (Cavalcanti and Joly, 2002).

Camera trapping

Between March and June 2008, we deployed 119 camera trap stations covering the entire ENP (Fig. 1) to estimate jaguar abundance and density in the study area (Sollmann et al., 2011). Distances between neighbouring stations were approximately 3.5 km, following recommendations for abundance estimation in jaguars (Silver, 2004). Cameras were predominately set along park roads; at off-road locations, we installed cameras along game trails. For unequivocal individual identification, each station consisted of two camera traps of the 35-mm LeafRiver C1-BU (Vibrashine Inc., Taylorsville, MS 3968, USA) facing each other with a lateral offset of approximately 30 cm to avoid flash interference. Camera traps were strapped to trees or stakes approximately 40–50 cm above ground. During approximately three months of sampling camera traps were checked at 10–14-day intervals for film roll and battery replacement. Since cameras were easily triggered by sunlight in the predominately open habitat of ENP, we programmed cameras to work 24 h day^{-1} in shady locations and only during night time in exposed locations. To avoid bias, we only used photographs taken at night for our analysis. We are confident that this choice did not influence our analysis as in ENP radio-telemetry showed that both species are predominantly nocturnal (Silveira 2004). An analysis of records from camera traps working 24 h day^{-1} confirmed this observation (data not shown).

Occupancy model

Occupancy models estimate the probability of a species occupying a sampling site while correcting for imperfect species detection based on repeated detection/non-detection data (MacKenzie et al., 2006). They can be formulated as hierarchical models (Royle and Dorazio, 2008) where the true occupancy state O_i (1 if present and 0 otherwise) of a sampling unit i is the outcome of a Bernoulli trial with probability of occupancy Ψ: $O_i \sim \text{Bernoulli}(\Psi)$.

Since non-detection of a species at a sampling unit can either be caused by true absence or by failure of detection, repeated visits to sampling units are used to estimate detection probability p conditional on occupancy. Using a logit link function on Ψ or p, both parameters can be modelled as linear functions of independent variables, as in regular logistic regression models (MacKenzie et al., 2006).

Implementation of the model in a Bayesian framework explicitly estimates the partially latent O, is straightforward and allows the definition of functions of the estimated occupancy state (MacKenzie et al., 2006; Royle and Dorazio, 2008). Thus, this approach enabled us to estimate the number of sites occupied by jaguars (J), pumas (P) and both species (B) as

$$J = \sum O_J;\, P = \sum O_P;\; B = \sum (O_J \times O_P)$$

where the subscripts "J" and "P" denote parameters for jaguars and pumas, respectively. We were interested in determining whether both species co-occurred more or less often than expected under the assumption that their distributions are independent. Two species, A and B, occur independently if the probability of occurrence of both species $\Psi(\text{A and B}) = \Psi(\text{A}) \times \Psi(\text{B})$. Thus, the expression $\varphi = \Psi(\text{A and B})/\Psi(\text{A})^{*}\,\Psi(\text{B})$ describes the degree of spatial interaction of both species. If $\varphi > 1$, species co-occur more often than expected; if $\varphi < 1$, species co-occur less often than expected (MacKenzie et al., 2006). In our approach, we used the actual rates of occurrence of jaguars and pumas, J_r and P_r, as the percentage of all sites estimated to be occupied instead of the probability of occurrence Ψ. We defined $J_r = J/N$, $P_r = P/N$ and $B_r = B/N$, where N is the total number of sampling sites, and

$$\varphi = \frac{B_r}{J_r \times P_r}$$

Single-season occupancy models assume that the true occupancy state of a sample unit does not change over the course of the study (MacKenzie et al., 2006). At the scale of the present study, where the occupancy state of a given sampling unit may largely depend on the within-home range movements of a single individual, the species might temporarily not be available for sampling at a given