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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.

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

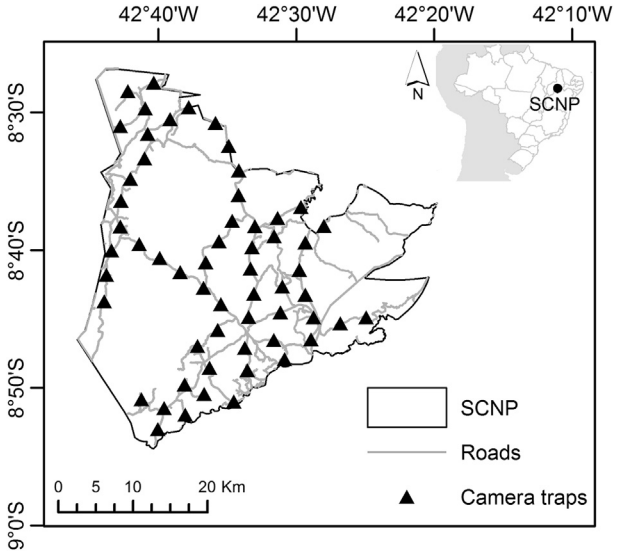

Fig. 1. Location of the Serra da Capivara National Park (SCNP) in Brazil and distribution of the camera-traps in the study between 2009 and 2011.