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Original investigation

Spatial requirements of jaguars and pumas in Southern Mexico

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ABSTRACT

Understanding how large felids use space is essential for the design of conservation plans that are required for their survival. Jaguars (*Panthera onca*) and pumas (*Puma concolor*) are the largest felids in the Neotropics, and they are sympatric throughout the entire range of the jaguar. However, there is very little information about the spatial requirements of these two species in the tropical rainforests of Central America. Using satellite GPS collars, we compared the spatial ecology of jaguars and pumas in a tropical rainforest in southern Mexico. We found that jaguars had home ranges that were 2–6 times larger than those of pumas. The mean annual home range was $181.4 \pm 4.0\,km^2$ for female jaguars and $431.6 \pm 152.6\,km^2$ for males. Annual home range for the only female puma tracked was $34.3\,km^2$, and $72.0 \pm 85.2\,km^2$ for males. Jaguars and pumas with overlapping home ranges showed little overlap of core areas and avoided using the same sites at the same time, which suggested that territoriality and avoidance were in play. Further evidence of avoidance was derived from our observation that pumas exhibited greater movement during the lightest periods of the day and jaguars moved most during the darkest. This temporal separation probably facilitates coexistence. Our data suggest that habitat destruction and fragmentation has more severe effects on jaguars than on pumas. According to our estimates, patches of at least $180\,km^2$ of primary forest are required to meet the annual spatial requirements of female jaguars. Thus, to conserve jaguars in this region, large tracts of primary forest should be preserved. Importantly, this population of jaguars depends on the adequate preservation of connectivity between natural reserves in Mexico and Guatemala.

Introduction

Understanding the details of how large felids use space is essential to develop and implement effective conservation plans for these species. Large felids require large home ranges for their survival and, thus, they exist at low population densities (Carbone and Gittleman, 2002; Woodroffe and Ginsberg, 1998). Diverse factors determine the patterns of space use of solitary large felids. Variables that dictate home range in these animals include body size (Carbone et al., 2007, 2005; Gittleman and Harvey, 1982; Gittleman, 1985; Jetz et al., 2004), prey availability (Herfindal et al., 2005; Marker and Dickman, 2005; Odden and Wegge, 2009; Schmidt, 2008), habitat suitability (Broomhall et al., 2003; Conde et al., 2010; Spong, 2002), and sociality (Azevedo and Murray, 2007; Cavalcanti and Gese, 2009; Goodrich et al., 2010; Logan and Sweanor, 2001; Seidensticker et al., 1973). Additionally, interactions between species, in particular other large carnivores, can influence patterns of space use. Co-occurring species of large carnivores may use different habitat types, actively avoid using the inhabited sites, or segregate their space use temporally (Bhattarai and Kindlmann, 2012; Foster et al., 2013; Harmsen et al., 2009; Odden et al., 2010; Scognamillo et al., 2003; Sollmann et al., 2012). Landscape configuration and connectivity are critical aspects that determine the space use in large felids as well (Colchero et al., 2011; Conde et al., 2010; de la Torre et al., in press; Zeilhofer et al., 2014).

Jaguars (*Panthera onca*) and pumas (*Puma concolor*) are the largest felids in the Neotropics, and are sympatric throughout the entire range of the jaguar. As with most large species of Carnivora, jaguar and puma populations are declining due to habitat destruction and human persecution (Ripple et al., 2014; Treves and Bruskotter, 2014; Woodroffe and Ginsberg, 1998). The present distribution of jaguars ranges from northern Mexico to northern Argentina, with some individuals occasionally reaching the southern portions of the United States (Arizona and New Mexico) (Sanderson et al., 2002; Sunquist and Sunquist, 2009). Throughout their range, jaguars occupy diverse habitat types, which include

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tropical rainforests, mangroves, wet grasslands, arid scrublands, and pine oak forests (Sanderson et al., 2002).

In comparison, pumas are found in an even wider range of habitat types and they have a larger distribution that ranges at present from Patagonia to Northern British Columbia (Sunquist and Sunquist, 2009). Pumas are smaller in areas where they live in sympatry with jaguars, and their body size is larger in areas outside the jaguar's distribution (Iriarte et al., 1990). Although jaguars are larger than pumas, there is overlap in their size and the size of prey they can hunt effectively and, thus, they are potentially competing species. Several studies have examined interactions between these species in areas of sympatry. It appears that coexistence between jaguars and pumas is facilitated by differential habitat use, active avoidance, temporal segregation of space, or by differential prey use (Aranda and Sánchez-Cordero, 1996; Emmons, 1987; Foster et al., 2010a, 2013; Harmsen et al., 2009; Novack et al., 2005; Nuñez et al., 2000; Romero-Muñoz et al., 2010; Scognamillo et al., 2003; Sollmann et al., 2012).

Recently, there have been significant advances in understanding jaguar and puma ecology in tropical ecosystems (Carvalho and Pezzuti, 2010; De Angelo et al., 2011; Di Bitetti et al., 2010; Foster et al., 2010a, 2010b, 2013; Harmsen et al., 2011, 2010, 2009; Hernández-saintmartín et al., 2013; Romero-Muñoz et al., 2010; Rosas-Rosas and Bender, 2012; Rueda et al., 2013; Scognamillo et al., 2003; Sollmann et al., 2012; Soto-Shoender and Main, 2013). However, information about spatial requirements, movement behavior, and the impact of habitat destruction is still lacking. Thus, current conservation and management plans for these species in Neotropical ecosystems suffer from insufficient information.

The aim of this study is to describe and compare the spatial ecology of jaguars and pumas in a tropical rainforest with heavy human activity in southern Mexico. Using GPS telemetry, we documented home range size, movement patterns, and interactions between jaguars and pumas. This is the first study that presents data on jaguars and pumas that were tracked simultaneously using GPS radio-telemetry, and the results presented in this study illustrate differences in the space use between these species that have not been documented previously. We were interested to know the home range characteristics of jaguars and pumas in the tropical rainforests of southern Mexico, to describe the spatial organization of both species, and to describe how jaguars and pumas share space when they coexist. Because home range size in large predators is determined by body size and energetic requirements (Gittleman and Harvey, 1982; Gittleman, 1985), we predicted that home range areas and movement rates will be greater in jaguars than in pumas. Given that coexisting felids show temporal segregation in their space use and actively avoid the same sites (Bhattarai and Kindlmann, 2012; Harmsen et al., 2009; Romero-Muñoz et al., 2010; Odden et al., 2010; Scognamillo et al., 2003), we predicted that jaguars and pumas with overlapping home ranges would show little overlap at core home range areas and they would avoid using sites at the same time.

Material and methods

Study site

Our study area was in the Greater Lacandona Ecosystem (GLE) in southeastern Mexico. This region contains the largest remaining portion of tropical rainforest in Mexico. Found in the most biodiverse region of Mexico, the GLE is a valuable natural resource and is part of what is called the 'Mayan Forest', given its important cultural associations (de la Torre and Medellín, 2011; Medellin, 1994). Despite importance for conservation of numerous species, the GLE continues to be subjected to anthropogenic destruction. Of its original 1,500,000 ha of rainforest, 2/3 has been lost due to human impact in the past 40 years (Jong et al., 2000; Mendoza and Dirzo, 1999).

There are seven Natural Protected Areas (NPAs) within the GLE. These cover the largest forested areas of this region: Montes Azules (3312 km^2), Lacantún (619 km^2), Bonampak (48 km^2), Yaxchilán (26 km^2), Chan-kin (122 km^2), Naha (38 km^2), and Metzabok (33 km^2) (Fig. 1). Our study area was in the north of GLE and covered approximately 2500 km^2, including Yaxchilán (Usumacinta river as the border with Guatemala on the north), Bonampak, Lacantún, and Montes Azules NPAs (Fig. 1). The study area also encompassed the Sierra la Cojolita, a tract of natural habitat in the north of GLE that is protected by local communities. Three indigenous communities inhabit the Mexican part of our study area: Lacanja Chansayab (~1000 people), Nueva Palestina (~20,000), and Frontera Corozal (~15,000). The main economic activities in this region include ranching, farming, and ecological and archeological tourism. The climate is hot (mean of 25 °C) and the mean rainfall per year is 2800 mm, with the greatest concentration in June-September, and the lowest in March–April (reviewed O'Brien (1998)).

Data collection

We captured jaguars and pumas using foot snares (Frank et al., 2003). At the site of each snare trap we also placed a VHF radio transmitter to monitor if traps were triggered (Halstead et al., 1995). Traps were checked every 4 h throughout the night and, depending on weather conditions, several times during the day. All capture and handling protocols followed the American Society of Mammalogists' IACUC guidelines (Sikes et al., 2011).

Upon capture, we immobilized animals using medetomidine (0.06 mg/kg) combined with ketamine (3.5 mg/kg) using a dart fired from a CO_2 pistol or rifle. While immobilized, we examined individual body condition and determined sex. We estimated age based on coat color, tooth wear (Stander, 1997), and gum-line recession (Laundré et al., 2000). Body mass and linear measurements were recorded. Weight was recorded using a portable scale.

We used satellite global positioning system (GPS) collars (i.e., Telonics® GEN IV, model TGW-4580). We programmed GPS collars to acquire a location every 4.8 h (4 locations/day), and to send data through the ARGOS system every 4 days. All collars included a programmable release mechanism (model CR-2a, Telonics®), and we scheduled the drop-off mechanism to release 12–14 months after capture. The GPS collars were recovered when possible using the locations that were obtained after their release through the ARGOS system and by searching the VHF pulse of the collars using a receiver.

Data analysis

For all analysis, we used only the 3D GPS fixes that were obtained by the collars, which are locations calculated from four or more GPS satellites that provided a location estimate for the GPS/ARGOS system with a typical accuracy of 2–10 m. For comparisons with other studies, we estimated annual home range size using 95% minimum convex polygon estimations (Mohr, 1947). However, to provide a more precise description of the home range use of jaguars and pumas, we also used the 50% and 95% fixed kernel estimators (Worton, 1989). We defined the core area within a home range as the area enclosed by the 50% isopleth. To prevent under-smoothing in kernel estimates, we utilized the rule-based ad hoc method of Kie (2013). We used the package "adehabitat HR" (Calenge, 2013) for R 3.1.1 (R Core Team, 2016) to estimate minimum convex polygons and kernel home ranges. We evaluated if the home range sizes were influenced by the number of fixes that were obtained per individual using Pearson's correlation analysis, and we tested if