Biological Conservation 228 (2018) 233–240

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Resource selection in an apex predator and variation in response to local landscape characteristics

R.G. Morato[a,b,c,*], G.M. Connette[b], J.A. Stabach[b], R.C. De Paula[a,c], K.M.P.M. Ferraz[c,d], D.L.Z. Kantek[e], S.S. Miyazaki[e], T.D.C. Pereira[e], L.C. Silva[f], A. Paviolo[g], C. De Angelo[g], M.S. Di Bitetti[g], P. Cruz[g], F. Lima[h,i], L. Cullen[i], D.A. Sana[c,j], E.E. Ramalho[c,k], M.M. Carvalho[l], M.X. da Silva[m], M.D.F. Moraes[m], A. Vogliotti[c,n], J.A. May Jr[o,p], M. Haberfeld[o], L. Rampim[o], L. Sartorello[o], G.R. Araujo[q], G. Wittemyer[r], M.C. Ribeiro[i], P. Leimgruber[b]

[a] *Centro Nacional de Pesquisa e Conservação de Mamíferos Carnívoros, Instituto Chico Mendes de Conservação da Biodiversidade, Atibaia, SP, Brazil*
[b] *Conservation Ecology Center, Smithsonian Conservation Biology Institute, National Zoological Park, Front Royal, VA, USA*
[c] *Instituto Pró-Carnívoros, Atibaia, SP, Brazil*
[d] *Escola Superior de Agricultura "Luiz de Queiroz", Universidade de São Paulo, Piracicaba, Brazil*
[e] *Estação Ecológica Taiamã, Instituto Chico Mendes de Conservação da Biodiversidade, Cáceres, MT, Brazil*
[f] *Departamento de Medicina Veterinária, Universidade Federal de Viçosa, Viçosa, MG, Brazil*
[g] *Instituto de Biología Subtropical, Universidad Nacional de Misiones, Asociación Civil Centro de Investigaciones del Bosque Atlántico (CeIBA) and CONICET, Puerto Iguazú, Misiones, Argentina*
[h] *IPÊ – Instituto de Pesquisas Ecológicas, Nazaré Paulista, SP, Brazil*
[i] *Laboratório de Ecologia Espacial e Conservação, Instituto de Biociências, Univesidade Estadual de São Paulo, Rio Claro, SP, Brazil*
[j] *Programa de Pós-graduação em Biologia Animal – Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil*
[k] *Instituto de Desenvolvimento Sustentável Mamirauá, Tefé, AM, Brazil*
[l] *Instituto de Defesa e Preservação dos Felídeos Brasileiros, Corumbá de Goiás, Go, Brazil*
[m] *Projeto Carnívoros do Iguaçu, Parque Nacional do Iguaçu, Instituto Chico Mendes de Conservação da Biodiversidade, Foz do Iguaçu, PR, Brazil*
[n] *Universidade Federal da Integração Latino-Americana, Foz do Iguaçu, PR, Brazil*
[o] *Associação Onçafari, São Paulo, SP, Brazil*
[p] *Universidade do Sul de Santa Catarina, SC, Brazil*
[q] *Faculdade de Medicina veterinária e Zooctecnia, Universidade Federal do Mato Grosso do Sul, Campo Grande, MS, Brazil*
[r] *Department of Fish, Wildlife and Conservation Biology, Colorado State University, CO, USA*

ARTICLE INFO

Keywords:
Resource selection function
Discrete choice models
Home range scale
Foraging scale
Functional response
Jaguar

ABSTRACT

Habitat loss and fragmentation represent major threats for the conservation of apex predators, such as the jaguar (*Panthera onca*). Investigating species' resource selection behavior in response to landscape alteration is critical for developing relevant conservation management plans. The jaguar is found across a variety of habitats with different gradients of human disturbance, making them a good candidate to study how apex predators respond to increasing intensity of human land use. We developed resource selection models to characterize patterns of jaguar resource selection at two different spatial scales, home range (coarse) and foraging scale (fine). This analysis was based on the largest existing GPS-location dataset for jaguars ($n = 40$ individuals, $n = 87{,}376$ locations), spanning the species' geographic range in Brazil and Argentina. We found that both males and females jaguars exhibited an overall preference for forests and areas close to watercourses at both the home range and foraging scale. At the foraging scale, areas of high livestock density "attracted" male jaguars. We also performed a follow-up analysis to test for context-dependent resource selection (i.e., functional responses) by relating individual behavior to local habitat characteristics. We found that jaguars in heavily-forested landscapes showed strong avoidance of non-forest. Furthermore, we found that only the individuals in closest proximity to watercourses showed positive selection for water. Our results highlight that jaguars display different patterns of resource selection in different areas, demonstrating a considerable ability to use or tolerate a wide variety of different conditions across the species geographic range. This plasticity may allow jaguars to adjust their behavior according to land use changes but also increases human-jaguar conflict and jaguar mortality, especially in areas with high livestock density.

---

[*] Corresponding author at: ICMBio-CENAP, Estrada Municipal Hisaichi Takebayashi 8600, 12952-011 Atibaia, SP, Brazil.
E-mail address: ronaldo.morato@icmbio.gov.br (R.G. Morato).

https://doi.org/10.1016/j.biocon.2018.10.022
Received 5 May 2018; Received in revised form 17 August 2018; Accepted 19 October 2018
0006-3207/

1. Introduction

Rapid changes in landscape composition and structure represent major threats to biodiversity worldwide (Candolin and Wong, 2012; Ripple et al., 2014, 2015). Typically leading to habitat loss (Barnosky et al., 2011), fragmentation (Fahrig, 2003), and increased barrier effects (Seidler et al., 2015), these changes may limit animal movement and dispersal and result in widespread reduction of core ecological processes (Haddad et al., 2015; Tucker et al., 2018). Investigating changes in species' resource selection behavior in response to landscape alteration is critical for developing relevant conservation management plans to facilitate species survival (Van Buskirk, 2012).

Natural or anthropogenic change in landscape structure, however, often vary across broad spatial scales (e.g. regions, biomes, continents), affecting individuals and populations in different ways (Mysterud and Ims, 1998). As a result, responses to temporally-dynamic and/or spatially heterogeneous resources may vary considerably across a species' geographic range, presenting significant challenges for land managers and decision makers (Boyce et al., 2002; Roever et al., 2012). Conversely, some resources may be used consistently across a species' geographic range, regardless of their underlying availability. African elephants (*Loxodonta africana*), for example, show consistent affinity for areas of low slope, high tree cover, and greater distance from human settlement (Roever et al., 2012). Despite the growing number of studies investigating how species "adjust" their resource selection across rapidly changing environments, few studies have performed analyses at a scale that encompasses a species' full geographic range (although see Parmesan, 2006), largely because range-wide, regional or continental-scale data are usually not available.

Resource selection functions (RSFs) have been widely applied to investigate species-habitat relationships (e.g., Boyce and McDonald, 1999; Gillies et al., 2006; Roever et al., 2012; Lehman et al., 2016; Stabach et al., 2016). For instance, RSFs are frequently used to compare used resources at observed telemetry locations (i.e., 'use' locations) with attributes of randomly-selected locations that are potentially available (i.e., 'pseudo-absence' locations). Resource selection functions may differ based on how the representative sample of available locations is selected, potentially influencing the scale of biologic inference (for a review of RSFs, see Lele et al., 2013).

Over the past decade, discrete choice models have emerged as a promising alternative to traditional logistic regression approaches for assessing resource preferences (Cooper and Millspaugh, 1999; McDonald et al., 2006; Thomas et al., 2006; Carter et al., 2010; Rota et al., 2014). Unlike logistic regression models, discrete choice models allow the researcher to develop different 'choice sets' for each independent observation. In doing so, discrete choice models provide a robust framework for accounting for changes in resource quality or availability through space and time. Furthermore, adjusting the spatial scale at which locally-available alternatives are selected allows the researcher to identify and compare drivers of resource selection behavior across a range of spatial scales (McDonald et al., 2006; Bonnot et al., 2011). Discrete choice models also provide an opportunity to test for

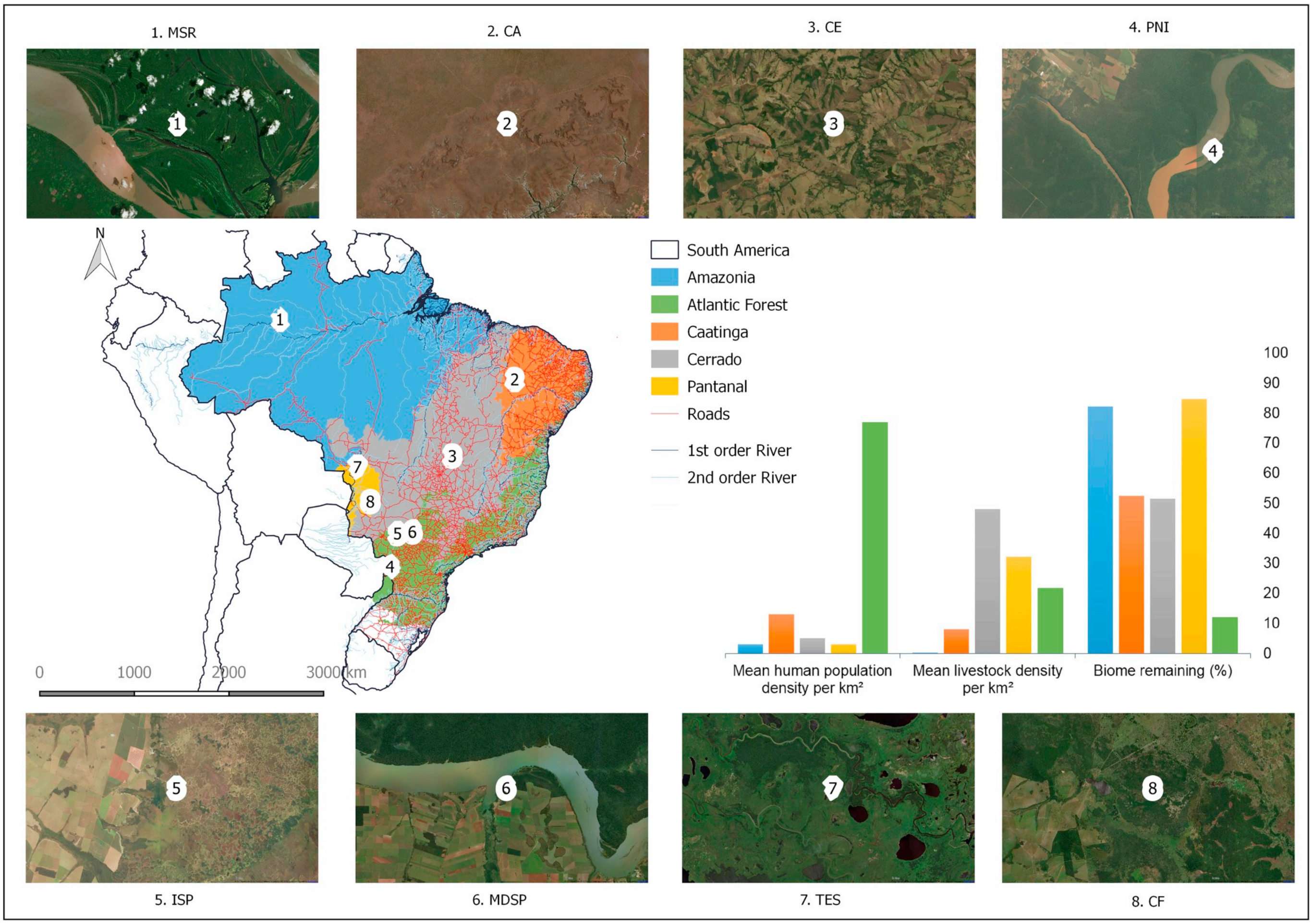

Fig. 1. Map of study area locations and associated aerial images depicting landscape characteristics of each study site. Histograms indicate mean human population density per km^2, mean livestock density per km^2 and % of biome remaining. Study sites were: 1) Mamirauá Sustainable Reserve (MSR, Amazon), 2) Serra da Capivara National Park (CA, Caatinga), 3) private lands at the Cerrado (CE), 4) Iguazú and Iguaçu National Parks (PNI, Atlantic Forest), 5) Invinhema State Park (ISP, Atlantic Forest), 6) Morro do Diabo State Park (MDSP, Atlantic Forest); 7) Taiama Ecological Station (TES, Pantanal); 8) Caiman Farm (CF, Pantanal).

potential functional responses, or context-dependent resource selection, by relating individual behavior to local habitat characteristics (e.g., Roever et al., 2012).

Jaguar (*Panthera onca*) is a widely-distributed apex predator, ranging across the Americas and inhabiting a wide variety of habitats, stretching from tropical moist forest to tropical dry forest or xeric areas (Sanderson et al., 2002). The species is found across a gradient of human disturbance (Jędrzejewski et al., 2018), which has been shown to affect its movement patterns and increase local extinction risk (Morato et al., 2016; Morato et al., 2013). Across many regions, jaguar populations have plummeted over the past few decades and are considered threatened in several countries (De La Torre et al., 2017a). The species, however, is also highly adaptable, making them a good candidate to study how apex predators respond to a gradient of land use change. While many resource selection studies exist on jaguar (e.g, Conde et al., 2010; Foster et al., 2010; Colchero et al., 2011; Cullen Jr et al., 2013; De La Torre et al., 2017b), none have addressed resource selection across a large range of biomes due to data limitations and the difficulty of combining datasets across a range of disturbance.

Here, we applied a Bayesian framework to the analysis of discrete choice models in order to characterize patterns of resource selection of the jaguar (*Panthera onca*), incorporating the largest telemetry dataset available to date for the species that covers approximately 30% of the species distribution. We developed resource selection models to compare resource selection between two different scales of inference: home range scale (coarse) and foraging scale (fine), corresponding to Johnson's (1980) 3rd and 4th order of resource selection, respectively. We were most interested in: 1) identifying primary drivers of jaguar resource use at multiple spatial scales and 2) examining how resource selection behaviors differ among gender and individual as a result of differences in resource availability across the landscape.

2. Material and methods

2.1. Study areas

Our study areas spanned the southern portion of the jaguar's distribution, covering areas in Brazil and NE Argentina (~900,000 ha), and included eight study sites encompassing five biomes: 1) Mamirauá Sustainable Reserve (MSR, Amazon, 1,124,000 ha), 2) Serra da Capivara National Park (CA, Caatinga, 100,000 ha), 3) private lands in the Cerrado (CE), 4) Iguazú and Iguaçu National Parks (PNI, Atlantic Forest, 200,000 ha), 5) Invinhema State Park (ISP, Atlantic Forest, 73,000 ha), 6) Morro do Diabo State Park (MDSP, Atlantic Forest, 34,000 ha); 7) Taiama Ecological Station (TES, Pantanal, 11,000 ha); 8) Caiman Farm (CF, Pantanal, 35,000 ha). The region included two tropical moist lowland forests (Amazon and Atlantic Forest), a tropical dry forest (Cerrado), an herbaceous lowland grassland (Pantanal), and a xeric scrubland area (Caatinga) (Sanderson et al., 2002) (Fig. 1). Habitat loss, human population density and livestock density varied considerably across study sites (see Fig. 1). In brief, MSR and TES are pristine areas with very low human activities. CA is a protected area surrounded by roads and sheep and goat farms. CE is an agricultural area with cattle farms and crop production. CF is a high-density cattle farm with low human population density. PNI, ISP, and MDSP are comprised of a mix of crop and cattle farms. These areas also have the highest human population and road density among the study sites (see Fig. 1).

2.2. Jaguar data

Adult jaguars ($n = 20$ males and $n = 20$ females) were captured and collared with GPS-satellite collars (Telonics-ARGOS, $n = 7$; Televilt-GPS, $n = 11$; Northstar-Globalstar, n = 1; Lotek-Globalstar, n = 2; Lotek-Iridium, $n = 19$) between 1998 and 2015. All individuals were reported to be in good health/body condition. Data collection schedules ranged from every half hour to one position per day. We gathered 87,376 individual locations from our sample of 40 jaguars (PNI, $n = 8634$; MDSP, $n = 561$; ISP, $n = 1306$; CA, $n = 6959$; CE, $n = 2432$; MSR, $n = 7196$; TES, $n = 41{,}554$; CF, $n = 18{,}734$). Fix success rate varied from 4% (Telonics-ARGOS) to 81% (Lotek-Iridium) and resulted in large variation in the total number of GPS locations per individual (range: 35 to 10,615). All animals were captured following standard protocols approved by the Instituto Chico Mendes de Conservação da Biodiversidade - Ministério do Meio Ambiente - Brazil (ICMBio-SISBIO license numbers: 30896–3, 46,031–4, 36,740–1, 44,677–1,14,202–4, 38,006–1, 30,053–1, 37,867–1), from Brazil, the Argentine National Park Administration (NPA license 03/09), and the Misiones Province Government (ME license 119/2012) from Argentina. Capture and collaring procedures followed guidelines approved by the American Society of Mammologists (Sikes and Gannon, 2011).

2.3. Home range scale

Home range extents were estimated for each individual using the autocorrelated kernel density estimator (AKDE) in the continuous time movement-modeling framework (package *ctmm*; Calabrese et al., 2016) in the R environment for statistical computing (R Core Team, 2016). This approach to home range estimation has several advantages over other existing methods, including the ability to incorporate data with irregular sampling intervals, data gaps, and complex autocorrelation structures. For each individual, we calculated the 95% AKDE contour and selected one random location per day to assess resource use ($n = 7643$ total locations). For the purpose of analysis, characteristics of each ‘used’ location were compared with five randomly-selected points within the home range.

2.4. Foraging scale

To delineate the foraging scale, we estimated the mean distance moved per day for each individual using the *ctmm* package (Fleming et al., 2015; Calabrese et al., 2016). We divided the derived mean distance moved per day for each individual by 24 to obtain the mean individual distance moved per hour. For each individual, we created a buffer around each telemetry location with a radius equal to the mean hourly distance moved by individuals within each study area (range: 165-m to 680-m). Each telemetry location was paired with five randomly-selected locations within this foraging radius for analysis.

2.5. Habitat covariates

Habitat covariates for our resource selection analysis were chosen based on their expected influence on jaguar movement. We used only covariates that could be applied across all populations, thereby avoiding site-specific variables: human population density, livestock density, distance to road, distance to water, and forest cover. Unless otherwise noted, all analyses were based on data layers with a 30-m spatial resolution.

Human population density has been reported to negatively affect jaguar presence (Conde et al., 2010; De Angelo et al., 2011; Jędrzejewski et al., 2018). Human density was estimated based on Bright et al. (2011) human population data (1 km resolution) and log (x + 1) transformed to account for a number of extreme outliers at high human population densities. The presence of livestock is suspected to attract jaguars (Zarco-González et al., 2013), with herd size having a positive effect on predation rates (Michalski et al., 2006). We used the Gridded Livestock of the World dataset (Robinson et al., 2014) to represent livestock density (1 km resolution). Distance to nearest road was calculated from road data provided by the Brazilian Institute of Geography and Statistics (IBGE, 2016) and a previous publication by De Angelo et al. (2013). Similar to other large mammals, jaguars avoid roads with high traffic (Colchero et al., 2011; De Angelo et al., 2013), which we expected to consequently affect patterns of space use (Conde et al., 2010). Non-primary roads were excluded from analyses. The MSR, ISP, TES, CF do not have roads within 10 km of any telemetry location from these study site. Because individuals at these sites were not expected to respond to roads > 10 km away, we fixed distance to roads for all used and available locations from these sites to an arbitrarily-large distance threshold of 10 km. This allowed us to retain distance to roads in the model while also reflecting that this variable should not influence the relative likelihood of any used or available location being selected at the four sites furthest from roads. Jaguar presence has been found to be positively associated with watercourses (Crawshaw and Quigley, 1991; Cullen Jr et al., 2005). Distance to the nearest river was estimated from a water (rivers) dataset obtained from the Brazilian National Agency of Water (ANA, 2012). Finally, forest cover is known to have a positive effect on jaguar presence (De Angelo et al., 2011), with probability of occurrence decreasing drastically in areas with low forest cover (Rodríguez-Soto et al., 2011; Morato et al., 2014). We used the Global Forest Change – tree cover dataset (Hansen et al., 2013) to represent percent forest cover in our analysis. This dataset defines forest cover as percent canopy coverage for all vegetation taller than 5-m.

2.6. Discrete choice models

We conducted Bayesian analyses of discrete choice models to characterize patterns of resource selection in jaguars based on telemetry data. Discrete choice models treat the probability of an individual selecting each used location as a function of that location's ‘utility’ relative to other locally-available, but unused (pseudo-absence), alternatives. Collectively, each set of used and unused alternatives is referred to as a ‘choice set’, and the utility of each alternative in the choice set is defined as a function of covariates. In our study, we treat the utility of each location (*i*) in a given choice set (*j*) for individual (*k*) as a function of location-specific covariates:

$$U_{ijk} = \beta_{1,k} PopDen_{ijk} + \beta_{2,k} Livestock_{ijk} + \beta_{3,k} River_{ijk} + \beta_{4,k} Road_{ijk} + \beta_{5,k} Forest_{ijk}$$

where $PopDen_{ijk}$ is log(human population density + 1), $Livestock_{ijk}$ is livestock density, $River_{ijk}$ is the distance to the nearest river (m), $Road_{ijk}$ is the distance to the nearest road (m) and $Forest_{ijk}$ is percent canopy cover. We modeled resource selection coefficients ($\beta_{1,\ k}, \ldots, \beta_{5,\ k}$) as individual-level random effects that are normally-distributed around the grand means for each coefficient across individuals (defined as μ_1,

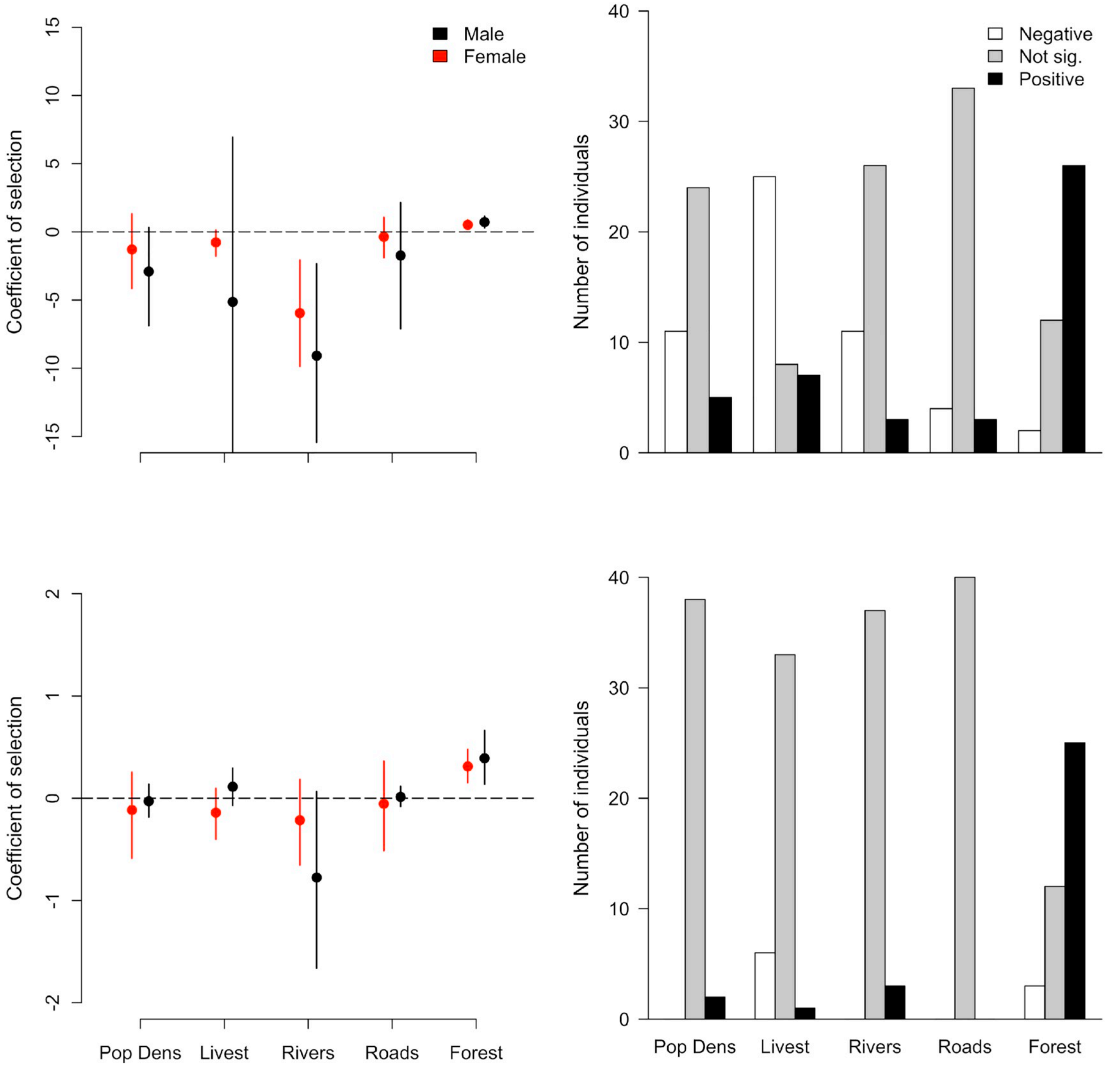

Fig. 2. Estimated overall selection coefficients by gender for each resource variable for the home range scale (top left) and foraging scale analysis (bottom left) (Points = Posterior Mean, lines = 95% HPDI interval). Number of jaguar showing positive, negative, or non-significant relationships for each habitat variable at the home range (top right) and foraging scale (bottom right) (based on 95% HPDI overlapping zero or not). Pop Dens = Human population density per km^2, Rivers = distance to rivers (m), Livest = livestock density per km^2, Roads = distance to roads (m) and Forest = forest cover (%).

…, μ_5). Corresponding variance parameters (σ_1^2, …, σ_5^2) describe the variation among individuals in the study. For example,

$$\beta_{1,k} \sim Normal(\mu_1, \sigma_1^2)$$

This specification of individual-specific regression coefficients accommodates variation among individuals in resource selection and accounts for the non-independence of repeated observations of each individual (Thomas et al., 2006, Rota et al., 2014). In our analysis, we also accomodated sex-related differences in habitat selection by estimating separate grand means and variance parameters for males and females. Thus, individual-level regression coefficients are considered random realizations of the population-level distributions corresponding to the individual's sex.

After defining the individual-specific utility of each alternative location (U_{ijk}), the relative probability ψ of an individual, k, selecting a particular location, i, in a given choice set, j, can then be expressed as

$$\psi_{ijk} = \left(\frac{\exp(U_{ijk})}{\sum_{i=1}^{I} \exp(U_{ijk})} \right)$$

where I defines the total number of locations in the choice set.

We used vague priors to reflect a lack of prior knowledge about the expected values of all parameters. The grand means for each resource selection coefficient, (μ_1, …, μ_5), were assigned diffuse normal priors (mean = 0, precision = 0.001) while corresponding precisions, $\left(\frac{1}{\sigma_1^2}, \ldots, \frac{1}{\sigma_5^2}\right)$, were assigned diffuse gamma priors (shape = 0.1, rate = 0.001).

We used all available jaguar locations to fit the model for resource selection at the foraging scale and one randomly-selected location per day, when available, to fit the model for resource selection at the home range scale. Models were fit in JAGS (Plummer, 2003) using the jagsUI (Kellner, 2015) package in R (R Core Team, 2014). We ran three parallel Markov chains for 20,000 iterations each. Our final sample from the joint posterior distribution was obtained by discarding the first 5000 iterations as burn-in and thinning the remaining samples to retain every 20th sample.

2.7. Functional response analysis

We followed the method described by Roever et al. (2012). In brief, after estimating individual-specific resource selection coefficients, we assessed how selection coefficients for a given covariate changed as a function of the average value of that covariate within the individual's home range. A relationship between the prevalence of a resource covariate and the corresponding strength of selection is interpreted as evidence for a functional response. Significance was evaluated using generalized additive models (Hastie and Tibshirani, 1986) in a Bayesian framework, since evidence existed for non-linear effects (Fig. S1). In addition, as our previous analysis didn't show evidence of differences between gender at home range scale, coefficients were pooled for the analysis. The fit of these generalized additive models was assessed by visually inspecting the plots of 30 curves drawn from the posterior distributions (e.g., Wood, 2016).

3. Results

3.1. Resource selection

At the home range scale, the relative probability of a jaguar using a location was positively associated with the local percent forest cover for both females ($\mu_5 =$ 0.51, 95% Highest Posterior Density Interval (HPDI) – [0.20, 0.86]) and males ($\mu_5 =$ 0.71, 95% HPDI = [0.30, 1.15]). Jaguars also selected for areas closer to rivers, with relative probability of use decreasing with increasing distance to river in both females ($\mu_3 =$ −5.95, 95% HPDI – [−9.86, −2.06]) and males ($\mu_3 =$ −9.16, 95% HPDI – [−15.43, −2.64]). Although the point estimate for the effect of

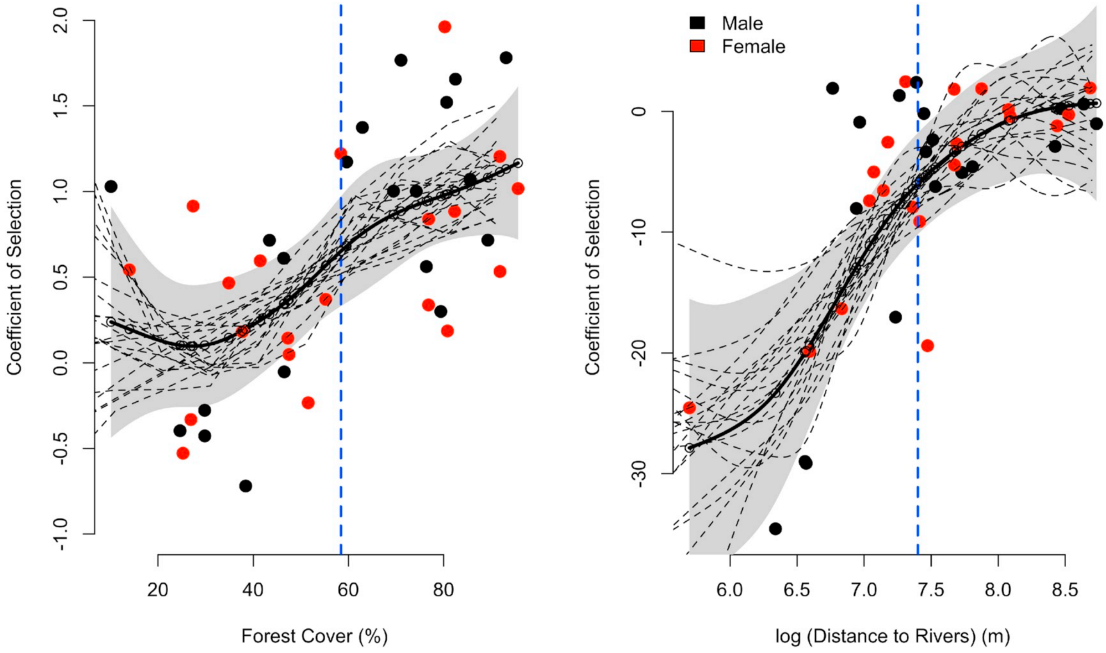

Fig. 3. The left panel is the estimate of the smooth function (black line) and 30 smooth curves drawn from the posterior (dotted lines) of a generalized additive model considering the coefficient of selection in relation to forest cover (%). The gray area indicates the 95% CI. The blue dashed line is the shifting point (58.4%). Notice the uncertainty of the response at low forest coverage and the tendency for jaguars in heavily-forested landscapes to more strongly avoid non-forest. The right panel is the estimate of the smooth function (black line) and 30 smooth curves drawn from the posterior (dotted lines) of a generalized additive model considering the coefficient of selection in relation to log distance to water (m). The blue dashed line is the shifting point (1685 m). The gray area indicates the 95% CI. Notice that jaguars further from watercourses move independently of water location. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

human population density was negative for both males and females ($\mu_1 = -1.29$ for males, $\mu_1 = -2.90$ for females), 95% HPDI overlapped zero for both sexes. Nonetheless, the probability of jaguar responding negatively to human population density was estimated at 0.84 for females and 0.97 for males. Estimated selection coefficients for individual jaguars also highlighted considerable variation among individuals in their response to habitat characteristics at the home range scale (Fig. 2).

At the foraging scale, we again observed that relative probability of habitat use increased with higher percent forest cover for both females ($\mu_5 = 0.31$, 95% HPDI – [0.15, 0.48]) and males ($\mu_5 = 0.39$, 95% HDPI – [0.13–0.66]; Fig. 2). Although the point estimate for the effect of distance to rivers was negative for both males and females ($\mu_3 = -0.77$ for males, $\mu_3 = -0.21$ for females), 95% HPDI overlapped zero for both sexes (Fig. 2). Nonetheless, the probability of jaguar responding negatively to distance to rivers was estimated at 0.85 for females and 0.96 for males. Males had a 0.9 probability of showing a positive coefficient towards livestock ($\mu_2 = 0.11$) while females showed 0.87 probability of showing negative coefficients towards livestock ($\mu_2 = -0.14$). Although we identified several meaningful predictors of resource selection, there was high uncertainty in the estimates of individual-specific selection coefficients (Fig. 2). With the exception of a majority of individuals showing increased relative probability of use for locations with higher percent forest cover, we were generally unable to identify clear positive or negative resource selection at the individual level for the other variables considered (Fig. 2).

3.2. Functional responses

Resource selection behavior varied considerably across individuals (Fig. S1). Nevertheless, we noticed that jaguars in heavily-forested areas (shift point = 58.4%) showed a stronger tendency to avoid non-forest than individuals in more open landscapes (Fig. 3). Individuals at three study sites (ISP, CA, MDSP, $n = 7$ jaguars) even showed negative coefficients of selection for forest cover. Individuals living closest to water also showed a preference for areas near primary and secondary watercourses while resource selection were independent of watercourse proximity for individuals at greater distances to water (shift point = 1635 m, Fig. 3).

We also tested for functional responses to human population, livestock density and distance to roads and found that these relationships were not significant based on generalized additive models, despite the overall tendency of jaguars to avoid human presence at the home range scale. Higher human population and livestock density did not result in increased strength of resource selection (Fig. S2). Similarly, jaguar showed a heterogeneous response to distance to roads, with no clear effect of road proximity on the strength of selection for or against roads (Figs. S2 and S3).

4. Discussion

Jaguars are widely recognized as a focal and umbrella species for biodiversity conservation planning at regional and countrywide scales (Rabinowitz and Zeller, 2010; Silveira et al., 2014). However, the effectiveness of jaguar conservation strategies depends on understanding how resource selection relates to landscape characteristics and how the response to these characteristics differs across the species' geographic range (Silveira et al., 2014; Watkins et al., 2015). Our approach allowed us to provide detailed information about resource selection patterns at two different spatial scales that lend new insights into the species' ecology.

In our overall evaluation of jaguar-resource associations, we found positive selection for increased forest cover at both home range and foraging scales, regardless of gender. Previous studies have highlighted the importance of forests for species survival (De La Torre et al., 2017b), with areas > 54% of forest cover being considered highly suitable for species persistence (Rodríguez-Soto et al., 2011; Morato et al., 2014). Similarly, our analysis showed that jaguars showed increasingly strong selection for forest in landscapes with > 58.4% forest cover. However, jaguars also showed significant variation in the strength of association with forest cover in different areas, demonstrating an ability to use a wide variety of habitats (Sanderson et al., 2002). The tendency for jaguars in heavily-forested landscapes to more strongly avoid non-forest areas suggests that the species may alter their resource selection behavior as a function of forest availability.

Jaguars showed an overall positive association with watercourses at both home range and foraging scales, confirming previous observations (Crawshaw and Quigley, 1991, Cullen Cullen Jr et al., 2005, De Angelo et al., 2011). Space use by jaguars with home ranges distant from watercourses (~1685 m) seemed to be independent of water source locations, reinforcing the idea of a positive functional response towards water if available. This result may be due in part to the limitations of our countrywide water source layer, which was restricted to primary and secondary rivers and lacked information about lower order streams, ponds, marshes and wetlands, and wells. However, the current distribution of jaguar includes extremely arid climates and habitat types where water is scarce. Jaguars cope with these harsh environmental conditions by changing their behavior, resulting in increased movement rates, home range size (McBride and McBride Jr and Thompson, 2018), nighttime activity, and greater use of forested valleys and caves to avoid hot temperatures and water loss (Astete et al., 2007, 2017).

The negative impact of human presence on jaguar occurrence and/or movement has been described by many authors (Conde et al., 2010; Rabinowitz and Zeller, 2010; Colchero et al., 2011; De Angelo et al., 2011, 2013; Morato et al., 2014, 2016). In our study, we noticed a tendency for jaguars to avoid high human population density areas at the home range scale. Although we were unable to find a similar trend at the foraging scale, we believe this was due in part to the lack of meaningful variation within choice sets for this coarse (1 km) resolution dataset. The lack of a functional response indicates that there was no evidence that avoidance of humans depends on the absolute human population density. Jędrzejewski et al. (2017) reported that the strength of human impact depends on ecosystem productivity, suggesting that the species might have higher probability of surviving in humid and high productivity areas even when human densities are high. In our study, individuals inhabiting high human population areas were associated with protected areas and remaining forest areas (Iguaçu National Park- Brazil, Iguazú National Park- Argentina and Morro do Diabo State Park), which are likely to provide conditions to hide, stalk prey, and reproduce.

Livestock density and herd size have also been reported to have positive effects on depredation risk by jaguar because of increased conspicuousness and higher encounter rates (Michalski et al., 2006; Zarco-González et al., 2013; Carvalho et al., 2015). Although, we did not observe a species functional response for livestock density, males seem to be “attracted” to these features at the foraging scale. Considering that male jaguars have larger home ranges and move longer distances per day than females (Morato et al., 2016), it is expected that they will have a higher probability of encountering livestock. A previous study, however, identified no difference in kill rates of livestock between male and female jaguar (Cavalcanti and Gese, 2010). The tendency of individual jaguar to exploit livestock may reflect variation in available prey species and their relative abundance across different biomes (De Azevedo, 2008; Cavalcanti and Gese, 2010; Perilli et al., 2016). In our study, all sites (except for MDSR and TES) have livestock density higher than 20 ind/km^2, with several individuals being in close contact with livestock even though natural prey is seemingly available in high proportions (De Azevedo, 2008; Cavalcanti and Gese, 2010; Astete, 2012; Ramalho, 2012).

Roads impact many terrestrial vertebrate species directly and indirectly (Trombulak and Frissel, 2000), through increased mortality after collision with vehicles (Srbek-Araujo et al., 2015), changing animal behavior, disrupting movement and migration, facilitating disease spread, and increasing hunting and poaching pressure (Trombulak and Frissel, 2000; De Angelo et al., 2013). Although previous research found that jaguars seemed to avoid moving close to roads (Colchero et al., 2011; Espinosa et al., 2018), our study found no consistent overall effect of roads on resource selection. Avoidance of roads by some individuals makes nearby habitat less usable while the failure to avoid roads would put jaguar at risk of encounters with humans/vehicles. Recent fatal collisions at Iguaçu National Park, Morro do Diabo State Park and Linhares-Soretama Block, and other areas within the species range, demonstrate that road kills are a major threat for the species long-term survival (Cullen Jr et al., 2016), regardless of whether they are perceived as a greater threat to some specific populations (Morato et al., 2013; Srbek-Araujo et al., 2015).

4.1. Conservation implications

Habitat models have formed the basis for planning jaguar conservation at broad (Rabinowitz and Zeller, 2010; Silveira et al., 2014) and local scales (Conde et al., 2010; Colchero et al., 2011; Rodríguez-Soto et al., 2011; De Angelo et al., 2013; Morato et al., 2014; De La Torre et al., 2017b). However, our understanding of variation in jaguar resource preferences across the species range has been limited. The preference for high forest cover and areas near watercourse, as found in our study, might support the use of riparian areas to establishing corridors connecting priority areas for the species conservation (Zeilhofer et al., 2014; Silveira et al., 2014). If not available, preserving natural habitats that have low human densities likely will aid jaguar survival because those areas are more likely to be used by jaguars.

Many individuals showed human-avoidance behavior regardless of human population density. This finding, combined with the species ability to use or tolerate a wide variety of different habitat conditions, suggests that jaguar may adopt compensatory mechanisms to survive in human-dominated landscapes by increasing distance travelled (Morato et al., 2016) to track the most favorable habitats within these areas and avoid human contact. These landscapes, however, have the potential to become ecological traps because of the increased likelihood of vehicle collisions and human-predator conflict, both of which lead to increased and mortality (Graham et al., 2005; De Angelo et al., 2013; Inskip et al., 2013; Cullen Jr et al., 2016). The jaguars' endangered status in almost every region in which they are found (De La Torre et al., 2017a; Jędrzejewski et al., 2018) reinforces this idea. In these landscapes, law enforcement and communication interventions, such as conservation outreach and education programs, are required and must play a central role in planning the species conservation, as others have previously suggested (Marchini and Macdonald, 2012; Jędrzejewski et al., 2017). In addition, wildlife passes/corridors should be planned before (and after) barriers are constructed to facilitate movement between protected areas and disparate populations (Colchero et al., 2011; Srbek-Araujo et al., 2015).

Finally, our study contributes to the growing state of knowledge related to resource selection of apex predators and provides an example for how to analyze large tracking data sets to evaluate resource selection at different spatial scales and across large geographic distributions. Our results provide wildlife managers with a better understanding of species responses to local habitat conditions and may improve the effectiveness of species conservation planning into the future, helping to develop landscape-based conservation plans for large predators in general and jaguars specifically.

Acknowledgements

We thank Antonio Carlos Csermak Junior, Apolonio N. S. Rodrigues, Cristina Gianni, Dale Anderson, Jorge Luiz Pegoraro, Ivan Carlos Baptiston, Leanes Silva, Mariella Burti, Paulo Roberto Amaral, Paulo Baptista, Pollyana Motinha, Rafael Garay, Raphael Xavier, Rogério Silva de Jesus, Silvano Gianni, Tarcizio Paula, Thiago Luczinski, Valdomiro Lemos, Wendy Debbas and the members and volunteers of Proyecto Yaguarete for supporting on animal capture and monitoring.

Studies were funded by FAPESP (2013-10029-6), Cat Heaven Endangered Species-Project Survival, Dallas World Aquarium, Orient Express Hotels do Brasil, WWF Switzerland-Fundacion Vida Silvestre Argentina, Panthera Foundation and Rufford Small Grant Foundation. RGM fellowship was funded by FAPESP (2014-24921-0). CNPq (Brazilian Government Research Council) provided a research grant for MCR (312045/2013-1) and RGM (301652/2015-5). MCR also thanks FAPESP (process 2013/50421-2), CNPq (process 312045/2013-1 and 312292/2016-3) and PROCAD/CAPES (project 88881.068425/2014-01) for their financial support.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.10.022.

References

ANA, 2012. Base Hidrográfica Ottocodificada Multiescalas. Available at: http://metadados.ana.gov.br/geonetwork/srv/en/resources.get?id=43&fname=geoft_bho_trechodrenagem.zip&access=private.

Astete, S.E.P., 2012. Ecologia e conservação da onça pintada e da onça parda no Parque Nacional da Serra da Capivara, Piauí. Thesis. Universidade de Brasília.

Astete, S., et al., 2007. Comparative ecology of jaguars in Brazil. CAT News 9–14.

Astete, S., et al., 2017. Living in extreme environments: modeling habitat suitability for jaguars, pumas, and their prey in a semiarid habitat. J. Mammal. 98, 464–474.

Barnosky, A.D., et al., 2011. Has the earth's sixth mass extinction already arrived? Nature 471, 51–57.

Bonnot, T.W., et al., 2011. Discrete choice modeling of shovelnose sturgeon habitat selection in the lower Missouri River. J. Appl. Ichthyol. 27, 291–300.

Boyce, M.S., McDonald, L.L., 1999. Relating populations to habitats using resource selection functions. Trends Ecol. Evol. 14, 268–272.

Boyce, M.S., et al., 2002. Evaluating resource selection functions. Ecol. Model. 157, 281–300.

Bright, E.A., et al., 2011. LandScan: Digit Dataset. Oakridge Natl Lab, Oakridge, TN, USA (web ornl gov/sci/landscan/index shtml. 2012).

Calabrese, J.M., et al., 2016. Ctmm: an R package for analyzing animal relocation data as a continuous-time stochastic process. Methods Ecol. Evol. 7, 1124–1132.

Candolin, U., Wong, B., 2012. In: Candolin, U., Wong, B. (Eds.), Behavioural Responses to a Changing World: Mechanisms and Consequences. Oxford University Press.

Carter, N.H., et al., 2010. American black bear habitat selection in northern Lower Peninsula, Michigan, USA, using discrete-choice modeling. Ursus 21, 57–71.

Carvalho, E.A.R., et al., 2015. Modelling the risk of livestock depredation by jaguar in the Transamazon Highway, Brazil. Basic Appl. Ecol. 16, 413–419.

Cavalcanti, S.M.C., Gese, E.M., 2010. Predation patterns of jaguars (*Panthera Onca*) in a seasonally flooded forest in the southern region of Pantanal, Brazil. J. Mammal. 91, 722–736.

Colchero, F., et al., 2011. Jaguars on the move: modeling movement to mitigate fragmentation from road expansion in the Mayan Forest. Anim. Conserv. 14, 158–166.

Conde, D.A., et al., 2010. Sex matters: modeling male and female habitat differences for jaguar conservation. Biol. Conserv. 143, 1980–1988.

Cooper, A., Millspaugh, J.J., 1999. The application of discrete choice models to wildlife resource selection studies. Ecology 80, 566–575.

Crawshaw, P.G., Quigley, H.B., 1991. Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. J. Zool. 223, 357–370.

Cullen Jr., L., et al., 2005. As onças-pintadas como detetives da paisagem no coredor do Alto Paraná, Brasil. Nat. e Conserv. 3, 43–58.

Cullen Jr., L., et al., 2013. Selection of habitat by the jaguar, *Panthera onca* (Carnivora: Felidae), in the upper Paraná River, Brazil. Zoologia 30, 379–387.

Cullen Jr., L., et al., 2016. Implications of fine-grained habitat fragmentation and road mortality for jaguar conservation in the Atlantic Forest, Brazil. PLoS One 11 (12), e0167372.

De Angelo, C., et al., 2011. Differential impact of landscape transformation on pumas (*Puma concolor*) and jaguars (*Panthera onca*) in the upper Paraná Atlantic Forest. Divers. Distrib. 17, 422–436.

De Angelo, C., et al., 2013. Understanding species persistence for defining conservation actions: a management landscape for jaguars in the Atlantic Forest. Biol. Conserv. 159, 422–433.

De Azevedo, F.C.C., 2008. Food habits and livestock depredation of sympatric jaguars and pumas in the Iguaçu food habits and livestock depredation of sympatric jaguars and pumas in the lguagu National Park Area, South Brazil. Biotropica 40, 494–500.

De La Torre, J., et al., 2017a. The jaguar's spots are darker than they apear: assessing the global conservation status of the jaguar *Panthera onca*. Oryx 1–16.

De La Torre, J., et al., 2017b. Habitat availability and connectivity for jaguars (*Panthera onca*) in the Southern Mayan Forest: conservation priorities for a fragmented landscape. Biol. Conserv. 206, 270–282.

Espinosa, S., et al., 2018. When roads appear jaguars decline: increased access to an Amazonian wilderness area reduces potential for jaguar conservation. PLoS One 13

(1), e0189740.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515.

Fleming, C.H., et al., 2015. Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. Ecology 96, 1182–1188.

Foster, R.J., et al., 2010. Habitat use by sympatric jaguars and pumas across a gradient of human disturbance in Belize. Biotropica 42, 724–731.

Gillies, C.S., et al., 2006. Application of random effects to the study of resource selection by animals. J. Anim. Ecol. 75, 887–898.

Graham, K., et al., 2005. Human-predator-prey conflicts: ecological correlates, prey losses and patterns of management. Biol. Conserv. 122, 159–171.

Haddad, N.M., et al., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1, e1500052.

Hansen, M.C., et al., 2013. High-resolution global maps of 21st-century forest cover change. Science 342, 850–854.

Hastie, T., Tibshirani, R., 1986. Generalized additive models. Stat. Sci. 1, 297–318.

IBGE, 2016. B_CIM Trecho rodoviário. Available at: http://www.geoservicos.ibge.gov.br:80/geoserver/wms?service=WFS&version=1.0.0&request=GetFeature&typeName=CCAR:BCIM_Trecho_Rodoviario_L&outputFormat=SHAPE-ZIP.

Inskip, C., et al., 2013. Human-Tiger conflict in context: risks to lives and livelihoods in the Bangladesh Sundarbans. Hum. Ecol. 41, 169–186.

Jędrzejewski, W., et al., 2017. Predicting carnivore distribution and extirpation rate based on human impacts and productivity factors; assessment of the state of jaguar (*Panthera onca*) in Venezuela. Biol. Conserv. 206, 132–142.

Jędrzejewski, W., et al., 2018. Estimating large carnivore populations at global scale based on spatial predictions of density and distribution: application to the jaguar (*Panthera onca*). PLoS One 13 (3), e0194719.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65–71.

Kellner, K., 2015. jagsUI: A Wraper around Rjags to Streamline JAGS Analyses. (R package version).

Lehman, C.P., et al., 2016. Elk resource selection at parturition sites, Black Hills, South Dakota. J. Wildl. Manag. 80, 465–478.

Lele, S.R., et al., 2013. Selection, use, choice and occupancy: clarifying concepts in resource selection studies (F Huettmann, Ed.). J. Anim. Ecol. 82, 1183–1191.

Marchini, S., Macdonald, D.W., 2012. Predicting ranchers' intention to kill jaguars: case studies in Amazonia and Pantanal. Biol. Conserv. 147, 213–221.

McBride Jr., R.T., Thompson, J.J., 2018. Space use and movement of jaguars (*Panthera onca*) in western Paraguay. Mammalia. https://doi.org/10.15.15/mammalia-2017-0040.

McDonald, T.L., et al., 2006. Discrete-choice modeling in wildlife studies exemplified by northern spotted owl nighttime habitat selection. J. Wildl. Manag. 70, 375–383.

Michalski, F., et al., 2006. Human-wildlife conflicts in a fragmented Amazonian forest landscape: determinants of large felid depredation on livestock. Anim. Conserv. 9, 179–188.

Morato, R.G., et al., 2013. Avaliação do risco de extinção da onça-pintada *Panthera onca* (Linnaeus, 1758) no Brasil. Biodiversidade Bras. 3, 122–132.

Morato, R.G., et al., 2014. Identification of priority conservation areas and potential corridors for jaguars in the Caatinga biome, Brazil. PLoS One 9 (4), e92950.

Morato, R.G., et al., 2016. Space use and movement of a Neotropical top predator: the endangered jaguar. PLoS One 11 (12), e0168176.

Mysterud, A., Ims, R.A., 1998. Functional responses in habitat use: availability influences related use in trade-off situations. Ecology 79, 1435–1441.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37, 637–669.

Perilli, M.L.L., et al., 2016. Can scat analysis describe the feeding habits of big cats? A case study with jaguars (*Panthera onca*) in southern Pantanal, Brazil. PLoS One 11 (3), e0151814.

Plummer, M., 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. http://citeseer.ist.psu.edu/plummer03jags.html.

R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria URL. https://www.R-project.org/.

R Development Core Team R, 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria URL. https://www.R-project.org/.

Rabinowitz, A., Zeller, K.A., 2010. A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. Biol. Conserv. 143, 939–945.

Ramalho, E.E., 2012. Jaguar (*Panthera onca*) Population Dynamics, Feeding Ecology, Human Induced Mortality, and Conservation in the Várzea Floodplain Forests of Amazonia. Thesis. University of Florida.

Ripple, W.J., et al., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 1241484.

Ripple, W.J., et al., 2015. Collapse of the world's largest herbivores. Sci. Adv. 1, e1400103.

Robinson, T.P., et al., 2014. Mapping the global distribution of livestock. PLoS One 9 (5), e96084.

Rodríguez-Soto, C., et al., 2011. Predicting potential distribution of the jaguar (*Panthera onca*) in Mexico: identification of priority areas for conservation. Divers. Distrib. 17, 350–361.

Roever, C.L., et al., 2012. Functional responses in the habitat selection of a generalist mega-herbivore, the African savannah elephant. Ecography 35, 972–982.

Rota, C.T., et al., 2014. Space-use and habitat associations of black-backed woodpeckers (*Picoides arcticus*) occupying recently disturbed forests in the Black Hills, South Dakota. For. Ecol. Manag. 313, 161–168.

Sanderson, E.W., et al., 2002. Planning to save a species: the jaguar as a model. Conserv. Biol. 16, 58–72.

Seidler, R.G., et al., 2015. Identifying impediments to long-distance mammal migrations. Conserv. Biol. 29, 99–109.

Sikes, R., Gannon, W., 2011. Mammalogists TAC and UC of the AS of. Guidelines of the American Society of Mammalogist for the use of wild mammals in research. J. Mammal. 1, 235–253.

Silveira, L., et al., 2014. The potential for large-scale wildlife corridors between protected areas in Brazil using the jaguar as a model species. Landsc. Ecol. 29, 1213–1223.

Srbek-Araujo, A., et al., 2015. Jaguar roadkill in Brazilian Atlantic Forest and implications for species conservation. Braz. J. Biol. 75, e1678–e4735.

Stabach, J.A., et al., 2016. Variation in habitat selection by white-bearded wildebeest across different degrees of human disturbance. Ecosphere. 7, 1–17.

Thomas, D.L., et al., 2006. A Bayesian random effects discrete-choice model for resource selection: population-level selection inference. J. Wildl. Manag. 70, 404–412.

Trombulak, S., Frissel, C., 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conserv. Biol. 14, 18–30.

Tucker, M.A., et al., 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. Science 359, 466–469.

Van Buskirk, J., 2012. Behavioural plasticity and environmental change. In: Candolin, U., Wong, B. (Eds.), Behavioural Responses to a Changing World: Mechanisms and Consequences, 1st ed. Oxford University Press, pp. 145–154.

Watkins, A., et al., 2015. A spatially explicit agent-based model of the interactions between jaguar populations and their habitats. Ecol. Model. 306, 268–277.

Wood, S.N., 2016. Just another Gibbs additive modeller: interfacing JAGS and mgcv. arXiv 1–14.

Zarco-González, M.M., et al., 2013. Spatial Model of Livestock Predation by Jaguar and Puma in Mexico: Conservation Planning. 159. pp. 80–87.

Zeilhofer, P., et al., 2014. Jaguar *Panthera onca* habitat modeling in landscapes facing high land-use transformation pressure—findings from Mato Grosso, Brazil. Biotropica 46, 98–105.