Influence of behavioral state, sex, and season on resource selection by jaguars (*Panthera onca*): Always on the prowl?

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Abstract. How a predator uses its landscape to move through its territory and acquire prey is a fundamental question for scientific research. The influence of abiotic and biotic factors on space use of large carnivores has profound implications for their future management and conservation. In the Pantanal, Brazil, jaguars (*Panthera onca*) are the apex predator, but conflicts with cattle depredations pose a risk to their future conservation. We examined whether behavioral state, sex, and season influenced how jaguars used the landscape in the Pantanal. To accomplish this, we radio-collared four females and six males; radio-collared jaguars were monitored for 76 radio-months with 11,787 GPS locations acquired. We developed resource selection functions (RSFs) examining how female and male jaguars used their landscape during three behavioral states (moving, killing native prey, killing cattle) during two seasons (dry, wet). From the RSF models, we found similar variables and relationships of landscape characteristics that jaguars selected for when moving and when depredating native prey and cattle. While moving, jaguars selected for locations that were either in dense cover or very near dense cover, with higher plant diversity and closer to water than available across the landscape. While null models suggested jaguars opportunistically depredated native prey in the dry season and cattle in the wet season, there was some indication they selected for specific landscape characteristics, mainly dense cover when killing cattle in the dry season and native prey in the wet season. Both sexes killed native prey and cattle within dense cover or close to dense cover as expected of an ambush predator. Particular habitat types were not important as long as there was dense cover for concealment. Additionally, jaguars killed prey closer to water than was available on the landscape. The similar variables across the models showed the importance of dense cover and distance to dense cover during all three behavioral states indicating jaguars in the Pantanal were "always on the prowl." Understanding the spatial requirements for jaguars during the acquisition of native prey and cattle may lead to improved management strategies to allow for continued coexistence of jaguars in an area of traditional cattle production.

Key words: behavioral state; generalized linear models; jaguar; kills; movements; Pantanal; *Panthera onca*; resource selection function.

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INTRODUCTION

Understanding how a predator uses the landscape to secure prey and other resources has been a source of interest for many decades (e.g., Rosenzweig 1966, Kruuk 1972, Schaller 1972). Space-use decisions made by both predator and prey influence "encounter rates, predation rates, and ultimately predator-prey population and community dynamics" (Sih 2005:241). While prey abundance and biomass ultimately influence the abundance of carnivores (e.g., Carbone and Gittleman 2002), habitat characteristics and the spatial structure of vegetation also impact movement patterns of predators and their prey (e.g., Caro and FitzGibbon 1992, Denno et al. 2005, Sih 2005). Hunting success for many ambush predators is dependent on landscape characteristics such as cover, distance to water, or vegetation structure and heterogeneity (e.g., Holmes and Laundré 2006, Merrill et al. 2010, Blake and Gese 2016). Evaluating how an animal selects habitats on the landscape to achieve increments of fitness depends on integrating multiple factors including the behavioral state of the individual, the season, or even the sex of the individual (e.g., Dickson et al. 2005, Squires et al. 2013, Zeller et al. 2014).

Jaguars (*Panthera onca*) are the apex predator throughout Central and South America, are the largest felid in the Americas, and once existed from the southwestern border of the United States to the Rio Negro in Argentina (Macdonald and Loveridge 2010). The "near threatened" status of jaguars (Quigley et al. 2017) in conjunction with their tendency to depredate cattle results in conflicts between conservationists and cattle ranchers and poses a challenge for effective management (Quigley and Crawshaw 1992, Cavalcanti and Gese 2010, Cavalcanti et al. 2010, Zanin et al. 2015). As stealth predators, jaguars must evaluate and determine which habitats provide sufficient cover to remain hidden but are not so dense that prey cannot conduct effective surveillance. Such habitats include the edge between dense cover (e.g., forests, dense marshland) and open cover (e.g., cultivated fields, low structured grasslands; Crawshaw and Quigley 1991, Laundré and Hernández 2003, Cullen et al. 2013). Identification of habitat selection for jaguars while preying on native vs. non-native prey (i.e., cattle) would aid managers in assessing situations or habitats that attract jaguars and cattle into close proximity. Resource managers could then focus their efforts on those potentially overlapping habitats with the goal of reducing cattle depredations and thus easing tensions among local ranchers and jaguar conservationists.

The Pantanal region in west-central Brazil harbors abundant wildlife and is considered critical for the long-term conservation of jaguars (Sanderson et al. 2002, Bernal-Escobar et al. 2015). The region is a vast 140,000-km^2 floodplain consisting of a mosaic of plant communities including the Cerrado savanna ecoregion, the Gran Chaco region, and the Amazon forest (Gese et al. 2016). The distinct dry and wet seasons influence the vegetation, spatially and temporally which likely influences interactions between jaguars and their prey. Although few studies have examined how the sex of a carnivore species influences habitat selection, it is biologically reasonable to theorize that female and male carnivores would interact differently with their environment. Although Conde et al. (2010) found that both female and male jaguars selected for dense cover in central and northern Belize and Mexico, males were more willing to move into areas with agriculture and cattle. In addition, male jaguars were less clustered across the landscape than females, which were spatially grouped and located closer to den sites and areas with high prey densities (Bernal-Escobar et al. 2015).

Identification of resource selection under different behavioral states has not been conducted for jaguars, although it has for other American felids, such as cougars (*Puma concolor*) and Canada lynx (*Lynx canadensis*). Zeller et al. (2014) found cougars selected against annual grasslands and barren land when using a resource patch (i.e., hunting or resting) but selected for those habitats when moving through a habitat. Conversely, lynx in northwestern Montana and cougars in southern California exhibited no difference in habitat selection, nor between seasons when resting and active (Dickson et al. 2005, Squires et al. 2013). Based on fine scale temporal and spatial information, Dickson et al. (2005) found cougars were more plastic in their habitat requirements for nocturnal and diel movements than in resting daybeds, but there was no statistical difference in the habitats selected for different

behavioral states. Wilmers et al. (2013) found cougars had large differences in their response to the density of houses when feeding or moving and denning or communication (i.e., scrapes) in the Santa Cruz Mountains of coastal California.

Seasons have been shown to influence habitat selection by felids although there does not seem to be a general pattern. Cougars in Montana and Wyoming selected habitat based on distance to water, slope, and vegetation type in the summer, but only on elevation and vegetation type in winter (Blake and Gese 2016). Jaguars in the western part of Sao Paulo State and the southeastern corner of Mato Grosso do Sul State in Brazil selected habitats differently depending on the season (dry or wet) and scale (Cullen et al. 2013). In a tropical semi-deciduous forest with few openings in the vegetation, season did not influence habitat selection by jaguars (Conde et al. 2010).

Resource selection functions (RSFs) determine which resources were selected by animals on the landscape (Manly et al. 2002, Gillies et al. 2006). In the past, selection was often assumed to be consistent across behavioral states, animal status (e.g., sex, age, and social status), season, or quality of the environment or resource. However, Squires et al. (2013), Wilmers et al. (2013), and Zeller et al. (2014) demonstrated more information was gained when the behavioral state of the animal was incorporated into the RSF framework with biologically meaningful variables, such as season (Smulders et al. 2010) and sex (Conde et al. 2010, Welch et al. 2015). Our objective was to assess whether behavioral state, sex, and season influenced how jaguars used the landscape in the Pantanal of Brazil. Specifically, we examined resource selection during three behavioral states: moving, killing native prey, and killing cattle (*Bos* spp.), for female and male jaguars across the dry and wet seasons. We generated used–available RSFs (Manly et al. 2002) to determine resource selection during movements and at kill sites with generalized, linear mixed model regression. Variables of interest included habitat type, percent dense cover, distance to dense cover, distance to dirt roads, and the distance to seasonally dependent water sources. We were not interested in prediction or hypothesis testing, but rather identifying the variables influencing how jaguars use the landscape during movement and depredation events (e.g., Zeller et al. 2014,

Blake and Gese 2016). Knowledge of how jaguars use the landscape may prove critical for future conservation efforts in the Pantanal as jaguars are the main predator on cattle (Cavalcanti and Gese 2010, Cavalcanti et al. 2010).

METHODS

Study area

The study area consisted of a 460-km^2 private cattle ranch in the southern Pantanal, Mato Grosso do Sul, Brazil (Fig. 1). The Pantanal is a tropical wetland that undergoes extensive habitat modifications between a dry (April–September) and wet (October–March) season. During the wet season, low-lying areas (89 m above sea level) are inundated with water, while higher elevation areas (120 m above sea level) form terrestrial islands or cordilheiras. In the dry season, low-lying areas become isolated ponds resulting in dense aggregations of animals. Although the extreme hydrologic seasonality of the Pantanal

Fig. 1. Location of the study area, indicated by the gray star, in the southern Pantanal region of Brazil (black area).

results in diverse vegetation, three broad habitat characteristics were evident: open areas, closed canopies, and wetland habitats (Prance and Schaller 1982). Open habitats consisted of grasslands, herbaceous fields, and savannas, while closed-canopy habitats consisted of dense upland and riparian forests. Wetlands had an intermediate canopy coverage and had water present year-round (see Gese et al. 2016 for an extensive description of the study area vegetation). Habitat classes were generated from an unsupervised classification scheme of wet- and dry-season Landsat Thematic Mapper images (1:100,000; Cavalcanti 2008) in ERDAS Imagine 8.7 (Leica Geosystems Geospatial Imaging, Norcross, Georgia, USA). We delineated five habitat types (Cavalcanti 2008): brushland, forest, herbaceous field, open field, and savanna. Brushland was characterized by different shrubs (e.g., *Vernonia scabra*, *Annona dioica*, *Bauhinia* spp., *Psidium guineense*, *Cordia insignis*) and small trees (e.g., *Erythroxylum suberosum*, *Banara argutta*, *Alchornea discolor*) varying in height from 2 to 4 m with dense cover. Forest consisted of gallery forests along river corridors, secondary forest, and open forest patches, with a high (6–20 m) thick canopy. The principal species were deciduous, semi-deciduous, and palm trees (e.g., *Ceiba samauma*, *Genipa americana*, *Guazuma ulmifolia*, *Sterculia apetala*). The understory varied from open to semi-closed to almost completely closed. Herbaceous field consisted of tall grassland species with wide leaves and soft stems (e.g., *Echinodorus macrophyllus*, *Heliconia* spp., *Cyperus giganteus*, *Ipomoea carnea fistulosa*), varying in height from 50 to 200 cm, according to the season; this habitat was submerged during the wet season. Open field was the most open habitat and included bare soil and various short grassland species, both native (e.g., *Andropogon bicornis*, *Leersia hexandra*, *Paspalum almum*) and introduced (e.g., *Brachiaria humidicula*) species, 50–100 cm in height. Savanna was similar to open field, but was interspersed with different species of deciduous, semi-deciduous, or palm trees (e.g., *Tabebuia* spp., *Ficus* spp., *Curatella americana*) and included small tree islands on slightly elevated ground which remained dry during the wet season.

The ranch supported approximately 6000 cattle and several native wildlife species including two species of peccary (*Tavassu* spp.), three species of deer (*Blastocerus dichotomus*, *Mazama americana*, and *Mazama gouazoubira*), feral hog (*Sus scrofa*), capybara (*Hydrochoerus hydrochaeris*), and a large population of caiman (*Caiman crocodilus yacare*). The only other large carnivores present in the study area were cougars (*Puma concolor*) and maned wolves (*Chrysocyon brachyurus*; see Cavalcanti and Gese 2010 for a complete list of species). During the study, the area supported an estimated density of 6.6–11.7 jaguars/100 km^2 (Soisalo and Cavalcanti 2006).

Capture and radio-collaring of jaguars

We captured jaguars after locating their tracks in the early morning and trailing them with hounds (Hornocker 1970, Ruth 2004). Once a jaguar was treed, we immobilized it with tiletamine hydrochloride and zolazepam hydrochloride (Telazol; Fort Dodge Animal Health, Fort Dodge, Iowa, USA), or a combination of Telazol and ketamine hydrochloride (Fort Dodge Animal Health) administered with a dart pistol or rifle (Cavalcanti and Gese 2009, 2010). We determined age, body condition, sex, and weight and fitted jaguars with a GPS radio-collar (Televilt International, Lindesberg, Sweden); all jaguars were released at the capture site. We placed jaguars into one of three age classes (adults: >24 months old; sub-adults: 11–24 months old; or kittens: <11 months old) based on the type and condition of the teeth (Ashman et al. 1983). Capture and handling protocols were reviewed and approved by the Institutional Animal Care and Use Committees at the National Wildlife Research Center (QA-1194) and Utah State University (permit #1202).

GPS locations, location identification, and home range estimation

Between October 2001 and September 2002, we obtained GPS locations every two hours during the night (7 locations/night). Between September 2002 and April 2004, we programmed the collars to obtain 12 locations/d (every two hours throughout the entire 24-h period). We downloaded the GPS locations every 21–24 d via a radio link between the GPS radio-collar and a remote receiver (Cavalcanti and Gese 2009, 2010). GPS locations had a high degree of accuracy and precision as indicated by errors of <10 m

obtained from ground tests with reference GPS radio-collars (Cavalcanti and Gese 2010). We designated each GPS location as belonging to a cluster or as a moving point based on spatial and temporal constraints. Clusters occurred when two or more consecutive locations were found <100 m from each other and within 12 h (Anderson and Lindzey 2003, Sand et al. 2005, Webb et al. 2008, Merrill et al. 2010, Blake and Gese 2016, Gese et al. 2016). Moving locations were those locations not identified as being part of a cluster. To determine whether a cluster was associated with a kill, clusters were searched within 21 d after initiation to a radius of 50 m from the approximate center of the cluster. The cluster was identified as a kill site if prey remains were found within 50 m from the approximate center of the cluster (Cavalcanti and Gese 2010, Gese et al. 2016). If no prey remains were located, the cluster was identified as a non-kill site and not included in the predation RSFs. It was not possible to identify which GPS location was the actual kill location, so we assumed that the area around the initial point establishing a cluster represented the kill site (Gese et al. 2016) and was considered the used point in the predation RSFs.

The dramatic changes in water levels and grassland habitat between the dry and wet seasons correspond to shifts in home ranges and habitat use for jaguars in the Pantanal (Crawshaw and Quigley 1991, Cavalcanti and Gese 2009, 2010). Therefore, we generated 95% isopleth home ranges separately for the dry and wet seasons for each jaguar using the least squares cross-validation (LSCV) bandwidth in the Geospatial Modeling Environment 0.7.3.0 (Beyer 2012). We evaluated several bandwidths (e.g., PLUGIN, smoothed cross-validation, biased cross-validation) at multiple quantiles and determined the LSCV bandwidth with the 0.95 quantile resulted in the most biologically relevant home range. One male jaguar did not have enough locations to generate a home range for the dry season, so we used the wet-season home range for analysis in both seasons. On our study area, female jaguars had smaller home ranges than male jaguars (Cavalcanti and Gese 2009), thus necessitating examination of the sexes separately. In addition, simple t-tests (Zar 1996) indicated there was a significant difference ($P \leq 0.05$) between female and male home ranges for most

landscape variables examined (see *Variable selection and model development* below).

Resource selection models

We employed used–available RSFs (RSFs; Manly et al. 2002) to determine how female and male jaguars selected habitats during three behavioral states (moving, predation of native prey, and predation of cattle) during two seasons (dry and wet). We constructed RSFs for females and males moving in the dry and wet seasons for a total of four moving RSFs. Because the sample sizes of kill locations were much smaller than those of the moving locations, we combined the sexes for the predation RSFs. Thus, we constructed four total RSFs to examine depredation: one for predation on native prey in the wet and one in the dry season; and one for predation on cattle in the wet and one in the dry season. All RSFs were constrained to the seasonal home range for each jaguar. Used points for the moving and predation RSFs were GPS locations identified as moving and kill sites, respectively. We calculated the mean distance between consecutive moving points in 2 h and used that distance (Klar et al. 2008, Forester et al. 2009) to limit available points to a biologically meaningful area for the moving RSFs (Boyce et al. 2002, Forester et al. 2009) and generated 25 available points for each used point (Northrup et al. 2013). Available points were not allowed to overlap each other or with the used point. As with the moving RSFs, we examined the mean distance between consecutive kill sites as a distance in which to constrain available points. However, the mean distance between kills encompassed the entire home range of the animal; thus, available points for the predation RSFs were randomly spaced throughout each individual's seasonal home range.

To evaluate how jaguars assess their landscape, we examined an area around each used and available point using a 35-m buffer. A 35-m buffer was considered appropriate because this distance was within the 50 m search radius used when investigating kill clusters (Cavalcanti and Gese 2010, Gese et al. 2016), and was likely to contain the kill site based upon reported drag distances of prey by jaguars (Brock 1963, McGrath 2004, Iserson and Francis 2015). The 35-m buffer also approximated the resolution of our habitat classification (i.e., a 30 × 30 m pixel). All buffered locations

were constrained within the seasonal home range of each jaguar. We determined the proportion of the five habitat types in each buffer in ArcGIS 10.2.2 (ESRI, Redlands, California, USA) and used the predominant habitat in the RSF models. We did not examine aspect, elevation, ruggedness, or slope because the Pantanal has little topographical relief and the study area was flat (Cavalcanti and Gese 2010).

Variable selection and model development

Dense cover has an important role for ambush predators for both successful predation and hiding cover (Sollmann et al. 2012, Cullen et al. 2013, Blake and Gese 2016). Therefore, not only did we examine habitat type in the RSFs, we also examined the percent dense cover in the 35-m buffered area. Dense cover consisted of the combination of brushland, dense riparian forest, and dense upland forest; therefore, habitat type and percent dense cover were not included in the same models. Other variables examined in the moving and predation RSFs included distance to the nearest dense cover, distance to the nearest dirt road (there were no paved roads), and the distance to the nearest water source specific to the wet and dry seasons. All distances were constrained within each jaguar's home range by season (dry and wet) and were standardized by subtracting the mean and dividing by the standard deviation (Zar 1996). Water sources during the dry season consisted of open water, while water sources during the wet season consisted of all possible watercourses including ephemeral streams, permanent streams, and open water. The only measurable variable of anthropogenic influence was distance to the nearest road, but the low density of roads in the area forced us to assess distance across the entire study area rather than by each jaguar's seasonal home range. Finally, we calculated the Simpson Diversity Index (Ricklefs and Relyea 2014) for each used and available location to quantify the complexity of the habitat within each buffered location.

We constructed the RSFs to examine seasonal effects only (dry vs. wet seasons) as these seasons correspond to changes in predation patterns and space use (Cavalcanti and Gese 2009, 2010). Daily patterns were not examined as Cavalcanti and Gese (2010) found no influence of time of day on when jaguars killed native prey (i.e., they

killed prey throughout the 24-h period). Similarly, while cattle were predominantly active during the day, jaguar predation on cattle occurred at a similar frequency during all times of the day and night (Cavalcanti and Gese 2010). In addition, the high amount of overlap among jaguar home ranges and the frequent social interactions (Cavalcanti and Gese 2009) suggested that intraspecies competition likely would not influence resource selection.

We developed and ranked additive generalized linear models examining the influence of habitat type, percent dense cover, distance to dense cover, distance to nearest road, distance to nearest water source, habitat diversity, and the null model, using Bayesian Information Criteria (Schwarz 1978). Generalized linear models were constructed and performed in R (R Core Team 2013). We plotted the proportion of used points as a function of percent dense cover, distance to dense cover, habitat diversity, and distance to water to assess these relationships. To assess model fit, we calculated the area under the cover for the receiver operating characteristics curve in R (Boyce et al. 2002). All distances and compositional data were obtained in ArcGIS 10.2.2 (ESRI).

Results

We captured, radio-collared, and monitored four adult female and six adult male jaguars between October 2001 and April 2004. Radio-collared jaguars were monitored for a total of 76 radio-months with 11,787 GPS locations acquired. The number of GPS locations used in the moving and predation RSFs varied considerably across season, sex, and prey type with females generally having more locations than males (Table 1).

Resource selection while moving

The top-performing resource selection model (Table 2) during the dry season for female jaguars while moving through the landscape included only one variable, percent dense cover ($\beta = 0.37$, $P < 0.01$). The second top-ranked model for females when moving in the dry season included percent dense cover ($\beta = 0.38$, $P < 0.01$) and distance to dense cover ($\beta = -0.95$, $P < 0.01$). These two top-ranked models contained 94% of the model weight (Table 2).

Table 1. The number of used points for GPS-collared jaguars (*n*, individuals in parenthesis) analyzed in the resource selection functions developed for three behavioral states (moving, predation on native prey, and predation on livestock) according to sex and season in the southern Pantanal, Brazil.

Behavior	Season	Females	Males
Moving	Dry	1,223 (2)	2,074 (5)
	Wet	2,357 (4)	779 (3)
	Total	3,580 (4)	2,853 (5)
Predation on native prey	Dry	68 (2)	97 (6)
	Wet	84 (3)	47 (3)
	Total	152 (3)	144 (6)
Predation on livestock	Dry	45 (2)	45 (5)
	Wet	30 (4)	12 (3)
	Total	75 (4)	57 (6)

Similarly, during the dry season when males moved through the landscape, the top-ranked model (Table 2) also included only percent dense cover ($\beta = 0.39$, $P < 0.01$), with the second highest ranked model containing percent dense cover ($\beta = 0.38$, $P < 0.01$) and distance to dense cover ($\beta = -0.61$, $P < 0.02$). These two top-ranked models contained 98% of the model weight.

Table 2. Top-performing resource selection function models for female and male jaguars when moving during the dry and wet seasons, southern Pantanal, Brazil.

Sex and season	Model	ΔBIC	df	Weight
Female				
Dry	Percent dense cover	0.0	2	0.59
	Percent dense cover + distance to dense cover	1.1	3	0.35
	Percent dense cover + diversity	5.1	3	0.05
Wet	Percent dense cover + distance to dense cover	0.0	3	0.55
	Percent dense cover + diversity	1.8	3	0.22
	Percent dense cover + distance to dense cover + diversity	2.0	4	0.20
Male				
Dry	Percent dense cover	0.0	2	0.90
	Percent dense cover + distance to dense cover	4.9	3	0.08
Wet	Percent dense cover	0.0	2	0.85
	Percent dense cover + distance to water	3.9	3	0.12

Notes: BIC, Bayesian Information Criteria. Only models with a weight ≥0.05 were included.

During the wet season, the top-ranked model for females while moving contained percent dense cover ($\beta = 0.47$, $P < 0.01$) and distance to dense cover ($\beta = -0.70$, $P < 0.01$), with the second-ranked model containing percent dense cover ($\beta = 0.47$, $P < 0.01$) and habitat diversity ($\beta = 0.20$, $P < 0.01$). The three top-ranked models all contained percent dense cover and distance to dense cover and explained 97% of the model weight combined (Table 2). The top-ranked model for male jaguars during the wet season included only percent dense cover ($\beta = 0.65$, $P < 0.01$), while the second-ranked model included percent dense cover ($\beta = 0.62$, $P < 0.01$) and distance to water ($\beta = -0.23$, $P < 0.02$); these two top-ranked models contained 97% of the model weight combined (Table 2). The distance to dirt roads and habitat type were not included in any of the ranked models for jaguars while moving during the dry or wet seasons. While moving through the landscape, both female and male jaguars selected for locations with dense cover (Figs. 2A, 3A). When using locations with low dense cover, they then selected locations close to dense cover (Figs. 2B, 3B). As the models and the percent of used locations indicate, if the jaguar was not in dense cover, they were very close to dense cover (88–93% of used locations were <200 m from dense cover). Female jaguars also selected for locations with higher diversity than available on the landscape, but generally used locations with low habitat diversity (Fig. 2C). During the wet season, male jaguars selected for locations closer to water sources (Fig. 3D).

Resource selection while killing native prey

The number of locations and GPS-collared jaguars used for the kill-site RSFs was somewhat more equitable across sex and season than those used for the moving RSFs, although more native prey were killed than cattle (Cavalcanti and Gese 2010) resulting in more locations for kill sites of native prey (Table 1). The top-performing model when female and male jaguars killed native prey in the dry season was the null model (Table 3). The second-ranked model in the dry season for females and males contained only a single variable, percent dense cover ($\beta = 0.42$, $P < 0.02$), which contained 18% of the model weight. In the wet season, the top-performing model (Table 3)
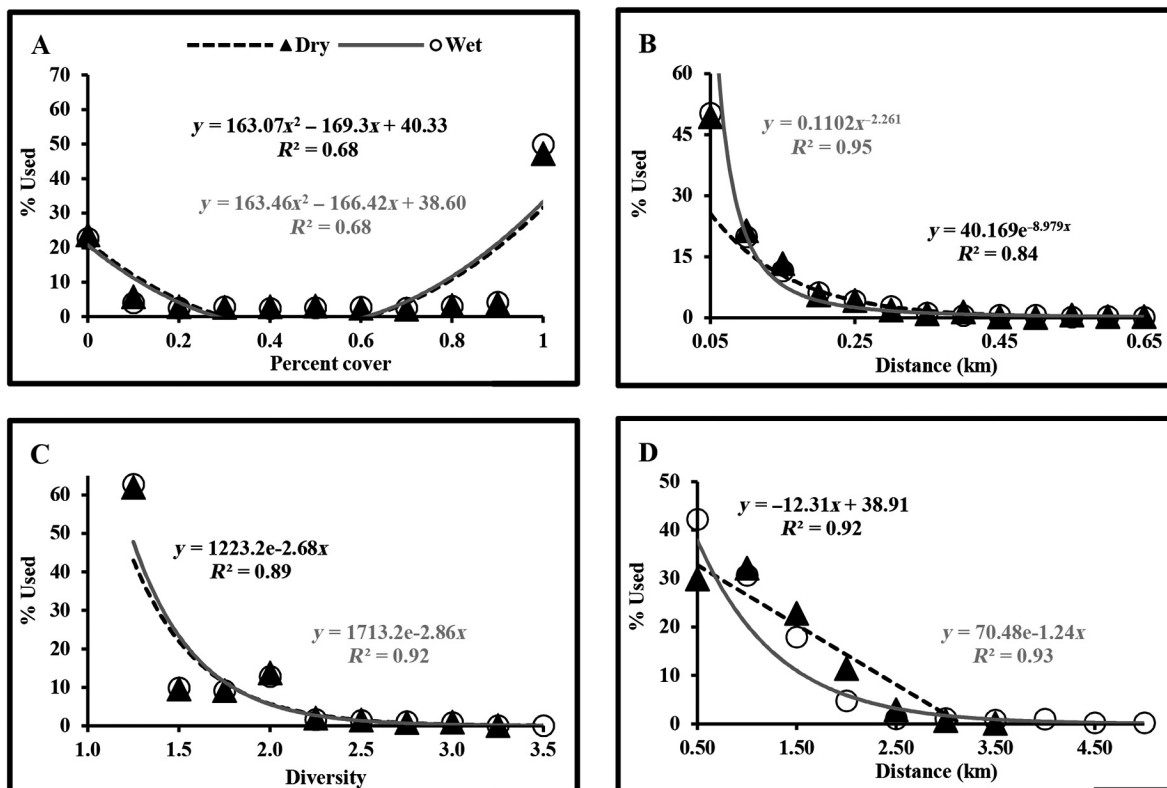
Fig. 2. Proportion of used points related to (A) percent dense cover, (B) distance to dense cover, (C) diversity, and (D) distance to water, for female jaguars while moving in the dry and wet seasons, southern Pantanal, Brazil.

included the percent dense cover ($\beta = 0.70$, $P < 0.01$) and habitat diversity ($\beta = 0.75$, $P < 0.01$). The second highest ranked model contained the percent dense cover ($\beta = 0.71$, $P < 0.01$) and distance to dense cover ($\beta = -2.25$, $P < 0.01$), with the two top-ranking models explaining 67% of the model weight. While the null model was the highest ranked model explaining resource selection while killing native prey during the dry season, the model from the wet season showed the importance of dense cover. Similar to when the jaguars are moving through the landscape, jaguars selected for locations within dense cover (Fig. 4A) or very close to dense cover (Fig. 4B) when killing native prey. The β-coefficients ($\beta = 0.16$, $P < 0.02$) suggest jaguars selected locations with higher habitat diversity than was available on the landscape, even though they had more used locations in areas of low diversity (Fig. 4C). They generally made kills close to water sources (Fig. 4D),

although distance to water sources was not in any of the ranked models (Table 3).

Resource selection while killing cattle

The null model was the top-performing model for jaguars when they killed cattle in the wet season (Table 3). The next two ranked models contained the distance to dense cover ($\beta = -2.71$, $P > 0.05$) and percent dense cover ($\beta = 0.58$, $P > 0.05$), but explained only 17% of the model weight combined (Table 3). During the dry season, the distance to dense cover ($\beta = -5.11$, $P < 0.01$) was the only model with a weight above 0.05 and explained 87% of the model weight for resource selection for jaguars when killing cattle (Table 3). Similar to the resource selection models while jaguars were moving, when killing cattle jaguars used locations within dense cover (Fig. 5A) or close to dense cover (Fig. 5B). While not ranked in the top-performing models, jaguars used more locations with
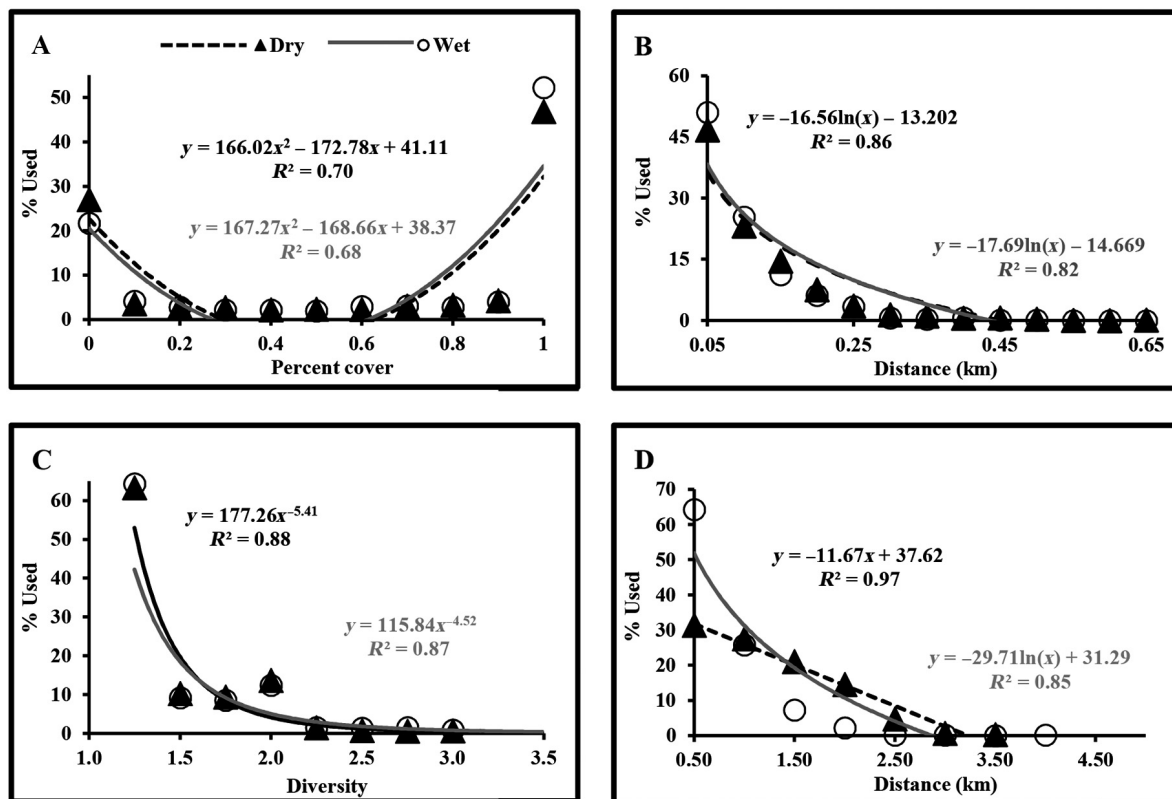
Fig. 3. Proportion of used points related to (A) percent dense cover, (B) distance to dense cover, (C) diversity, and (D) distance to water, for male jaguars while moving in the dry and wet seasons, southern Pantanal, Brazil.

low habitat diversity (Fig. 5C) and closer to water (Fig. 5D), but the models indicated these were not driving factors when killing cattle.

Variable preferences

The percent dense cover was present in all of the top-performing models generated for jaguars while moving through the landscape, with distance to dense cover in several of the ranked models for both female and male jaguars (Table 2). These same variables were included in several of the highest ranked models for jaguars when killing cattle and native prey (Table 3). The greater use of dense cover and locations close to dense cover while moving and killing indicates the overwhelming influence of dense cover to this large ambush predator. The Simpson Diversity Index was present in several of the ranked models for resource selection but exhibited considerable variation between behavioral states, sex, and seasons (Tables 2 and 3). The distance to the nearest water

source variable was present in only one of the highest ranked models for resource selection for male jaguars in the wet season. The predominant habitat type variable was not present in any of the ranked models for resource selection, suggesting that dense cover rather than a particular habitat type was most important to landscape use by jaguars in the Pantanal.

DISCUSSION

Our objective was to assess how jaguars use the Pantanal landscape during three behavioral states (moving, depredating native prey, or depredating cattle) during two seasons (dry and wet) for females and males. In general, when jaguars, female or male, were moving across the landscape, they selected areas that were in dense cover or near to dense cover, preferred areas of higher habitat diversity, and used locations closer to water than what was available on the

Table 3. Top-performing resource selection function models for jaguars when killing native prey and cattle in the dry and wet seasons, southern Pantanal, Brazil.

Prey and season	Model	ΔBIC	df	Weight
Cattle				
Dry	Distance to dense cover	0.0	2	0.87
Wet	Null	0.0	1	0.67
	Distance to dense cover	4.0	2	0.09
	Percent dense cover	4.2	2	0.08
	Diversity	5.1	2	0.05
Native				
Dry	Null	0.0	1	0.70
	Percent dense cover	2.7	2	0.18
	Distance to dense cover	5.3	2	0.05
Wet	Percent dense cover + diversity	0.0	3	0.56
	Percent dense cover + distance to dense cover	3.2	3	0.11
	Percent dense cover + distance to dense cover + diversity	3.9	4	0.08
	Percent dense cover	4.0	2	0.07
	Diversity	4.2	2	0.07

Notes: BIC, Bayesian Information Criteria. Only models with a weight ≥0.05 were included.

landscape, similar to other studies (Crawshaw and Quigley 1991, Sollmann et al. 2012, De Lázari et al. 2013). The top-ranking RSF models showed that when jaguars were moving through the landscape and killing prey or cattle, the models were relatively simple with consistent variables among the models. Although the null model was the highest ranked in two of the four predation RSFs, the sub-ranked models included percent dense cover and distance to dense cover, albeit at very low model weights. Essentially, the similarity of relationships between the use of dense cover and distance to dense cover for all three behavioral states suggests the familiar phrase always on the prowl is an apt description of resource selection for jaguars in the Pantanal. Similarly, Blake and Gese (2016) found cougars in central Montana, USA, did not change preferred habitats between behavioral states and had simpler RSF models for depredation events than while moving. The presence of two null models in the best-performing kill-site RSFs suggested that neither female nor male jaguars consistently selected for a particular landscape feature when killing cattle in the wet season or native prey in the dry season. We recognize the limitations of low sample sizes of jaguars in certain seasons (i.e., two females in the dry season), and in any subsequent analyses and conclusions drawn from sub-ranked models contain greater uncertainty.

Female and male jaguars did not select for any particular habitat when depredating on native prey or making cattle kills, but they did select for locations based on the amount of dense cover and the distance to dense cover and habitat diversity. Jaguars likely select locations close to dense cover from which to depredate prey due to the hiding cover it provides while allowing the jaguars to assess prey vulnerability (Holmes and Laundré 2006, Klar et al. 2008). Cattle were placed in open pastures at the start of the dry season and dispersed throughout the study area during the remainder of the season. Thus, at the start of the dry season, cattle are clustered and in high densities making them susceptible to depredation by jaguars (Zarco-González et al. 2013, Carvalho et al. 2015). Jaguars usually hunt grazing livestock that can freely disperse (Zarco-González et al. 2013); thus, jaguars likely stayed within or near to dense cover while evaluating livestock in the open fields. As the dry season continues, the cattle become less clustered but remain near available water sources, such as river edges and isolated ponds, which again provide concentrated sources of prey for jaguars (Crawshaw and Quigley 1991, Klar et al. 2008). During the wet season, cordilheiras concentrate prey and likely cause jaguars to focus their hunting efforts to these areas. The cordilheiras generated in the wet season provide a refuge for terrestrial mammals, which they leave for the more nutrient-rich marshes in the dry season (De Lázari et al. 2013). Prior researchers have found that Pantanal jaguars were rarely away from water (Crawshaw and Quigley 1991, Cullen et al. 2005), and our data suggest they are generally <2.5 km from water (Fig. 2D), similar to the patterns cattle exhibit. During the wet season, although cattle are able to forage in chest-deep water, they need dry ground on which to spend the night. Therefore, cattle spend more time closer to islands and strips of forests, which are characterized by higher and drier ground during the wet season. Additionally, native prey are more likely adapted to submerged and partially submerged vegetation (Mamede and Alho 2006)
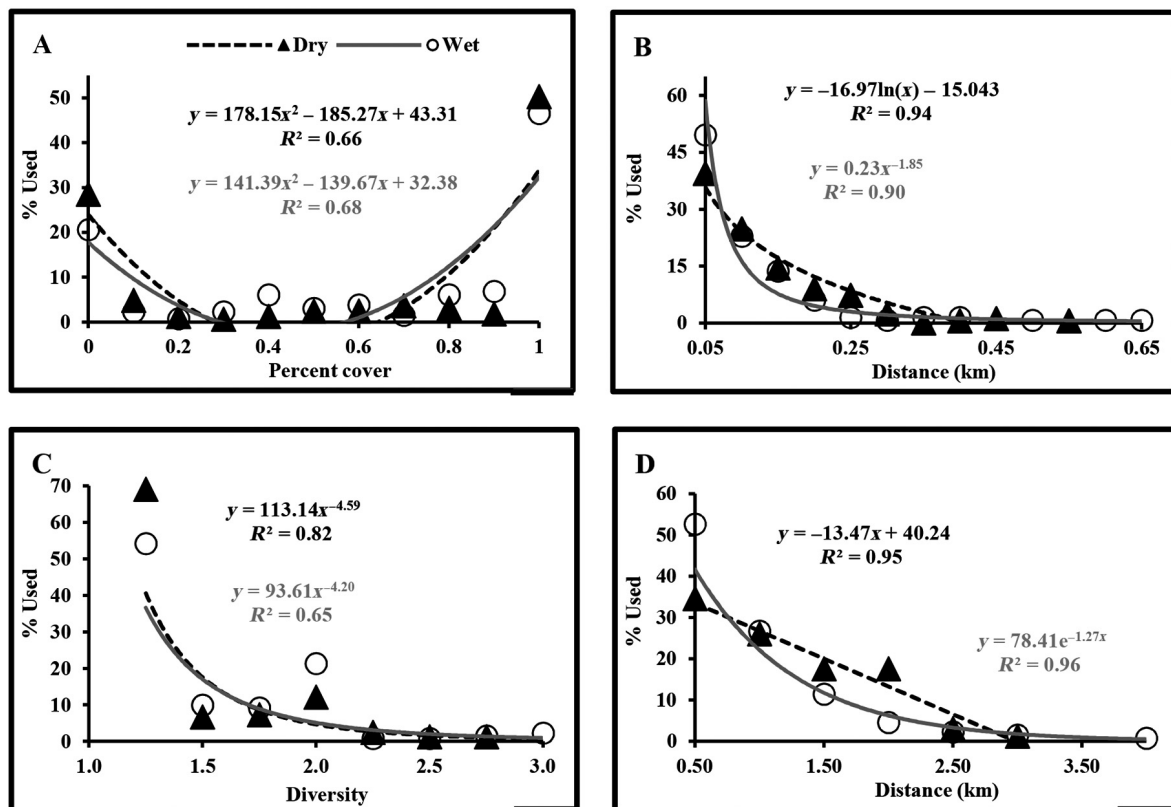
Fig. 4. Proportion of used points related to (A) percent dense cover, (B) distance to dense cover, (C) diversity, and (D) distance to water, for jaguars while killing native prey in the dry and wet seasons, southern Pantanal, Brazil.

and thus were not constrained exclusively to the cordilheiras in the wet season.

Another major environmental characteristic influencing jaguars when hunting either native prey or cattle, regardless of season, was their distance to dense cover. We found both sexes equally using dense cover or located very close to dense cover when depredating native prey and cattle, although males did have some locations further from dense cover than females. Male jaguars, with a larger body size, are considered less risk-averse than females and less sensitive to uncertain habitats (Colchero et al. 2011) and will travel farther than females (Crawshaw and Quigley 1991). Additionally, as native prey is more likely to be found in submerged and partially submerged vegetation in the wet season (Mamede and Alho 2006), male jaguars are not forced to focus the search for prey to the isolated cordilheiras.

The similarity of relationships between the use of dense cover and distance to dense cover for all three behavioral states suggests that jaguars in the Pantanal are always in hunting mode. Several authors have suggested keeping cattle herds away from forests as a strategy to minimize jaguar attacks (Rabinowitz 1986, Quigley 1987, Hoogesteijn et al. 1993, Michalski et al. 2006, Palmeira et al. 2008). Hoogesteijn et al. (1993) compared three ranches in Venezuela with depredation problems and found cattle losses were associated with forested areas. Accordingly, the ranch with the lowest rates of jaguar predation on cattle was comprised of narrow strips of gallery forests along rivers and streams which were completely fenced, keeping cattle out of the forest. Rabinowitz (1986) reported jaguars readily killed livestock when they came into forested areas, but not when they were in open pastures. Quigley (1987) reported in the Pantanal all cattle kills were
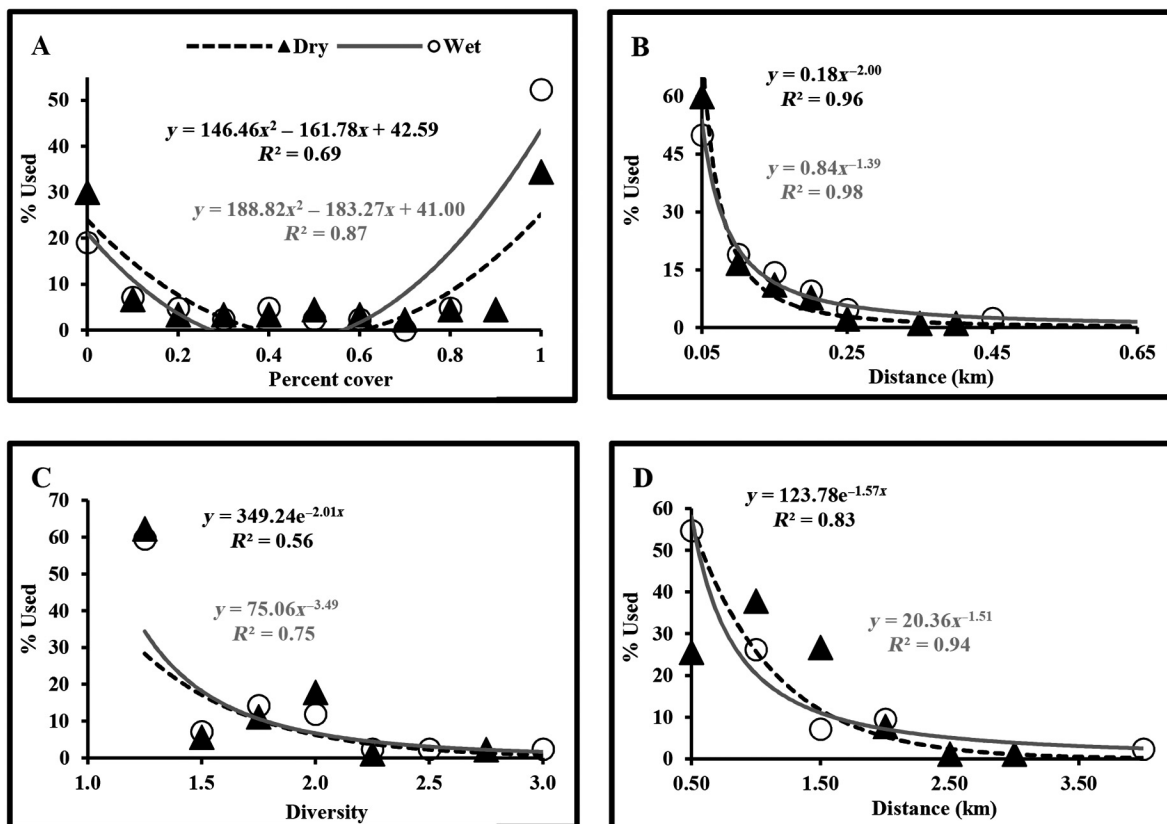
Fig. 5. Proportion of used points related to (A) percent dense cover, (B) distance to dense cover, (C) diversity, and (D) distance to water, for jaguars while killing cattle in the dry and wet seasons, southern Pantanal, Brazil.

located in gallery forests and forest patches, although a few were made at forest edges and dragged into cover. However, we recorded jaguar kills on cattle in all habitats. Principally, we found that dense cover was the main driver of resource selection, be it in the form of forests, brushland, or dense shrublands. In addition, given the heterogeneous patterns of vegetation distribution in the Pantanal, keeping cattle away from dense cover is impractical. Some authors have suggested introducing exotic grasses in the Pantanal in areas originally covered by shrublands and native grasses as a way to minimize the impact on arboreal vegetation (Comastri-Filho and Pott 1993, Comastri-Filho 1997).

Prior research has indicated that hunting success of jaguars is affected by factors other than vegetation cover; for example, prey vulnerability is equally important (Taylor 1976, Temple 1987). Jaguars in the Pantanal kill a variety of species

that exhibit a wide diversity of movement behaviors. Caiman is a primary prey for jaguars in the study area (Cavalcanti and Gese 2010) that make extensive seasonal movements between permanent and temporary lakes and rivers (Coutinho and Campos 1996, Campos et al. 2005). These long-range movements between different habitats expose them to greater amounts of edge habitats and likely make them more vulnerable to predation by jaguars.

Our kill-site analyses were based on the assumption that prey were equally distributed in the various habitat types across the study area. We determined available locations based on the used locations within each home range rather than specific prey distributions. In addition, the variables we selected may not reflect the general distribution of prey. Although we did not have detailed information on prey distribution in the study area, the predation models were based on

428 prey items killed by jaguars (Cavalcanti and Gese 2010). Furthermore, studies suggest prey species use a variety of habitats in the Pantanal. Caiman, for example, can build their nests in lake-surrounding forests, isolated islands of forests, open pasture fields, or floating vegetation (Campos 1993). Adult caiman reside in many different types of aquatic habitats from temporary to permanent lakes and small to large rivers (Campos 1993, Coutinho and Campos 1996). Although peccaries are frugivores and are found primarily in the forest, they are frequently observed in other habitats as well, from open fields with sparse trees to shrubland to wetland vegetation (Keuroghlian et al. 2004, Desbiez 2007). Future studies examining the spatial distribution of jaguar's kills should consider the abundance and distribution of native species if possible.

The preservation of large undisturbed blocks of forests is considered vital for the conservation of jaguars (Rabinowitz 1986, Crawshaw et al. 2004, Cullen et al. 2005, Michalski et al. 2006). The intermingling of different habitats and the dynamic cyclical nature of the wet and dry seasons in the Pantanal play a critical role in the relationships between jaguars and their prey. Finding the balance between the traditional ranching communities and maintaining a robust jaguar population will require integrating ecological and social values to formulate effective management plans, as well as recognizing the issues of different scales required for management. Our findings on resource selection were at a relatively small scale (i.e., a 35-m buffer within the extent of an individual jaguar home range). Ranchers attempting to mitigate cattle losses through habitat modification at a larger scale (i.e., across a ranch) may find focusing management actions to areas containing valuable calves more practical. Management at the ranch scale seems impractical given that dense cover in any form provides ambush cover for jaguars. On a larger scale, habitat conservation in the Pantanal must go beyond preserving small amounts of habitat but should consider management at a landscape scale. On the coarsest scale, maintaining connectivity of jaguar sub-populations will require knowledge of regional-scale movement patterns. Acknowledging the issues of different scales (e.g., kill site, home range, ranch, landscape, region) could prove valuable when formulating management plans. Connections among scales may also prove useful as they relate to the management objective. For example, attempts to reduce predation risk to livestock on a ranch are also related to population management (i.e., reduces killing of jaguars) and are therefore informative at fine and coarser scales. Likewise, managing jaguars occupying several ranches scales up to management of the sub-population necessary to maintain range-wide connectivity.

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