

Jaguar *Panthera onca* Habitat Modeling in Landscapes Facing High Land-use Transformation Pressure—Findings from Mato Grosso, Brazil

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ABSTRACT

The modeling of top predators' habitats and the understanding of their environmental requirements in landscapes facing high land-use transformation pressure have long-standing importance for the development of conservation strategies. Multi-distance spatial cluster analysis and logistic regression with environmental weighting for pseudo-absence designation were applied to understand spatial patterns of jaguar occurrence in Mato Grosso state (Central Western Brazil). This location has been under intense deforestation pressure since the 1970s and is historically one of the most important jaguar habitats in the world. By using a model of five independent variables, we were able to achieve a 73.2 percent success rate of case/non-case classification and indicate not only a general loss of habitat suitability, but also an increasing interruption of potential migration corridors in the state. Our analysis on a regional scale demonstrates the importance of forest and savannah woodland for jaguar habitat maintenance in the Mato Grosso state. The jaguar species demonstrates a sensitivity to landscape fragmentation, which can be parameterized for improved model building by metrics such as edge density and patch size. Comparisons with previous studies in South America show that parameter selection for jaguar habitat modeling is highly scale-dependent and that habitat suitability in partially transformed landscapes could be maintained if fragmentation is minimized. Recent land-use transformation, however, has significantly weakened the conservation status of the Pantanal-Amazon corridor.

Abstract in Portuguese is available in the online version of this article.

Key words: corridors; GIS; habitat mapping; landscape metrics; land-use change; *Panthera onca*.

BRAZILIAN ECOSYSTEMS, MAINLY THE LOWLAND FORESTS OF THE AMAZON, sustain about 50 percent of the jaguar (*Panthera onca*) population worldwide (Sollmann *et al.* 2008). Adjacent regions of tropical savanna (*i.e.*, Cerrado) and transitional forests have historically been an extension of the jaguar habitats of the Central Amazon. Cerrado regions, when undisturbed, are suitable for jaguars (Torres *et al.* 2008, 2012) and connect the Amazon to the Pantanal floodplain, another important refuge (Cavalcanti 2008). The development of agricultural technology suited to soils of the Cerrado and forests of the southern Amazon has triggered land-use transformation at a virtually unprecedented speed. Between 1988 and 2010, Mato Grosso state lost about 135,000 km² of its forest and savanna woodlands, mainly to cattle and crop farming, causing widespread habitat reduction and fragmentation (Carvalho *et al.* 2009). The type and intensity of land-use transformation and fragmentation in both the Cerrado and adjacent southern Amazon, however, have not occurred in a spatially uniform manner. Rather, they are related to both environmental and socio-economic factors, including land-occupation programs, road development, and designation of protected areas (Soares-Filho *et al.* 2006, Brannstrom *et al.* 2008). The prediction

of habitat suitability of top predators that integrates multiple aspects influencing land transformation can be used as an indicator of ecosystem health or integrity and strengthen conservation strategies.

Studies have shown that the percentage loss of natural vegetation cannot be used as a proxy for habitat suitability of carnivores (Carvalho *et al.* 2009). Instead, the type of agricultural land-use in deforested landscapes has a complex influence on species presence. As jaguars are known to substitute their natural prey for domestic livestock (Schaller & Crawshaw 1980, Rabinowitz 1986, Sanderson *et al.* 2002, Silveira *et al.* 2008), the species should be more present in areas of cattle farming than in crop farming regions. Yet, persecution by ranchers has been reported as a consistent threat to jaguar persistence. Other important aspects are the spatial distribution of vegetation relative to other landscape elements. For example, Crawshaw and Quigley (1991) point out the importance of proximity of vegetation to riparian areas, while the availability of smaller clearings can favor movement and hunting (Maffei *et al.* 2004). Finally, the degradation of vegetation or selective use of remaining forest patches can decrease habitat suitability (Michalski & Peres 2005).

Jaguars have home ranges of up to 150 km² in the Cerrado (Silveira 2004), and therefore large areas are needed to maintain viable populations. Habitat fragmentation and other discontinu-

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ities in their preferred environment are important threats to populations of large carnivores, including jaguars (Crooks 2002, Fahrig 2003, Hatten *et al.* 2005, Haag *et al.* 2010, Colchero *et al.* 2011). Fragmentation is the result of interactions between physical, biological, economic, political, and social factors, and independent of its driving forces; it can be parameterized by landscape metrics derived from land-use and vegetation-cover mapping. These metrics were constructed to measure the effects of fragmentation on the number of habitats, number of patches, patch size, and the isolation between patches (Fahrig 2003). Jackson *et al.* (2005) found a significant relationship between mean patch area and edge width to ocelot habitat suitability, while Michalski and Peres (2005) showed that forest patch area was a highly significant predictor for jaguar presence/absence in fragmented forest habitat in northern Mato Grosso.

We combined multiple landscape metrics and socio-environmental variables obtained from Remote Sensing and GIS-implemented spatial analysis through group-discrimination techniques to map jaguar habitat. Historic jaguar occurrences are compared with spatial data layers to: (1) determine if natural and anthropogenic landscape features and landscape metrics are reliable predictors of jaguar habitat in the Cerrado and forest biomes of Mato Grosso state; and (2) develop and validate a habitat suitability map for this region.

METHODS

STUDY AREA AND JAGUAR OCCURRENCE.—The state of Mato Grosso is located in the central-west of Brazil (900,000 km²; 6°00'S to 19°45'S and 50°06'W to 62°44'W) and includes three of the main Brazilian biomes: the Amazon forest, the Cerrado savannas, and the Pantanal floodplain (Fig. S1). Annual precipitation ranges from about 2300 mm in the extreme north to less than 1100 mm in the Pantanal. Elevations (except for the lower lying alluvial Pantanal floodplain in the southwest) range between 150 m at the transition to the northern Pantanal and about 800 m in the uplands of the 'Chapada dos Parecis' and 'Chapada dos Guimarães.'

The spatial database of jaguar occurrence was obtained from the Jaguar Conservation Fund (JCF), which has compiled historical and contemporary jaguar records from published research and web-based databases such as the Global Biodiversity Information Facility (<http://www.gbif.org/>), SpeciesLink (<http://splink.cria.org.br>), and the Museum of Vertebrate Zoology (<http://www.mip.berkeley.edu/>), in addition to information obtained from camera-trapping and interviews with locals conducted by JCF scientists (Torres *et al.* 2012).

To minimize bias due to time-related inconsistencies between available spatial data sets and jaguar occurrences, we only considered records from 2005 through 2009. Predictive landscape models assume spatial stationarity with respect to habitat-selection patterns, which mean that a species has similar habitat preferences over the spatial extent of the simulated study area (Fielding & Bell 1997, Osborne & Suárez-Seoane 2002). The Pantanal floodplain in the south of the state has different socio-environ-

mental characteristics determining jaguar habitat suitability (Sanderson *et al.* 2002, Silveira 2004). Model development was therefore restricted to the state's forest and Cerrado biomes, which encompass about 93 percent of the state's territory (Fig. S1) and include 219 jaguar records. Following Birch *et al.* (2007), the landscape was discretized by hexagonal grids, which follow the theoretic movement and dispersion pattern of a species in a isotropic landscape and have the same length common borders with all neighbors. Therefore, hexagonal discretization represents an equal strength of neighborhood interactions (Holland *et al.* 2007) and does not produce artificial edge effects in landscape metrics calculations (Jackson *et al.* 2005). Similar to previous studies (Silveira 2004, Astete *et al.* 2008, McRae *et al.* 2008, Wisz & Guisan 2009), the hexagon size was set to 200 km², corresponding to the maximum jaguar home range in the region. This spatial resolution assures that habitat suitability of a unique cell approximates the maximum potential of a jaguar home range.

SPATIAL DATA SETS AND LANDSCAPE METRICS.—All spatial data sets, jaguar occurrences, and explanatory data sets were processed by ArcGIS, v. 9.3 (ESRI). Hexagonal discretization and extraction of landscape metrics were conducted by using the Patch Analyst ArcGIS extension, version 4.2 (Elkie *et al.* 1999).

Both mean Euclidian distance from the hydrographic network (DIS_HYD) and road density (DEN_ROAD) were extracted from the respective 1:250,000 scale layers of the Socio-economical Ecological Zoning (ZSEE) of the state (Mato Grosso 2011) and adopted for the year 2008 (Table 1). As the 3 'SRTM digital elevation model (DEM) showed artifacts biasing elevation and slope with increasing landscape fragmentation (Kellndorfer *et al.* 2004), we used the 30' GTOPO30 (www.usgs.gov) DEM to parameterize mean terrain altitude (ALTITUDE), mean slope (ME_SLOPE), maximum slope (MA_SLOPE), and the slope standard deviation (SD_SLOPE).

Natural vegetation (VEG_NAT) and main land use (MAIN_USE) are two key data sets for jaguar habitat mapping (Lyra-Jorge *et al.* 2010, Rabinowitz & Zeller 2010, Colchero *et al.* 2011). Therefore, special care was taken in the adjustment of these layers. Natural vegetation represents the natural habitat before relevant anthropogenization and is the input layer for the calculations of landscape metrics. Annual deforestation layers (1:100,000) between 2004 and 2009 from Mato Grosso state environmental agency (SEMA) were intersected and manually corrected for inconsistencies by comparing polygons with co-registered multitemporal Landsat TM imagery from 2007 and 2008. The final habitat model was then calculated for the deforestation situation in 2009.

The variable of the main land use (MAIN_USE) represents the classification of each deforestation polygon according to its main land use based on the 1:250,000 land-use map presented by Mato Grosso (2011), differentiating four ordinally coded units: (1) crop farming on vast properties; (2) cattle farming on vast properties; (3) mixed farming on small properties; (4) and mostly natural vegetation. Attributes of each land-use polygon were

TABLE 1. Independent variables (without landscape metrics) evaluated for jaguar habitat suitability modeling by Logistic Regression. All values per hexagonal (200 km²).

Index	Acronym	Meaning and how obtained or computed	Unit
Distance to streams	DIS_HYD	Mean Euclidian distance from the double-lined, 1:250,000 scale, state hydrographic network (Mato Grosso 2011)	km
Road density	DEN_ROAD	Road Density obtained from 1:250,000 scale, state road map, paved and unpaved (Mato Grosso 2011)	km/200 km ²
Mean altitude	ALTITUDE	Mean altitude according to GTOPO digital elevation model, Vers. 2.1 (30 arc sec)	m
Mean slope	ME_SLOPE	Mean slope according to GTOPO digital elevation model, Vers. 2.1 (30 arc sec)	%
Maximum slope	MA_SLOPE	Maximum slope according to GTOPO digital elevation model, Vers. 2.1 (30 arc sec)	%
Standard deviation slope	SD_SLOPE	Standard deviation of slope according to GTOPO digital elevation model, Vers. 2.1 (30 arc sec)	%
Natural vegetation	VEG_NAT	Percentage of natural vegetation for each year of jaguar occurrences (2004–2009). 1:250,000 scale PRODES deforestation database (Câmara <i>et al.</i> 2006). Validated by Landsat TM imagery	%
Main land use	MAIN_USE	Predominant land use in deforested areas. Intersection of year-by-year PRODES database with the ZSEE land use and cover mapping (Mato Grosso 2011). Validated by Landsat TM imagery	4 classes

conferred and eventually corrected by visual inspection of the Landsat TM imagery.

LANDSCAPE METRICS.—Cushman *et al.* (2008) emphasized the high autocorrelation between landscape metrics, indicating the need for previous variable reduction to reduce overfitting in predictive modeling. In accordance with previous studies on the use of landscape metrics for predator habitat characterization (Jackson *et al.* 2005, Michalski & Peres 2005, Lyra-Jorge *et al.* 2010), we pre-selected nine metrics calculated for the VEG_NAT class (forest/woodland patches per hexagonal), and four metrics for patch density and size (DS), such as the number of patches (NP), mean patch size (MPS), patch size coefficient of variance (PScov), and the patch size standard deviation (PSSD). The mean patch edge (MPE) and edge density (ED) parameterize patch edges (E), and three of them, the mean shape index (MSI), the area weighted mean shape index (AWMSI), and the area weighted mean patch fractal dimension (MPSFD), are measures of patch shapes (S) (Table 2). All metrics were calculated for patches of natural vegetation inside the hexagons.

LANDSCAPE MODEL.—Logistic regression (LR) is the most widely used group-discrimination technique for the prediction of potential species distributions (Guisan *et al.* 2006). LR allows for the identification of the relative importance of each predictor variable on species response and estimates the spatial uncertainty patterns and their association with the model parameters (Wisiz & Guisan 2009). Coarse-scale feline habitat mapping studies are based in general on presence-only field

observations (Hatten *et al.* 2005). As in classification techniques, machine learning approaches and other regression modeling techniques (Barbet-Massin *et al.* 2012), LRs depend on presence/absence data. Therefore, the known locations of feline records (presence-only data) must be completed with ‘pseudo-absences’ (Zaniewski *et al.* 2002). As a consequence, results describe only the relative likelihood of occurrence (Pearce & Boyce 2006).

The selection of pseudo-absence data directly influences habitat maps and their performance indicators (Pearce & Boyce 2006, Wisiz & Guisan 2009, Barbet-Massin *et al.* 2012). Van Der Wal *et al.* (2009) and Zaniewski *et al.* (2002) showed that pseudo-absence designation should be meaningful as it concerns knowledge on species habitat, meaning that randomly designated pseudo-absence should be checked for its reliability. As natural savannas and forested biomes are known jaguar habitats in Mato Grosso, we adopted a two-fold criterion in this selection. First, 219 hexagons without jaguar records were randomly selected. Next, we maintained only those hexagons as pseudo-absences were which had less than 70 percent of natural vegetation, as such areas are likely to sustain specimens in the study area (Silveira *et al.* 2008, Sollmann *et al.* 2008, Torres *et al.* 2008, 2012).

Logistic regression (LR) landscape habitat models are susceptible to overfitting by auto-correlation of independents or an excessive use of independents (Betts *et al.* 2006). For variable reduction, univariate LR models were run for each independent variable (Table 1) and only those with significance at a 0.9 CI were maintained. Then Spearman Rank correlations were evaluated separately for non-landscape and landscape metrics. Remain-

TABLE 2. Class landscape metrics of natural vegetation patches for prediction of jaguar habitat suitability.

Índex	Acronym	Type	Meaning (for forest/woodland patches per hexagonal)	Unit
Number of Patches	NP	DS	Number of patches	n
Mean patch size	MPS	DS	Mean size of patches	ha
Patch size coefficient of variance	PScoV	DS	Relative variability (as percentage) about the mean size of patches	%
Patch size standard deviation	PSSD	DS	Absolute variation of patches	ha
Mean Patch Edge	MPE	E	Average edge length per patch	m
Edge density	ED	E	Total length of edge in landscape involving patch type divided by total landscape area	m/ha
Mean shape index	MSI	S	Mean of perimeter-to-minimum perimeter ratio	-
Area weighted mean shape index	AWMSI	S	Mean of perimeter-to-area ratio, weighted by the size	-
Area weighted mean patch fractal dimension	MPSFD	S	Mean of fractal dimension of each patch weighted by the size	-

DS, Density/size; E, Edge; S, Shape. All values calculated for 200 km² hexagons.

ing variables were introduced in multiple LR, using the conditional backward stepwise procedure for variable selection.

A further pre-requisite is the absence of spatial autocorrelation in observation data. After removing possible repeated occurrences of the same specimens (more than one point in the assumed home range), the global spatial autocorrelation was tested using Ripley's K-function (Ripley 1976), a multi-distance spatial cluster analysis for presence data which counts the number of points in increasing search radius to compare the observed spatial pattern to the pattern expected from a homogenous Poisson point process (Lancaster & Downes 2004, Fortin & Dale 2005).

RESULTS

SPATIAL STRUCTURE OF JAGUAR OCCURRENCE DATA.—Jaguar occurrences without repeated records inside a hexagon have an average minimum distance of about 39.8 km between them. L (h), and a standardization of Ripleys K function for the presence data does not show significant grouping of jaguar records (Fig. 1). Observations are dispersed up to a distance of about 50 km, with observed L (h) values (solid line) lower than the 99% significance level (dashed line). This dispersion pattern in small distances occurs due to the extended home range of the species. Further, low distanced records from the original dataset in a single 200 km² hexagonal have been removed from analysis as they are possible repeated sights of the same individual. In distances longer than about 50 km, observed L (h) values are inside the significance limits, indicating a purely random distribution throughout the evaluated biomes. With this spatial structure, a logistic regression without a spatial auto-correlation term can be applied for habitat mapping (Betts *et al.* 2006).

HABITAT SUITABILITY MODEL.—With the exception of the average, maximum, and standard deviation of slope, all independent variables (without landscape metrics) were found to be significant predictors of jaguar absence/presence in univariate LR models ($P < 0.10$). The explanatory variables of the average distance to the hydrographic network (DIS_HYD), average density of road

network (DEN_ROAD), average elevation (ALTITUDE), percentage of forested area (VEG_NAT), and percentage of predominant land use and cover ordered in four classes (MAIN_USE) all show partially significant Spearman coefficients (Table 3). Given that maximum rank correlations did not exceed ± 0.41 , all these variables were initially considered in LR.

Landscape metrics of the size/density (NP, MPS, PSCOV, PSSD) and the border (MPE, ED) group showed significant rank correlation between them (Table 4). Shape metrics (MSI, AWMSI, MPSFD) are less correlated, but showed generally lower Wald statistics (e.g, less predictive power) in univariate LR models (not shown) than evaluated metrics of the size/density and border groups. Therefore, we pre-selected the patch metric of the highest predictive power for each metric group.

After extensive testing, an LR model was developed accepting randomly selected pseudo-absences in hexagons with a maximum of 70 percent of forest/cerrado woodlands, which included five variables using a 90% confidence interval as inclusion criteria (Table 4). With the exception of VEG_NAT, all independent

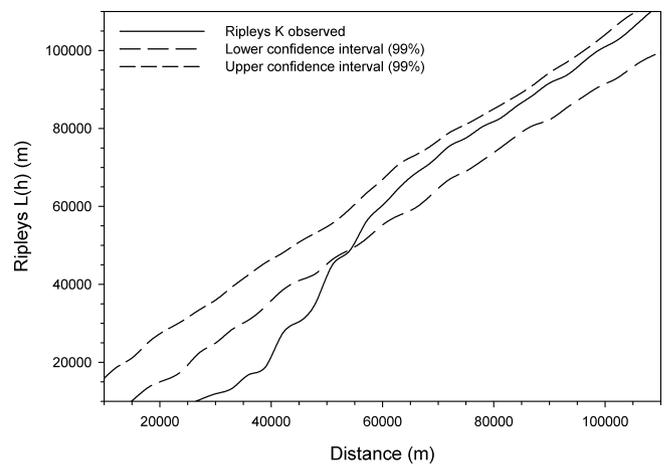


FIGURE 1. Standardized Ripley K-function (L[h]) of multiple distance spatial autocorrelation of jaguar occurrences in the Forest and Savannah biomes of MT.

variables were ln-transformed as they differ significantly from normal distribution according to the Shapiro–Wilk statistics (Bornmann *et al.* 2008). MAIN_USE, VEG_NAT, DEN_ROAD, ED, and MPS were included in the model resulting in an overall accuracy of 73.2 and the Nagelkerke R Square of 0.434. VEG_NAT shows the highest Wald statistics. Fewer than 2 percent of the occurrences were recorded in hexagons with less than 15 percent of VEG NAT, whereas more than 10 percent of random pseudo-absence hexagons have a significantly low percentage of natural vegetation (Fig. 2). Presences increasingly exceed pseudo-absences in hexagons with more than 50 percent of VEG_NAT.

Jaguar presence is lower than pseudo-absence on vast properties, regardless of whether they are used for crop (CRG) or cattle farming (CAG). On small mixed properties (MFS), presence is higher than absence. The negative coefficient of road density shows the inverse relation with jaguar habitat suitability. Presence percentages are higher than pseudo-absence percentages in densities of 1.5 km per hexagon or less.

Mean patch size (MPS) and edge density (ED) were found to be significant predictors in both models. Greater natural vegetation patches are positively related to habitat suitability and presence is higher than pseudo-absence in hexagons with a MPS greater than 10 km². ED at the class level as a measure of total edge length of natural vegetation patches (VEG_NAT) is inversely correlated with habitat suitability and presence hexagons override absence hexagons at values less than 0.8 km per hexagon. ED has the second highest Wald statistics, indicating a strong negative impact of habitat fragmentation on habitat suitability.

The first plane resulting map of habitat suitability represents the distribution of natural vegetation in the state (Fig. S2). Values higher than 0.5 stand for hexagons where the likelihood of species presence is relatively higher than its absence. Highest suitabilities are observed in protected areas (*Juruena* National Park, *Kaibi* Indigenous Area) in the extreme north of the State, and in several protected environmental areas, indigenous reserves, and adjacent areas in the north-west of the state (A1), and the lower valleys of the *Xingu* (A2) and *Araguaia* Rivers (A3).

The state's south-eastern savannas, which are on Mesozoic and tertiary sandstone and now used intensely for farming, have generally lost their status as suitable jaguar habitats (B1). The two other crop farming regions are located in the center of the state along a highway (BR-163) (B2) and the 'Parecis' plateau (B3). In

another widely deforested area in the central north (B4), hexagonal sample areas have only partially lower suitability due to their mixed land use with predominant cattle farming.

DISCUSSION

Jaguar records in Mato Grosso (2005–2009) are dispersed up to about 50 km and show no spatial grouping at higher distances. This occurs despite the heterogeneous patterns of deforestation in the state; deforestation is concentrated on the Brazilian Plateau, where there is more agriculture. With the exception of the southeast, jaguar occurrences have been recorded throughout the state and records are not significantly grouped in well-defined clusters of environmentally protected areas or indigenous reserves. This means that even in strongly deforested regions there is the potential for jaguar conservation initiatives.

Adjacent occurrences inside well-preserved areas (VEG_NAT > 70%), however, have an average distance of about 48.2 km. Even considering our non-systematic sampling approach, this indicates that conserved regions may not sustain their original populations, possibly due to the ongoing degradation of reserves by unauthorized logging and farming (Cavalcanti 2008, Torres *et al.* 2008).

High habitat suitability in densely vegetated landscape units underpins the importance of protected areas and Indian reserves for species conservation (Sollmann *et al.* 2008). Current spatial patterns of habitat suitability also validate former projections (Torres *et al.* 2008) of extensive loss of habitat quality in the 'arc

TABLE 4. Coefficients (B), standard error (SE), Wald statistics, and significance levels (Sig.) of independent variables included in the jaguar habitat suitability Logistic regression (LR) model. Pseudo-absences in hexagons with less than 70% of natural vegetation.

	B	SE	Wald	Sig.
MAIN_USE	0.710	0.219	10.519	0.001
VEG_NAT	4.847	0.839	33.380	0.000
DEN_ROAD	-0.015	0.007	5.107	0.024
ED	-1.625	0.354	21.035	0.000
MPS	-0.476	0.153	9.664	0.002
Constant	11.201	2.934	14.572	0.000

TABLE 3. Spearman rank correlation between independent variables (without landscape metrics) (** P < 0.01) with significant (P < 0.10) predictive power in univariate Logistic regression (LR) models.

	DIS_HYD	DEN_ROAD	ALTITUDE	VEG_NAT	MAIN_USE
DIS_HYD	1	-0.054	0.264**	-0.312**	-0.078
DEN_ROAD	-0.054	1	0.221**	-0.410**	-0.285**
ALTITUDE	0.264**	0.221**	1	-0.333**	-0.409**
VEG_NAT	-0.312**	-0.410**	-0.333**	1	0.368**
MAIN_USE	-0.078	-0.285**	-0.409**	0.368**	1

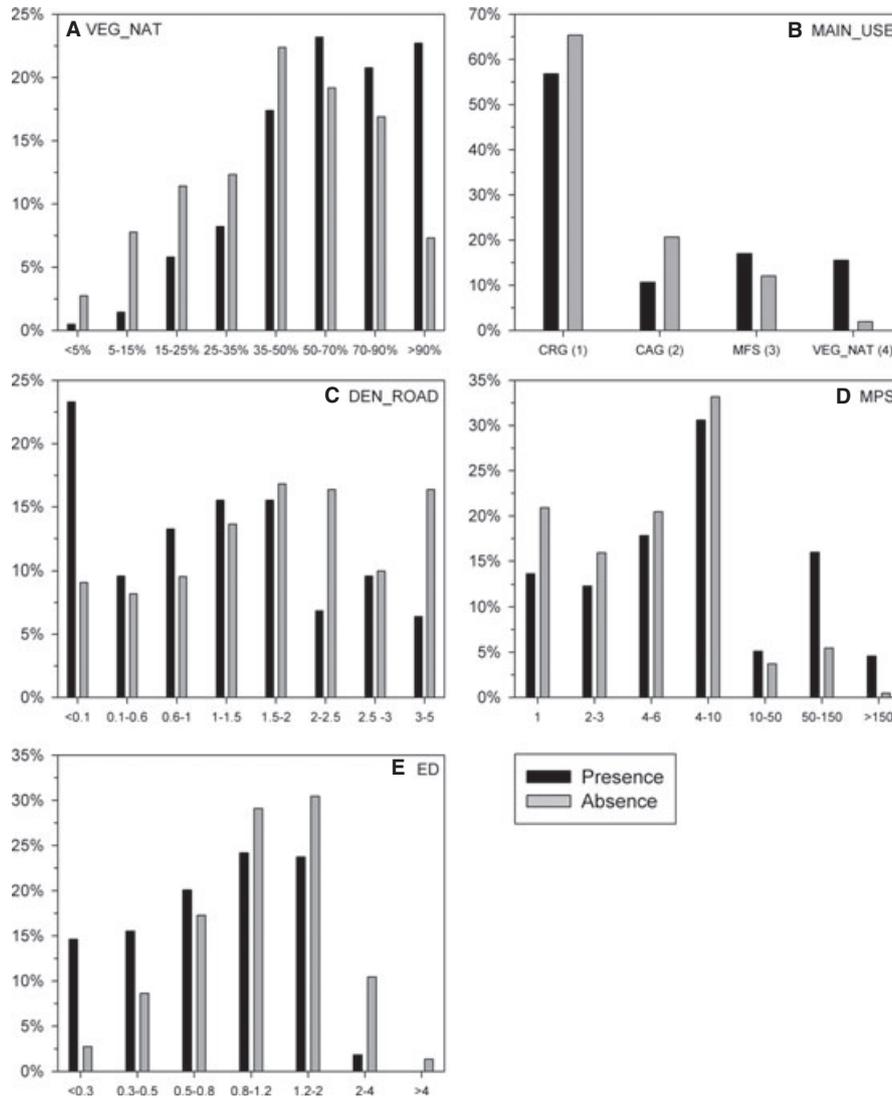


FIGURE 2. Class percentages of significant independent variables in jaguar habitat suitability models for presence and random pseudo-absence hexagons. (A) Natural vegetation, (B) Main land use (CRG, Crop farming on vast properties; CAG, Cattle farming on vast properties; MFS, farming on small properties; VEG_NAT, Natural vegetation), (C) Road density, (D) Mean patch size, (E) Edge density.

of deforestation’ in northern Mato Grosso (Fig S2, B4 and adjacent western areas). These results underscore that the maintenance of current jaguar populations is unrealistic from the perspective of ongoing and progressive deforestation in the Cerrado and forest ecosystems in central-western Brazil. Given the recent pressure to weaken conservation initiatives in Brazil’s Federal Forest Code efforts to stop or at least curtail this deforestation will be a major challenge.

Beyond the reduction in habitat suitability due to deforestation, an additional concern is the loss of corridors, which could sustain inter-population movement and genetic integrity (Rabinowitz & Zeller 2010). These corridors are determined by the geographical characteristics of the region. The main Amazonian river courses, such as the Xingu, Juruena, and Araguaia, have partially intact riparian forests and almost parallel, north-south

flows (see Fig. S2). The upper Juruena River and Guapore are an almost intact north-south corridor between the Amazon, Cerrado, and Pantanal, while the Xingu and the mid- and lower-Araguaia are important links between the Cerrado and the Amazon. Zones between these main connections are increasingly interrupted, however, potentially impeding latitudinal migration.

Secondary predictors improve overall percentage of case classification success—from about 61 percent (not shown) with VEG_NAT as unique predictor to more than 73 percent in the LR model. The importance of landscape metrics—the main land use in deforested areas and road density for suitability prediction—shows that conservation strategies in presently human-dominated landscapes can improve jaguar habitat quality. Hexagons sampling areas with less than 60 percent of remanant forest have a suitability higher than the average (>0.5) in almost 21,000 km²

of the study area if edge densities of their forest patches are low (<0.6). Reducing habitat loss in partially deforested areas—for example by reduced the fragmentation of remnant vegetation—could help establish migration corridors between reserves where agricultural land use is already tightly restricted by law.

We showed landscape metrics are better indicators of fragmentation and therefore jaguar habitat suitability than road network density. The absence of roads in partially deforested hexagons results in a suitability higher than 0.5 in just 11 cases (2200 km²), and this happens only if edge density is very low (<0.4 km/hexagon). We infer that this result is related to the limited traffic density on most of the secondary road networks in the state, most of which are not yet paved. Exceptions are the main routes for the outflow of agricultural production (e.g., the BR-163 highway), which experience intense truck traffic and potentially create barriers for jaguar movement (Colchero *et al.* 2011).

Results of LR parameter selection show high dependence on regional socio-environmental conditions and spatial scale when compared with prior studies (Sanderson *et al.* 2002). For instance, the importance of hydrographic network proximity for jaguar habitat suitability in most Brazilian biomes has been emphasized by Astete *et al.* (2008), but we show that this variable has limited predictive power. On a continental scale, however, climate and hydrographic densities vary greatly, and may therefore predict habitat suitability better (Torres *et al.* 2012). In local studies (e.g., by telemetry), one can also expect occurrences to be concentrated near streams, since individuals will frequently visit these sites (Hatten *et al.* 2005, Sollmann *et al.* 2008). At our scale of analysis, regions with small cattle ranching have higher likelihoods of jaguar presence than those with crop farming as the predominant land use following deforestation. As widely reported, jaguars are attracted by cattle for food, which is documented by the high persecution pressure of landholders in the ‘arc of deforestation’ where non-native pasture is the primary land use (Silveira *et al.* 2008).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

FIGURE S1. Jaguar occurrence between 2005 and 2009 in the Cerrado and forest biomes of Mato Grosso, overlaid with deforestation in 2009.

FIGURE S2. Logistic regression (LR) model of Jaguar habitat suitability in Mato Grosso state.

TABLE S1. Spearman rank correlation between nine landscape metrics with significant ($P < 0.10$) predictive power in univariate LR models.

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