


Chapter 10

Using Camera-Trap Data to Simultaneously Estimate Jaguar (*Panthera onca*) Density and Resource Selection in the Paraguayan Dry Chaco



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Abstract Habitat loss and human-caused mortality have led to an approximate 50% reduction of the distribution of the jaguar (*Panthera onca*). The large contraction in the jaguar's occurrence points to a need to understand its population size and habitat preferences to apply to the species' conservation. Typically, jaguar densities are estimated with capture–recapture modeling of photographic captures of individually identifiable individuals, while habitat selection is estimated from telemetry data. However, advances in spatial capture-recapture modeling now permit the simultaneous estimation of density and habitat selection based solely upon photographic detection data from camera-trapping grids. Here, we used data from 356 double camera-trap stations across five sites in the Paraguayan Dry Chaco to simultaneously estimate jaguar density and resource selection. We found that jaguar densities ranged from 0.58 to 1.39 individuals/100 km². At the spatial scale of our analysis, jaguars showed a strong preference for forest cover, while space use was not affected by the Human Footprint Index. Our density estimates were consistent with previous estimates based upon a subset of our data, as well as with estimates for jaguar populations in other dryland ecosystems. Furthermore, the strong selection for forest was also consistent with range-wide patterns in jaguar space use and habitat selection derived from telemetry data. Due to extensive and ongoing deforestation in the Dry

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Chaco, combined with high human-caused mortality, the jaguar is critically endangered in Paraguay. Although we show that jaguars can persist in anthropogenically altered landscapes in Paraguay, their long-term survival at the national level is strongly dependent upon the effective enforcement of the national jaguar conservation law, and application of the national jaguar management plan, to mitigate negative population effects from habitat loss and human-caused mortality.

Keywords Dry Chaco · Jaguar · Medanos · Paraguay · Resource selection · Spatial capture-recapture

10.1 Introduction

Apex predators are often used as conservation surrogates as they may play important roles in affecting ecosystem function and serve as bioindicators (Sergio et al. 2008). In the Neotropics, the occurrence of the jaguar (*Panthera onca*), the largest felid in the Americas, is associated with high levels of biodiversity, the provision of multiple ecosystem services, and consequently serves as an indicator of the conservation value of landscapes (Thornton et al. 2016; Burke et al. 2019). Since the jaguar is a forest-associated species throughout its range and across ecosystems types, and is sensitive to landscape-scale anthropogenic factors (Morato et al. 2018; Alvarenga et al. 2021; Thompson et al. 2021), it is a logical species to be used to examine the ecological effects of forest loss and other landscape-scale anthropogenic factors. However, the jaguar's distribution has been reduced by about 50% range-wide and by 80% outside of Amazonia due to habitat loss and human–jaguar conflict driven persecution (de la Torre et al. 2018). This reduction in distribution indicates an important need to understand the effects of habitat loss and degradation on jaguar populations, the implications for their conservation, and in turn the ecosystem services with which they are associated.

Within the jaguar's distribution, habitat conversion from expanding agricultural production has been acute during the last 20 years in dry forest and savanna systems in southern South America, particularly in the Dry Chaco of Argentina, Bolivia, and Paraguay which has undergone some of the highest rates of forest loss in the world (Curtis et al. 2018; Zalles et al. 2021; Da Ponte et al. 2021; Buchadas et al. 2022). Despite its high levels of habitat loss and often high levels of biodiversity, the Dry Chaco receives relatively little attention from the global conservation community due to a strong focus upon tropical humid systems (Redford et al. 1990; Kuemmerle et al. 2017; Qin et al. 2022). This pattern was discussed by Redford et al. (1990) who, in referring to the Dry Chaco, pointed out that “the attention to rainforest has acted like blinders” and “The concentration on rainforests, and the rhetoric that accompanies it, has led to the neglect of other severely threatened ecosystems.”

The statements of Redford et al. (1990) were prescient as they foresaw the forthcoming deforestation in the Dry Chaco and its implications for conservation that were to occur during the twenty-first century. However, in recent years, there has been an increasing amount of research on the effects of deforestation on multiple



Fig. 10.1 Camera-trap record of Jaguar (*Panthera onca*) in the Paraguayan Medanos

taxa and communities in the Dry Chaco (Periago et al. 2014; Cartes et al. 2015; Núñez-Regueiro et al. 2015; Semper-Pascual et al. 2018, 2020; Camino et al. 2020, 2022; de la Sancha et al. 2021), including the jaguar (Fig. 10.1) (Altrichter et al. 2006; Noss et al. 2012; Quiroga et al. 2014; Thompson and Velilla 2017; McBride and Thompson 2018; Romero-Muñoz et al. 2019; Thompson et al. 2020, 2021, 2022). Importantly, for the jaguar, although forest availability is key, it is not the sole factor determining jaguar occurrence in the Dry Chaco. Anthropogenic factors have a disproportionately strong negative influence on jaguar occurrence despite sufficient habitat and prey availability (Quiroga et al. 2014; McBride and Thompson 2018; Romero-Muñoz et al. 2019, 2020; Thompson et al. 2020). Consequently, evaluating the relative importance of both environmental and anthropogenic factors on jaguar density and habitat use is a necessary precursor to understand how deforestation in the Dry Chaco is affecting the jaguar population.

Advances in spatial capture–recapture (SCR) modeling allow for the simultaneous estimation of density, habitat selection, and connectivity (Royle et al. 2013b; Sutherland et al. 2015; Morin et al. 2017), providing a powerful framework to integrate population and landscape ecology (Royle et al. 2018). We previously took advantage of this framework and found that jaguar density and landscape connectivity in the Paraguayan Dry Chaco were negatively affected by increases in deforestation within landscapes (Thompson et al. 2022), which was consistent with expectations based upon patterns in jaguar space use (Thompson et al. 2021). Furthermore, we illustrated the importance and value of accounting for potential bias stemming from habitat-driven space use by jaguars when estimating density in a spatial capture–recapture modeling framework (Thompson et al. 2022).

Historically, the movements of animals within their home range (third-order habitat selection; Johnson 1980), and the drivers of those movements (Manly et al. 2002), have typically been estimated using telemetry data. However, SCR modeling has been extended to estimate resource selection by taking advantage of the spatial information provided by spatial recaptures of individuals (Royle et al. 2013b;

Sollmann et al. 2016; Linden et al. 2018). This advance consequently allows for the estimation of habitat use within activity areas using Resource Selection Functions (RSF; Manly et al. 2002) based solely upon spatial capture-recapture data, while allowing to simultaneously estimate density (Royle et al. 2013b).

We took advantage of the capabilities of SCR modeling to include RSFs to simultaneously estimate habitat selection within activity areas and density of jaguars in the Paraguayan Dry Chaco. This allowed us to explore how jaguar space use was affected by forest availability and landscape-scale anthropogenic factors across landscapes with differing intensities of forest conversion. Our sampling areas included landscapes with varying levels of deforestation, as well as the Medanos, a mixed matorral – savanna – forest system within the Bolivian–Paraguayan Dry Chaco, where in Paraguay jaguars have yet to be studied. Recognizing that jaguars demonstrate a general preference for forest cover, avoidance of pastures, reduced occurrence in response to anthropogenic factors, and in the Paraguayan Dry Chaco reduced densities in relation to deforestation (Morato et al. 2018; Thompson et al. 2020, 2021, 2022; Alvarenga et al. 2021), we expected that (1) within their activity areas, jaguars will select forest regardless if the heterogeneity in forest availability was natural or due to deforestation, while (2) areas with higher anthropogenic impacts will be avoided. Furthermore, we intended to show the capabilities of SCR modeling to expand its utility beyond density estimation to address key conservation questions, such as resource selection, solely from camera-trap-based capture–recapture data.

10.2 Methods

10.2.1 Study Site

The Dry Chaco extends across $\sim 787,000$ km² in parts of Argentina (62%), Paraguay (22%), and Bolivia (16%) and is the largest subtropical dry forest system in the world (Olson et al. 2001). The Dry Chaco is a global deforestation hotspot, whereby ranching and row crop agriculture have driven the deforestation of about 27% of the ecoregion's forest (Caldas et al. 2015; Da Ponte et al. 2021; Hansen et al. 2013; Vallejos et al. 2015). In Paraguay, 64,000–77,000 km² ($\sim 45\%$) of its Dry Chaco forest area was lost by 2020, mostly due to pasture creation for cattle raising, equating to an annual forest transformation rate of about 4% or ~ 500 ha/day/year since 2000 (Fig. 10.2; Hansen et al. 2013; Caldas et al. 2015; Vallejos et al. 2015; Baumann et al. 2017; Da Ponte et al. 2021). Importantly, from a conservation perspective, the forest loss during the past two decades has occurred in wilderness areas of high conservation value, so that since 2000 the area of intact forest landscapes in the Paraguayan Dry Chaco has decreased by 76% (Watson et al. 2018; Williams et al. 2020).

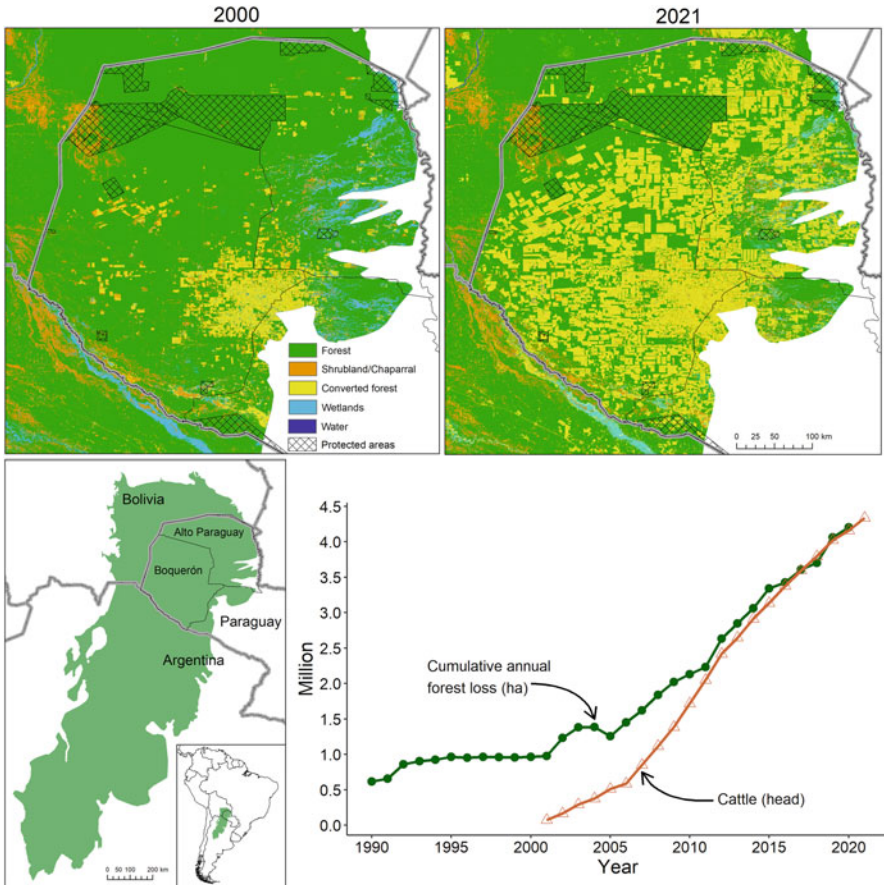


Fig. 10.2 Location of the Dry Chaco within South America and land cover and protected areas in the Paraguayan Dry Chaco for the years 2000 and 2021. The graph shows the cumulative annual forest loss and cattle population from 1990 to 2021 for the Paraguayan departments of Alto Paraguay and Boquerón, which encompass the large majority of the Dry Chaco in Paraguay. (Data from: <https://www.senacsa.gov.py/index.php/informacion-publica/estadistica-pecuaria>)

10.2.2 Camera-Trap Sampling

During the austral fall to winter (May–September) 2016–2018, we employed camera-trap sampling at four sites with semideciduous xeric forest in the Dry Chaco (Mereles 2005; Mereles et al. 2019) along a gradient of deforestation intensity ranging from 17% to 51% deforested. We employed 335 double camera-trap stations located on roads, firebreaks, or along fence lines (Fig. 10.3, Table 10.1; Thompson et al. 2022). Additionally, during 2018 we also sampled a site in the Medanos within the Dry Chaco, a matorral – savanna system interspersed with xeric forest (Mereles 2005; Mereles et al. 2019) which previously had not been sampled for jaguars in Paraguay (Fig. 10.3, Table 10.1). The initial four sampling sites were all located on

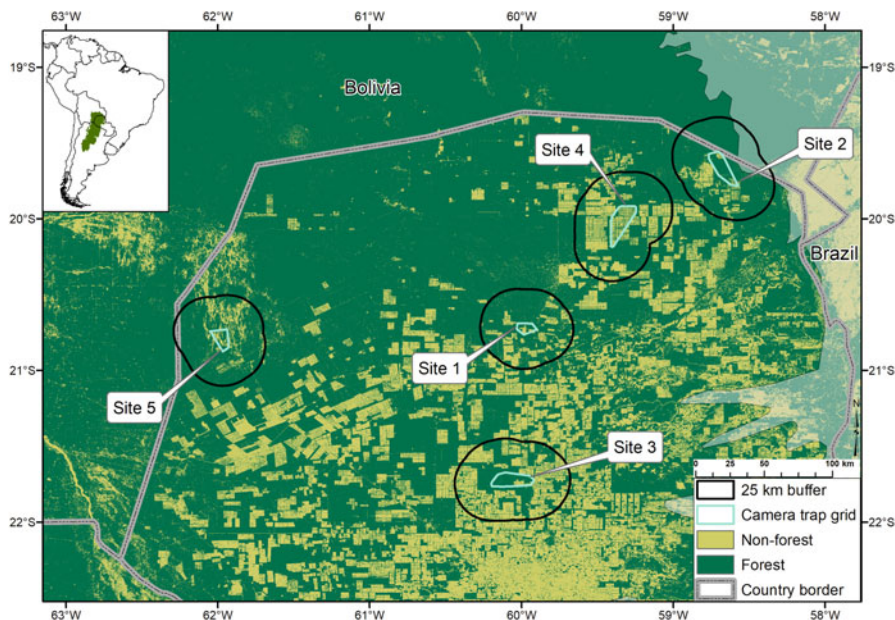


Fig. 10.3 Locations of camera-trap grids and their 25 km buffers in the Paraguayan Dry Chaco (Olson et al. 2001) in relation to forest cover in 2017 (Hansen et al. 2013). Shaded areas are outside the limit of the Dry Chaco. Inset shows the location of the Dry Chaco within South America

private ranchlands and the site in the Medanos was on a private protected area and adjoining indigenous land.

Sampling periods ranged from 98 to 279 days, with a mean of 100 operational days per station per site (Table 10.1). The site with the longest sampling period (Site 4) resulted from its sampling grid being divided into two temporally overlapping sections (48 and 27 stations). The long sampling periods were justifiable to increase detections (Dupont et al. 2019; Tobler and Powell 2013), while we see no reason to expect any effect on density as a function of sampling year as there were no abnormal differences in temperature or precipitation among the 2016–2018 sampling periods (www.meteorologia.gov.py). Moreover, in our analysis we accounted for potential site-specific differences in detectability and space use (see Data analysis).

Minimum convex polygons of our trapping grids ranged between 80 and 282 km² and, as discussed by Thompson et al. (2022), were sufficiently large related to jaguar activity areas to minimize bias in density estimates (Sollmann et al. 2011; Tobler and Powell 2013). We defined our modeling state space with a 25-km buffer around our trapping grids (see Data analysis), with our initial four sampling sites having a proportional area deforested ranging from 17% to 51% (Hansen et al. 2013). At the fifth site in the Medanos, the majority of unforested land was naturally occurring matorral with some deforested areas, so 18% of the modeled state space did not include forest (Fig. 10.3, Table 10.1).

Table 10.1 Site-specific sampling characteristics of camera-trap grids in the Paraguayan Dry Chaco, including sex-specific number of individuals captured and recaptured (n), count of total captures, and count of spatial recaptures per site

Site	% area in forest	Mean HFI ^a	Number of sampling stations	Trap days	Mean operational days/station	Females				Males			
						Total captures		Spatial recaptures		Total captures		Spatial recaptures	
						n	Count	n	Count	n	Count	n	Count
1	73	236	86	9712	113	4	39	3	31	8	152	7	85
2	83	60	62	4038	65	4	38	4	17	9	47	4	29
3	49	428	112	12,552	112	4	100	4	47	2	97	2	50
4	59	262	75	8554	114	5	18	4	14	4	71	4	24
5	82	169	21	2037	97	3	17	3	13	6	56	4	25

^aHFI Human Footprint Index

10.2.3 Data Analysis

We used spatial capture-recapture modeling framework incorporating resource selection (hereafter SCR–RS) to explore the effect of forest cover and anthropogenic pressures on jaguar resource selection while simultaneously estimating jaguar densities (Royle et al. 2013b; Sollmann et al. 2016). The SCR–RS modeling framework accommodates resource selection models by incorporating the resource selection information spatially inherent in camera-trapping data. This permits the estimation of resource selection parameters while relaxing the assumption of symmetrical distance in the SCR detection function, allowing for space use to be a function of differential habitat preferences. Apart from being able to estimate third-order habitat use directly from camera-trap data, accounting for habitat-driven differences in space use reduces bias in detectability when estimating density (Royle et al. 2013b). We considered this important given the preferred use of the forest by jaguars (Alvarenga et al. 2021; Morato et al. 2018; Thompson et al. 2021), and previous modeling of a subset of our data which demonstrated the importance of accounting for asymmetrical space use when estimating jaguar density in fragmented Dry Chaco forest (Thompson et al. 2022).

Using the photographic captures from our sampling we developed individual daily encounter histories for jaguars by assigning jaguar photographs to each sampling station by date and individual. Jaguars were identified by their spot patterns and sexed by genitalia, with juveniles accompanied by their mother excluded from the data set. Using these spatial encounter histories, we estimated densities for each site in a multisite (multisession) model in R (R Core Team 2019) using the *oSCR* package (Sutherland et al. 2015) with a state space delimited by a 25-km buffer from traps at a resolution of 1 km. Although in previous modeling of a subset of our data a resolution of 2 km was used (Thompson et al. 2022), we found that estimates were sensitive to resolutions greater than 1 km, which we attribute to the fine-grain nature of habitat heterogeneity in the additional site from the Medanos. Since jaguars in the Paraguayan Dry Chaco can move more than 14 km per day on average (McBride and Thompson 2018; Thompson et al. 2021) a 1 km resolution is consistent with the scale of jaguar space use in our study areas.

As in Thompson et al. (2022), we used the mean proportional area of forest as a biologically relevant metric to characterize forest availability. We developed maps of forest occurrence from 1 arc-second spatial data on forest canopy density corresponding to the year of our sampling (Hansen et al. 2013), classifying all areas with a forest canopy density of $\geq 15\%$ as forest (based upon ground truthing and our familiarity with the study system), and then deriving the mean proportional forest area for each grid cell of our 1 km resolution state space. To quantify anthropogenic influences within our state spaces we used the Human Footprint Index (HFI) (Sanderson et al. 2002; Venter et al. 2016; [wchumanfootprint.org](http://www.worldpop.org)), taking the average value at the 1 km resolution for the year corresponding to the beginning of sampling for each site.

We tested a set of models that evaluated the probability of space use as a function of the proportional forest area and the HFI, additively or separately. Models always included a site (session) effect on density, to meet closure assumptions, and on σ (scale parameter of decline in p with distance) and detection (p) to account for potential differences in space use and detection, respectively among sites. The scale parameter σ describes the rate that the probability of detection (p) decreases with distance from the estimated activity center of individuals, whereby p_0 is the baseline detection probability at an individual's activity center. We also evaluated the effect of sex on σ and p_0 . Model selection was based on rankings of Akaike Information Criteria (AIC) weights (Burnham and Anderson 2002). Since AIC has a tendency to select models with uninformative parameters with no ecological effects that do not reduce AIC but increase model complexity (Burnham and Anderson 2002; Arnold 2010), we excluded models with uninformative parameters from the final model set (Arnold 2010). A parameter was considered uninformative when its significance level was $<85\%$ since the effect of such parameters is insufficient to warrant their inclusion in a model (Arnold 2010).

Similar to Sollmann et al. (2016), we used linear discriminant analysis (Manly and Alberto 2016) to evaluate how modeling state spaces differ in anthropogenic and environmental characteristics to potentially explain the difference in jaguar densities among sites. We examined differences in proportional forest area, HFI, estimated net primary productivity (Zhao et al. 2005), and estimated mean annual precipitation along with its coefficient of variation (Fick and Hijmans 2017), using the mean values at the 1 km resolution of the modeling state spaces. We evaluated correlations among covariates from the discriminant functions that explained at least 95% of the between-group variance. We considered a strong correlation between covariables where coefficients were ≥ 0.7 and a p -value <0.05 . The linear discriminant analysis was undertaken in R using the *MASS* package (Venables and Ripley 2002).

10.3 Results

We detected between 6 and 13 individual jaguars per site. One GPS collared individual from site 3 was censored because it was killed after moving outside our sampling area. The total number of recaptures per site ranged from 73 to 197 and the total spatial recaptures per site ranged from 38 to 116 (Table 10.1). Of the models evaluated, three contained 100% of the model weights, with the model including the effect of forest cover on resource selection, and no sex effect on detection probability (p_0) or on the spatial scale factor (σ); being the highest ranked supported by 53% of model weights (Table 10.2). This model indicated a preference by jaguars for areas with increasing proportional forest cover ($\alpha = 1.31$, SE = 0.2; Table 10.3). The other two models included an uninformative parameter for the sex (-0.18 , SE = 0.21) on detection probability (p_0) or HFI ($\alpha = 0.06$, SE = 0.29) on resource selection and consequently were excluded. Based upon the best supported model, density estimates ranged from 0.58 to 1.39 individuals/100 km² and fully forested areas were

Table 10.2 Top-ranking spatial capture–recapture models from the examined model set based upon the covariates used in the resource selection component of the capture–recapture model

Model	K	AIC	ΔAIC	weight
Forest cover	21	2543.87	0.00	0.53
Forest cover + sex	22	2545.15	1.28	0.28
Forest cover + HFI	22	2545.83	1.96	0.19

All models evaluated included the effect of site on density, detection, and σ (scale parameter of decline in detectability (p) with distance)

Table 10.3 Parameter estimates, standard errors (SE), and lower (95 L) and upper (95 U) 95% confidence intervals from the top ranked model

Parameter	Estimate	SE	95 L	95 U
p_0 (intercept)	−0.32	0.31	−0.93	0.29
p_0 (site 2)	−0.16	0.40	−0.94	0.62
p_0 (site 3)	−0.08	0.26	−0.59	0.43
p_0 (site 4)	−0.75	0.49	−1.71	0.21
p_0 (site 5)	−0.52	0.32	−1.15	0.11
σ (intercept)	8.50	0.12	8.26	8.74
σ (site 2)	−0.31	0.16	−0.62	0.00
σ (site 3)	−0.40	0.13	−0.65	−0.15
σ (site 4)	−0.11	0.15	−0.40	0.18
σ (site 5)	0.13	0.20	−0.26	0.52
α (forest cover)	1.31	0.20	0.91	1.69
D (intercept)	−4.50	0.36	−5.21	−3.79
D (site 2)	0.25	0.48	−0.69	1.19
D (site 3)	−0.55	0.55	−1.63	0.53
D (site 4)	−0.62	0.50	−1.60	0.36
D (site 5)	−0.58	0.55	−1.66	0.50
Ψ (site 1)	0.69	0.61	−0.51	1.89
Ψ (site 2)	0.81	0.60	−0.37	1.99
Ψ (site 3)	−0.69	0.87	−2.40	1.02
Ψ (site 4)	−0.22	0.67	−1.53	1.09
Ψ (site 5)	0.51	0.73	−0.92	1.94

D and σ are on the log scale and relate to density per grid cell and km, respectively. p_0 , α (Forest cover), and ψ , the baseline detectability probability, coefficient on space use for proportional forest cover, and probability of being a male, respectively, are on the logit scale

estimated to be used 3.7 times more than completely deforested areas (Fig. 10.4). Baseline detectability at the mean forest cover value from each site was estimated to be between 62% and 80% (Table 10.4). Estimates of σ ranged from 3.3 to 5.6 km and sex ratio estimates had high uncertainty, but the estimated probability of being a male varied from 33% to 67% across sites (Table 10.4).

The first two discriminant functions of the habitat analysis explained 98.19% of the between-group variance among the five state spaces. The first discriminant function of the habitat analysis explained 84.07% of the between-group variance

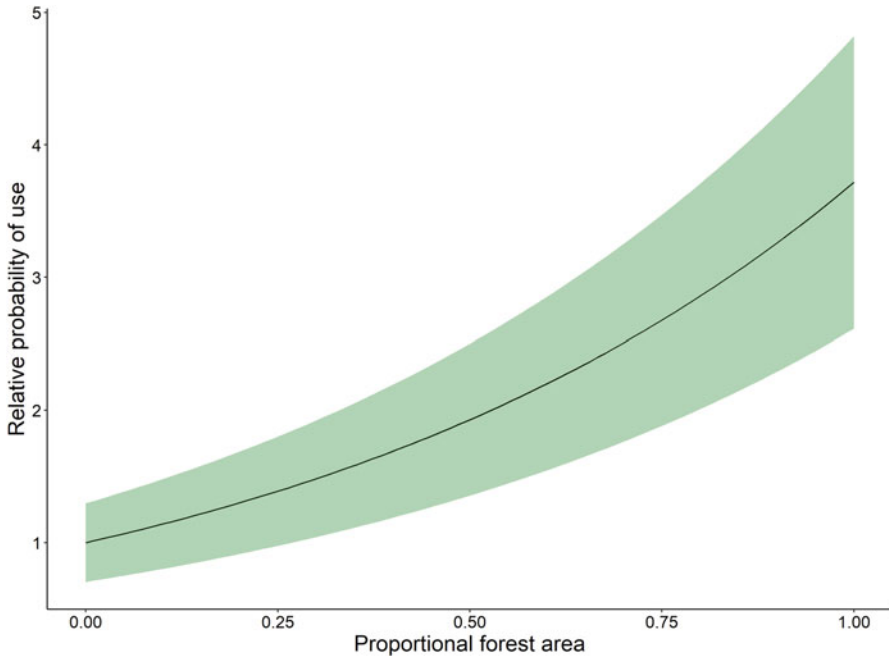


Fig. 10.4 Prediction of relative probability of site use by jaguars as a function of proportional forest area. Shaded area represents the 95% confidence interval

and was strongly negatively correlated with the coefficient of variance of annual precipitation and strongly positively correlated with mean annual precipitation (Table 10.5). The second discriminant function explained 14.12% of the variance between sites, with no strong correlations with covariates; however, net primary productivity showed a moderate correlation (Table 10.5). The effect of mean annual precipitation and its coefficient of variation grouped Sites 1–4 together, albeit with some among-site differences, while Site 5 from the Medanos was distinctly separated from the other sites (Fig. 10.5).

10.4 Discussion

By using the capacity of the SCR–RS model to estimate resource selection we further confirm the importance of forest cover for jaguars documented both range-wide (Morato et al. 2018; Thompson et al. 2021) and in the Dry Chaco (Romero-Muñoz et al. 2019; Thompson et al. 2022). We found strong third-order habitat selection for forested areas by jaguars in the Paraguayan Dry Chaco. Importantly, this relationship was evident in areas with forest fragmented through deforestation or naturally heterogeneous as in the matorral – savanna – forest system of the Medanos.

Table 10.4 Estimates and 95% confidence intervals (CI) from the best supported model for density, baseline detectability with the mean forest cover for each site (p_0 (mean forest cover)), scale parameter (σ) and sex ratio (expressed as the probability of an individual being a male)

Site	Density (individuals/100 km ²)		Detectability (p_0 (mean forest cover))		σ (km)		Sex ratio (probability of being a male)	
	Estimate	95% CI	estimate	95% CI	Estimate	95% CI	Estimate	95% CI
1	1.08	0.54–2.20	0.69	0.59–0.78	5.0	3.9–6.2	0.67	0.38–0.87
2	1.39	0.74–2.60	0.68	0.53–0.80	3.6	2.9–4.5	0.69	0.41–0.88
3	0.63	0.29–1.40	0.62	0.57–0.67	3.3	3.0–3.7	0.33	0.09–0.73
4	0.58	0.20–1.14	0.79	0.62–0.89	4.6	3.8–5.3	0.44	0.18–0.75
5	0.61	0.27–1.38	0.80	0.72–0.86	5.6	4.1–7.8	0.63	0.28–0.88

Table 10.5 Results of the functions of the linear discriminant analysis of landscape covariates for the five modeling state spaces in the Paraguayan Dry Chaco

	LD1	LD2	LD3	LD4
Landscape characteristic	<i>84.07</i>	<i>14.12</i>	<i>1.55</i>	<i>0.26</i>
Proportional forest area	-0.020 (0.008)	0.268 (<0.001)	0.038 (<0.001)	0.880 (<0.001)
Human footprint index	-0.068 (<0.001)	-0.387 (<0.001)	-0.201 (<0.001)	-0.702 (<0.001)
Net primary productivity	0.266 (<0.001)	0.649 (<0.001)	0.635 (<0.001)	-0.292 (<0.001)
Mean annual precipitation	0.974 (<0.001)	0.219 (<0.001)	-0.047 (<0.001)	-0.004 (<0.001)
Coefficient of variation mean annual precipitation	-0.943 (<0.001)	0.331 (<0.001)	-0.054 (<0.001)	0.002 (0.760)

Values in italics associated with the linear discriminant functions (LD) are the percentage of between-state space variance explained by each function, while column values are Pearson correlation coefficients and associated *p*-values (in parentheses) for the correlation of the discriminant function with each landscape covariate

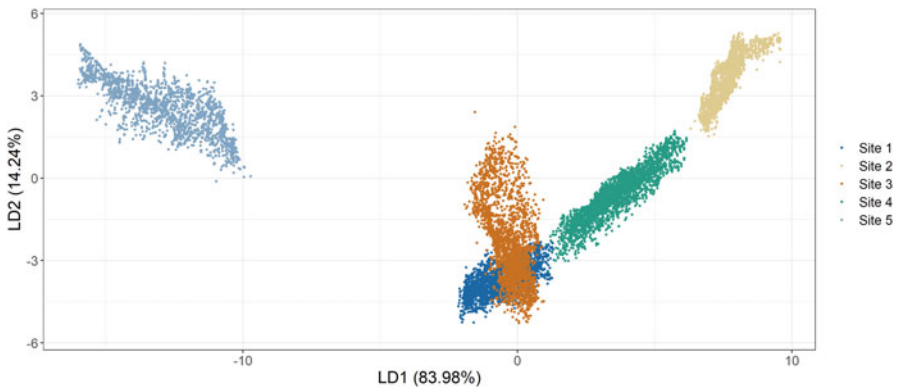


Fig. 10.5 Plot of the first and second linear discriminant functions for the habitat covariables from the spatial capture-recapture modeling state spaces. The first discriminant function was strongly negatively correlated with the coefficient of variation of annual precipitation and strongly positively correlated with mean annual precipitation. The second discriminant function only had a moderate positive correlation with net primary productivity

At the same time, we found no avoidance of anthropogenic factors represented by the HFI. Given the known negative relationship of anthropogenic factors on the occurrence and density of jaguars in the Dry Chaco (McBride and Thompson 2018; Romero-Muñoz et al. 2019; Thompson et al. 2020, 2022) this was unexpected and is likely due to the spatial scale of the HFI, or the information comprising the HFI, not capturing the relevant effects of jaguar space use.

Previously, in four of our five sites a negative relationship of deforestation on jaguar density was shown between the most and least deforested sites, as well as a strong negative effect of deforestation on population connectivity (Thompson et al.

2022). However, with the inclusion of the naturally heterogeneous site from the Medanos (Site 5), this relationship was not evident as its estimated density was similar to the most deforested of our sites (Sites 3 and 4). Nor did the linear discriminant analysis find a strong difference in net primary productivity among sites, which has been shown to decrease jaguar spatial needs, and in turn lead to increased density (Thompson et al. 2021). However, the analysis did show that the site from the Medanos (Site 5) received less, and much more variable, precipitation than the other sites. This suggests that the intra- and interannual variability of water is an important driver in limiting jaguar density in the Medanos despite ample forest cover and relatively low anthropogenic pressures. As our study areas are at the arid extreme of the jaguar habitat, and our density estimates are consistent with those from protected areas in other dryland systems with high variability in precipitation (Sollmann et al. 2011, 2013; Noss et al. 2012; Gutiérrez-González et al. 2015; Finnegan et al. 2020), our results provide valuable inferences on habitat needs for the conservation of jaguar in arid systems throughout its range and in support of potential reintroduction efforts for jaguars in arid systems such as in the southwestern United States (Sanderson et al. 2021, 2022).

We found no sex effect on either detectability or σ which was consistent with previous modeling that included our data (Thompson et al. 2022), but unexpected compared to general patterns in estimates of jaguar space use from spatial capture–recapture modeling and telemetry data (Sollmann et al. 2011; Tobler et al. 2013, 2018; Boron et al. 2016; Morato et al. 2016; Alvarenga et al. 2021; Thompson et al. 2021). Differences in sex ratios among sites may cause abundance related effects on detectability by sex which collectively offset the effect of sex on detection since both males and females were detected more frequently dependent upon the site (Table 10.1).

We note that our estimates of σ were larger than previous estimates (Thompson et al. 2022) for sites 1–4 which we attribute to differences in the modeling framework, whereby Thompson et al. (2022) explicitly modeled asymmetrical, non-Euclidean space use and connectivity as a function of forest cover, and here we used SCR–RS to estimate habitat driven differences in space use within activity areas. Regardless, both modeling approaches generated similar density estimates, while showing the importance of forest cover for jaguars from different perspectives while reducing potential bias by accounting for asymmetrical space use (Royle et al. 2013a, b; Sutherland et al. 2015).

Although we show a strong selection for forest cover by jaguars, anthropogenic factors negatively affect jaguar survival and occurrence in the Dry Chaco, driving complex source–sink dynamics (McBride and Thompson 2018; Romero-Muñoz et al. 2019, 2020; Thompson et al. 2020). The large movements of jaguars and the maintenance of connectivity in relation to forest loss (McBride and Thompson 2018; Thompson et al. 2021), suggest that the sites with high levels of forest loss are population sinks, with their populations being maintained by immigration (Romero-Muñoz et al. 2019; Thompson et al. 2022). This highlights the importance of considering anthropogenic effects on jaguar occurrence in the Dry Chaco which is further evident in the functional extinction of the jaguar in the Argentine Dry Chaco

despite high forest cover and sufficient prey availability (Quiroga et al. 2014; Thompson et al. 2020).

Consequently, our results may not be fully representative of the population trajectory in our study sites. Our sites could be demonstrating extinction debt, whereby individual longevity and immigration are masking negative population trends (Tilman and Lehman 1994; Semper-Pascual et al. 2018; Romero-Muñoz et al. 2019; Thompson et al. 2022). For example, despite similar estimates of density, as well as similarities in anthropogenic influences, the status of the jaguar populations in the more deforested sites (Sites 3 and 4) and in the Medanos (Site 5) is not clear based solely on density estimates. This illustrates the limitations of static estimates of density for conservation evaluations, highlighting the need for long-term studies to quantify survival, recruitment, and immigration to characterize the conservation value of the various landscapes for jaguars (Harihar et al. 2020).

The high rate of forest loss in the Paraguayan Dry Chaco is not only a concern for the conservation of the jaguar, but raises concerns for other forest dependent and endemic species in the Dry Chaco (Romero-Muñoz et al. 2020) such as the Chacoan peccary (*Catagonus wagneri*), Quebracho crested tinamou (*Eudromia formosa*), and Chacoan naked-tailed armadillo (*Cabassous chacoensis*). Furthermore, the forest loss in the Paraguayan Dry Chaco, apart from generating important concerns for biological conservation, has additional cultural and human rights implications as the Paraguayan Dry Chaco is the ancestral lands of multiple indigenous peoples, including the Ayoreo Totobiegosode, the last indigenous peoples outside of the Amazon Basin with members living in isolation (DGECC 2004).

Considering the jaguar's effective role as an umbrella and flagship for biodiversity conservation (Thornton et al. 2016), its conservation, which is dependent upon forest conservation and the fostering of coexistence, has significant ecological and cultural implications (United Nations Development Program et al. 2019). However, within Paraguay, the jaguar is listed as critically endangered due to continuing high rates of habitat loss and direct human-caused mortality (Giordano et al. 2017), pointing to the urgent need for the Paraguayan government to better implement the national jaguar conservation plan (Secretaría del Ambiente et al. 2016) and national jaguar conservation law (Congreso de la Nación Paraguaya 2014) to ensure the long-term survival of the species and the services that it provides.

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