Title: Jaguar density in the Argentine Yungas: overcoming camera trap failure

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Author contributions

Conception and design of the study: PGP, CS-Z; securing funding and managing project PGP, CS-Z; data collection: JIR, PGP, FC, GAEC, SdB, JPA; data organization, animal identification: JIR, PGP; data analysis: JIR; writing first draft: JIR, PGP, CS-Z. comments on the manuscript: all authors

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Declarations

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Abstract

The Yungas ecoregion supports an important jaguar population, of particular conservation relevance due to its location in the extreme SW of the species distribution, with potential for range extension and population recovery. Detailed population estimates are lacking. To evaluate jaguar density in the Argentine Yungas we conducted a camera trap survey in Baritú National Park and surrounding private lands. We deployed 32 sampling stations with a pair of camera traps each, obtaining a sampling effort of 2,080 trap/nights. Camera malfunction translated in several individual jaguars' photo-captured only from one side, thus preventing unequivocal identification to apply traditional spatially explicit capture-recapture models. We used 2-flank SPIM, a partial identity spatially explicit capture-recapture model, we estimated a density of 0.75 jaguars per 100 km^2, with a probability of detecting one side and both sides of 0.01 and 0.02 respectively. Our density estimates are low, but within the range of other studies, especially those on the fringes of the species distribution. This study offers as a baseline for a monitoring programme, much needed in a priority jaguar population.

Keywords: 2-flank SPIM, abundance, Argentina, population, spatial capture recapture

Introduction

Large carnivores play an important role in ecosystem functioning, but unfortunately their populations are often declining and retracting (Ripple et al. 2014; Wolf and Ripple 2017), which renders their population assessment and monitoring particularly relevant, particularly in key areas on their distribution (Karanth 2016). Studying classic large carnivore parameters such as abundance, density, and distribution are important to produce sound management plans and guide conservation actions. Moreover, monitoring these parameters over time enables a better understanding of a species response to environmental changes (Thompson et al. 1998; O'Brian 2011).

Jaguars (*Panthera onca*) are typically solitary, although they can tolerate other individuals at high densities (Nowell and Jackson 1996; Cavalcanti and Gese 2009). Given their wide distribution, from Arizona in the US to northern Argentina, jaguars present high variability in size (Nowell and Jackson 1996), home range (Quigley et al. 2017), food habits (de Oliveira 2002), habitat preferences (Morato et al. 2018), activity patterns (Harmsen et al. 2010), social interactions and space use (Cavalcanti and Gese 2009).

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Despite jaguars being legally protected their populations are declining in most of their range. They are listed by the IUCN as Near Threatened (Quigley et al 2017), threatened by habitat loss and fragmentation, retaliatory killing, poaching associated with the illegal trade of body parts (Di Bitetti et al. 2016; de la Torre et al. 2017; Quigley et al. 2017; Fraser 2018) and competition for wild meat with humans (Perovic 2002; Foster et al. 2014). In Argentina jaguars are listed as Critically Endangered (Paviolo et al. 2019) and provide one of the most severe examples of range decline, with a 95% reduction in their historical range (Di Bitetti et al. 2016). They persist in three regions of Argentina; the Chaco region adjacent to Bolivia and Paraguay, with very few recent records despite extensive survey efforts (Quiroga et al. 2014), the Atlantic Forest in the border with Brazil and Paraguay with low estimated density (Paviolo et al. 2008; Di Bitetti et al. 2016), high fragmentation and an estimated high extinction probability in the next 50 years (Bertrand et al. 2011). This region has been the focus of most research and conservation efforts in Argentina in the last few years. The Yungas ecoregion is comparatively less fragmented, and assumed to support the largest jaguar population in the country (Perovic et al. 2015; Di Bitetti et al. 2016), but to date there are no quantitative surveys to support this assumption.

The main threats to jaguars in the Argentine Yungas are large-scale deforestation, poaching, linear infrastructures, extensive livestock farming, selective logging, and wildfires (Perovic et al. 2015). Although the ecology of Yungas jaguars is poorly known (Perovic et al. 2015), due to its location in the extreme of their distribution we would expect low population numbers (Brown 1984) and larger home ranges (Lindstedt et al. 1986; Huggett 2004).

Jaguars, in common with other large felids, are highly mobile and elusive, thus difficult to detect. Camera trapping offers a suitable method to study jaguars (Tobler et al. 2008), especially in combination with modern capture-recapture analytical approaches that enable the relaxation of some traditional assumptions (Foster and Harmsen 2012; Tobler and Powell 2013). To contribute to the understanding and eventual monitoring of jaguars in the Argentine Yungas we carried out camera trap surveys in and around Baritú National Park and used the identities of photographed jaguars to estimate population density.

Methods

Study area. —We conducted the survey in a portion of the Yungas or Subtropical Mountain Forest ecoregion in Salta, northwest Argentina. Climate is subtropical with a dry season, yearly rainfall of 1,000-1,500mm, with fog

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adding an important water supplement (Brown et al. 2001). Three forest floors are present along an altitudinal gradient, namely the Piedmont Forest (between 400-700m *a.s.l.*) - the most degraded because the topography allows easy access and use for crops and intensive logging; the Montane Forest (700-1,500m *a.s.l.*) representing the largest extension of Yungas; and the Upper Montane Forest (1,500-3,000m *a.s.l.*) characterized by dense fog and alternating forest with grasslands (Cabrera 1976; Brown et al. 2001).

The survey covered part of Baritú National Park encompassing 724 km^2 of Yungas Forest, with an elevation ranging from 650-2,000m and private surrounding lands (Fig. 1). The park has little infrastructure and human use is concentrated in the northwest, on the east, where the park borders with Bolivia there are major agricultural developments, small towns and a paved road. The surrounding private lands are used for cattle rising, with human presence characterized by small ranches, and secondary dirt roads.

Survey design. —We overlaid the study site with a 5×5 km grid and identified the center point within each cell to be a potential sampling station location. During September 2013, five teams installed cameras reaching locations on foot, some with great difficulty (up to 10 walking days). Each sampling station was installed within 800m from the potential location, choosing the site to maximize detection probability. Thirty-five sampling station were installed, all but two composed of two camera traps on each side of the expected animal trajectory (Fig. 1). Heat and motion, infrared-triggered cameras were used (mostly Bushnell Trophy Cam HD, Bushnell Corporation, Overland Park, Kansas and Reconyx HC500, Reconyx, Inc., Holmen, Wisconsin), set to take three pictures in each detection, 24h/day with a 3-min delay between exposures. We choose that relatively long period, to reduce the number of pictures of the same event in case of large herds, or animals staying for long time in front of the camera traps (very common with cattle). The average distance between the closest stations was 4.6 km (range=2.6-6.8). Around 60% of the survey area was located inside the protected area, and the remaining area was made up of privately owned land used for cattle grazing (Fig. 1).

Data analysis. —Due to the high rate of camera malfunction, that resulted in a low number of detections of both flanks in the same capture event, it was not possible to construct individual capture histories needed for traditional spatial capture-recapture analysis. Thus, we used a spatial partial identity model (2-flank SPIM, Augustine et al.

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2018). The 2-flank SPIM uses the spatial information associated with each detection to jointly model completely identified (photographed both sides) and partially identified captures (left-only or right-only photographs) while accounting for the uncertain identity of partial identity samples within a Spatial Capture-Recapture (SCR) framework (Borchers and Efford 2008; Royle and Young 2008; Royle et al. 2014). This model has been shown to perform better than other alternatives to deal with single-sided detections (Kalle et al. 2011; Nair et al. 2012; Augustine et al. 2018).

The 2-flank SPIM model detection process is the same as traditional SCR assuming a Gaussian Hazard detection function and with capture probabilities depending on the capture type and the number of camera traps on the sampling station. Activity centers are assumed to be distributed uniformly across a rectangular state space *S* according to $s_i \sim Uniform(S)$. A partially latent binomial capture process was assumed for each capture type, $Y_{ij}^{(m)} \; Binomial(K, p_{ij}^{(m)})$ being *K* the number of trapping occasions and $p_{ij}^{(m)}$ the capture probability of individual *i* at trap *j* on occasion *k* for event type m (both sides, left side or right side). Capture histories were augmented up to a large amount *M*, and using a partially latent indicator variable *z* to indicate which individuals are in the population $z_i \sim Bernoulli(\psi)$, and $N \sim Binomial(M, \psi)$, where N (population abundance) is derived using Markov Chain Monte Carlo (MCMC) methods by $N^{curr} = \sum_{i}^{M} z_i^{curr}$ and population density as $D^{curr} = N^{curr} / ¿|s| \vee ¿¿$.

Detection probability was considered equal for each detected side, therefore we set detection rates $\lambda_0^{(S)} := \lambda_0^{(R)} = \lambda_0^{(L)}$, where *S, R*, and *L* indicates a single side, right or left capture respectively. During MCMC sampling the identity of partially identified histories is swapped producing posterior distributions for the SCR accounting for uncertainty in individual identification. See Augustine et al. (2018) for a detailed formulation of the model.

2-flank SPIM model was fitted using the SPIM package (Augustine and Royle 2015) implemented in R (R. Development Core Team 2019). We ran one MCMC chains with 200K iterations, discarding the first 2K. In the SPIMs, we set the search radius to swap IDs to 35 km and the number of IDs swapped per iteration to 10, an augmentation of 140 histories, and created a state-space imposing a 25 km rectangular buffer around sampling

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station locations. To construct captures histories, we grouped eight consecutive capture days into each sampling occasion and built a matrix specifying individual ID, sampling occasion, trap ID and capture type (right, left, or both sides) for each jaguar detection. A *J* x *K* matrix (sampling station by sampling session) was constructed with entries indicating the sampling station status on each sampling session (2 = both cameras active, 1 = one camera active, 0 = both cameras inactive). Assuming a bivariate normal distribution for individual home ranges, the shape parameter σ can be converted in a home range radius estimation (Royle et al. 2011) including 95% of the locations. We assessed the convergence of the MCMC chains using a combination of visual assessment of trace plots and by the Geweke convergence diagnostic (Ntzoufras 2009).

Additionally, we report the capture frequency of other medium-large mammals that are potential jaguar preys, as well as cows. To account for the unequal sampling period at different camera trap stations we normalized capture frequency as: number of independent cow detections / number of effective trap nights x 100. Additionally, we calculated richness at every camera trap station.

Results

Some of the sampling stations produced less data than expected due to cameras being stolen, disturbed by livestock, covered by growing vegetation, flooded, or malfunctioning. All data was lost from three stations (excluded in the analysis), while other remained active for less time than expected or with only one camera active. In total, 26% of sampling days at station level (when all cameras in the station stopped working) were lost, and 41% at camera level (including stations left with one camera). After addressing these drawbacks, 23 stations were left with at least one sampling occasion with two cameras active, and nine stations with only one active camera. This resulted in an overall camera trap effort of 2,080 trap/nights. Camera traps were active for a mean of 65.78 days.

We obtained 24 independent jaguar detections (Fig. 1). Capture histories were composed of five individuals captured on both flanks simultaneously at least once producing a complete identity, and eight partially identified capture histories (five left-only and three right-only). We recaptured completely identified individuals eight times and partially identified individuals three times. In total we obtained eight spatial recaptures (captures of the same individual in different locations).

Estimated abundance was 52.03 (95% confidence intervals [CI] 17-103) derived in a density of 0.75 (CI 0.25–1.49) jaguars per 100 km^2 (Table 1). The obtained baseline encounter rates (λ_0^S and λ_0^B for single or both sides respectively) and the derived capture probabilities (p_0^S and p_0^B *for single ∧ boh sides respectively*), showed that capturing both sides of a jaguar was less likely than capturing a single side (λ_0^S=0.01 and λ_0^B=0.02; p_0^S=0.01 and p_0^B =0.02). The scale parameter, σ was 8.24 (CI 5.04-16.59) (Table 1). Transforming the scale parameter into a home range radius led to an estimated home range area of 1,459 km^2 (CI 318.3-3,782.1). For all the MCMC runs the Geweke diagnostic statistic Z, provided values from -0.21 to 0.43. The combination of these values, along with the visual inspection of trace plots of parameters, indicates satisfactory convergence of the MCMC chain on each run.

Besides jaguars we detected another 19 native mammals as well as three non-native species (cows, domestic dogs and horses) the latter almost exclusively outside of the park limits while native species were distributed in all the area. The cow was the species that was detected more frequently (234 independent detections). The next two most frequently detected species were the common tapeti (*Sylvilagus brasilensis*) and the tapir (*Tapirus terrestris*), with counts of 186 and 109 independent detection, respectively (Table 2). Figure 2 shows the spatial arrangement of normalized cows frequency and normalized medium-large mammal richness.

Discussion

Abundance estimations are an essential attribute in population biology, necessary for management and conservation planning (Thompson et al. 1998; O'Brien 2011) as well as to assess conservation status (Quigley et al. 2017; Paviolo et al. 2019). This study presents the first jaguar abundance estimate for the Yungas region.

Jaguars are widely distributed, inhabiting a variety of habitats, thus it is expected that their abundance would present broad variation, with densities as high as 12.2 jaguar/100 km^2 (Peruvian Amazon - Tobler et al. 2013), 5.44 jaguar/100 km^2 (Ecuadorian Amazon - Espinosa et al. 2018), 4.40 to 0.46 jaguar/100 km^2 (Ecuatorian Amazon - Gil-Sánchez et al. 2021), 3.6-3.4 jaguar/100 km^2 (Belize - Borches et al. 2014) and 2.20 jaguar/100 km^2 (north-western Amazon - Mena et al. 2020), all these estimates used spatially explicit methods. Our estimate of 0.75 jaguar/100 km^2 is one of the lowest reported for the species. Similar densities were reported in the Bolivian Chaco - (0.31-1.82

jaguar/100 km2 - Noss et al. 2012), and were as low as 0.29 in one of Mena et al. (2020) Amazonian site that was closest to roads and accessible to hunters.

Comparing with studies at a similar latitude, Paviolo et al. (2008) reported densities ranging 0.2-1.46 jaguar/100 km^2 in the Atlantic Forest region (Misiones Province, Argentina), using minimum density for the lower value and non-spatial capture-recapture for the higher. Non-spatial methods are known to produce higher estimates (Reppucci et al. 2011; Noss et al. 2012; Jędrzejewski et al. 2018), but applying the linear relationship found by Jędrzejewski et. al (2018) the result would be 0.87 jaguar/100 km^2 (for the higher capture-recapture estimation) for Iguazú National Park in the Atlantic Forest.

Lodeiro Ocampo et al. (2019) carried out a non-probabilistic estimation in a section of our study area averaging yearly data from 2014 to 2017, yielding a minimum density of 1 jaguar/100 km^2. Even though these results are not directly comparable, they are not far apart from our study. Some differences would be due to different analytical methods, but a biological difference is also expected, since Lodeiro Ocampo et al. (2019) study mostly focused in the most pristine areas of Baritú National Park.

Since our study site is at the fringes of the jaguar's distribution one would expect density to be in the lower range for the species (Brown 1984), although it could be argued that this is not a natural edge, since less than a hundred years ago the jaguar distribution reached 1500 km further south (Di Bitetti et al. 2016). Some of the factors influencing the low jaguar density in Baritú might be the relatively high altitude and highly broken topography of the sampled area (Di Bitetti et al. 2013), cattle ranching and poaching, especially in areas close to main roads and Los Toldos town (Falke and Lodeiro Ocampo 2008; Perovic et al. 2015).

Our estimate for home range size (1,459 km^2) is the largest that we are aware of. There is limited information on home range size near the study site to compare, only one study motored a female during 193 days yielding an estimation of 148 km^2 (Perovic et al 2015). Reported GPS telemetry results for other areas showed great variation, ranging from 5.4 to 1,291 km^2; home range size ratio between sexes also varied greatly, from 1.1:1 to 3.1:1 (Tobler et al 2013, Morato et al 2016). Given the strong assumptions of the modelling process (circular shape of home range and bivariate normal distribution of use), unlikely to agree with animal behavior it was not unexpected that both methods (GPS telemetry vs SCR) would disagree. We still report our large home range estimate to allow comparison with other studies, but we caution against direct biological interpretations of home range area based on telemetry. We are aware of multiple jaguar detections approximately 40 km apart (Lodeiro Ocampo et al 2009 and

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our unpublished data) supporting our high home range size estimate; i.e., if we assume the unlikely situation that we capture both individuals in the more distant points of their home range and assume a circular home range, we would derive a home range of 1,257 km^2. Is more likely this calculation and our estimation (since was calculated over a short time) can greatly overestimate home range size (in the biological sense, more than latent variable in the model) when excursions occurs.

The jaguar population in Chaco region was assumed to be the largest in Argentina, due to the vast extension of this biome, but extensive surveys showed it to be the sparsest and most threatened in the country (Altrichter et al. 2006; Quiroga et al. 2014). Population numbers are increasing slowly in Atlantic Forests but numbers are small (Paviolo et al. 2016). The Yungas offers a stronghold for Argentina's jaguars (Di Bitetti et al. 2016), and our results lend support to that assumption. This is additionally supported by capture frequency data and from identified individuals reported from other regions in the Yungas (Perovic et al. 2015).

Overall, the habitat in areas where jaguar is present in the Argentine Yungas is in reasonably good condition, with low fragmentation, many areas of difficulty of access and well-preserved, rendering this region as of great importance for jaguar conservation. Moreover, the population of jaguars in Baritú and surroundings offers a good springboard for population expansion to the south and east, with suitable habitats serving as stepping stones for expansion, as already evidenced by opportunistic sightings. It is remarkable that most of the cameras that detected jaguars were located outside of the protected area. But the camera that captured the most jaguars was located around the center of the park. Is difficult to establish patter with our data, but this clearly shows the importance of private land for jaguar conservation and additionally sets an interesting direction for future studies. Additionally other mammals' capture frequency was quite homogeneous and widespread on these private lands corroborating its importance. It is certain that preys can coexist with cattle raising, showing an extensive spatial overlap and relatively homogeneous richness in sites inside and outside the national park and with or without cow presence. Some studies had found different effects both negative and positive for different species and depending on cow abundance (e.g. Perovic 2002, Black-Decima et al. 2019, Marás 2020, Cuyckens et al. 2022), this is an interesting factor that would be important to keep exploring in future studies. It is also worth noticing that contrary to our expectation we did not detect any white-lipped peccary (*Tayassu pecari*), considered one of the main jaguar preys; either inside or outside of the park. It seems that species faced a great reduction in the last years (de Bustos et al. 2019), but this situation might be reversing in the present (Reppucci et al. 2022).

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The popularization of camera trapping as a sampling method had increased greatly in the last 20 years, following an improvement in technology and a decrease in equipment cost (Tobler et al. 2008). The use of camera traps has become an invaluable tool for the study of wildlife, and a game changer especially for those working on cryptic, low abundance species, which are difficult to detect or require great sampling effort. There also has been important development and improvement of statistical methods that allows researchers to relax assumptions and make the most of their data (e.g., Royle et al. 2014; MacKenzie et al. 2017; Augustine et al. 2018; Satter et al. 2019). In our case, 2-flank SPIM (Augustine et al. 2018) enabled us to use our incomplete dataset to estimate density. Traditional SCR models would not have been applicable due to the high camera malfunction rate we encountered, which not only reduced the number of sampling days but also our ability to identify some individuals with certainty. Those setbacks are rarely reported in the literature, often researchers use alternatives to deal with uncertainty in individual recognition that require discarding data (Wang and Macdonald 2009; Nair et al. 2012; Srivathsa et al. 2015). The 2-flank SPIM route yielded a density estimation not possible otherwise with traditional SCR models, and spared us using models with stronger assumptions that we were not comfortable making.

There are some considerations to consider for future studies. First, it would be desirable to increase the sampling area, given the large σ result compared with similar studies on the species (which conduct to a large home range size estimated). A rule of thumb proposed is that density surveys should cover an area of at least one home range (Tobler and Powell 2013); while we do not have home range data for the area, we covered 767 km^2, which exceeds the recommendation for south America (500-600 km^2) where home range then go be larger than central America (Maffei et al 2011). Especially if we consider the home range estimation for a female of 148 km^2 (Perovic et al 2015) and the sex ratios in other areas (maximum 1:3.1; Tobler et al 2013, Morato et al 2016) would result in a male home range smaller than the sampled area. Moreover Sollman et al. (2012) showed that SECR models perform well even when using a trapping array smaller than an average home range. Secondly, use some technique to improve the number of spatial recaptures providing more data to the model. Efford et al. (2004) suggest a minimum of 20 recaptures to estimate density using spatially explicit capture recapture models and inverse prediction. Other ways to increase detectability would be reducing camera malfunctions, installing camera at location more frequently used and/or increasing sampling period. Lastly, and if the amount of data is enough it would be desirable to include other

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variables such as sex, different home range shapes, or habitat types that would make the model more biologically sound.

In many studies, sampling sites are commonly biased towards areas of easy access, but our study includes a gradient for easily accessible to highly remote areas (with no access tracks or trails), covering some of the land use heterogeneity. For those reasons, we do not expect considerable bias regarding the sampling area.

Given the remoteness of the sampling area, which necessitates a significant amount of effort to survey, it would be impractical to repeat this survey annually. However, considering the strategic importance of this area for jaguars it would be imperative to conduct surveys parodically, albeit at a lower frequency, e.g., every five years. Government agencies and other actors frequently request abundance estimations at the landscape level, but the figures and the techniques used to derive them are often speculative and distract from the protection of priority areas (Karanth 2016). We would recommend that, in order for research to feed into jaguar conservation planning, population estimations and monitoring should target those critical priority areas.

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Figure 1 Baritú National Park and international borders, showing study area with camera trap locations and jaguar detection frequency

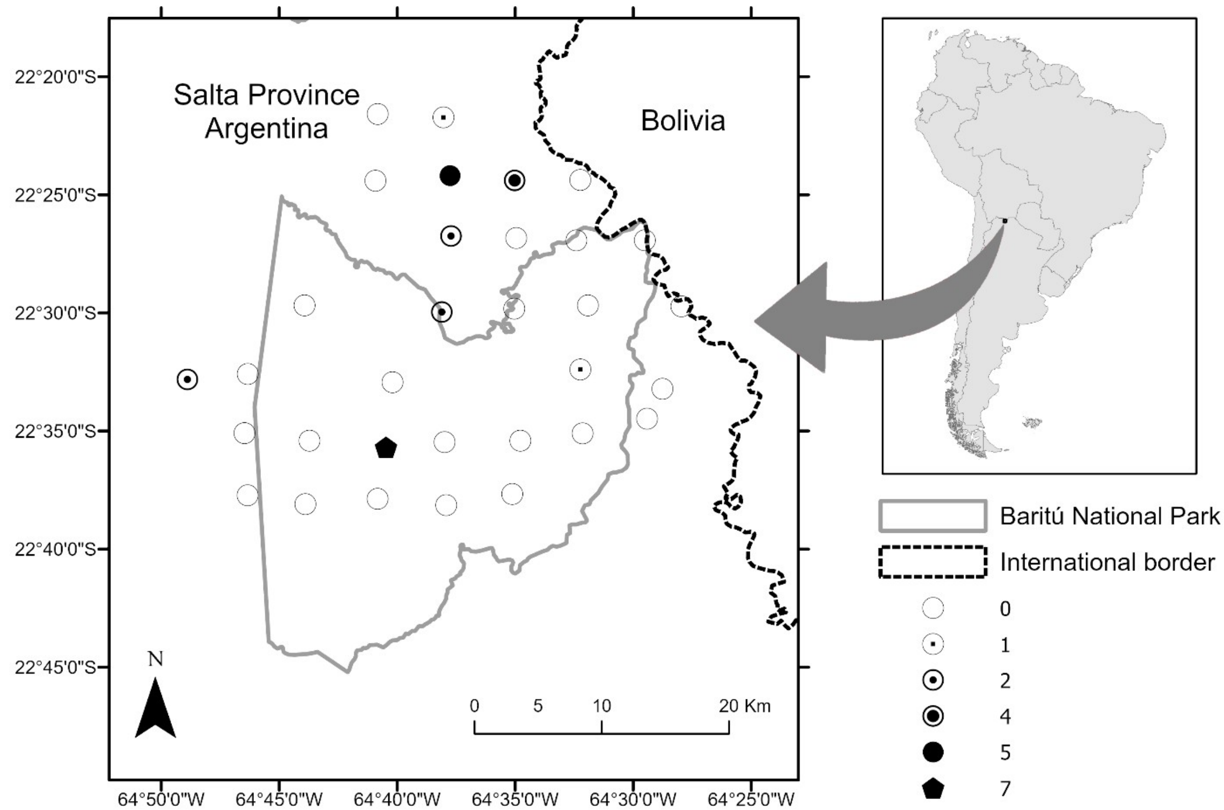

Figure 2 Baritú National Park and international borders, showing study area with camera trap locations, medium-large mammal richness and normalized cow detection frequency.

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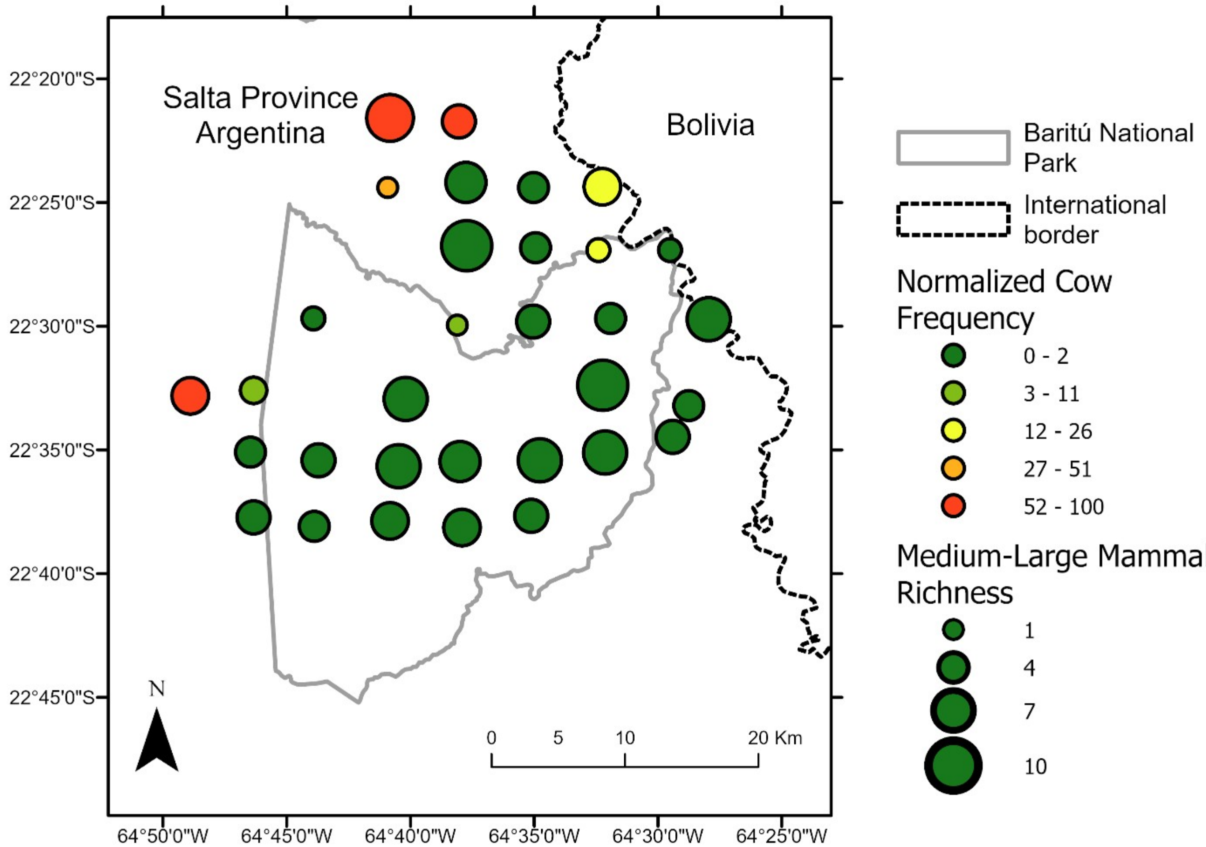
Salta Province
Argentina
Bolivia
22°20'0"S
22°25'0"S
22°30'0"S
22°35'0"S
22°40'0"S
22°45'0"S
64°50'0"W
64°45'0"W
64°40'0"W
64°35'0"W
64°30'0"W
64°25'0"W
N
0
5
10
20 Km
Baritú National Park
International border
Normalized Cow Frequency
0 - 2
3 - 11
12 - 26
27 - 51
52 - 100
Medium-Large Mammal Richness
1
4
7
10

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Tables

	P_0^S	P_0^B	σ	N	D
Posterior Mean	0.01	0.02	8.24	52.03	0.752
95% CI	(0.00-0.02)	(0.01-0.05)	(5.042-16.594)	(17-103)	(0.246-1.490)

Table 1. Posterior summaries (Posterior Mean and 95% Confidence Interval, CI) of SPIM model parameters. Single side detection probability (P_0^S), both sides detection probability (P_0^B ¿ *, shape parameter* ¿σ), abundance (N) and density (D) as number of jaguars per 100km^2.

Species	Independent detections
Bos taurus	234
Canis familiaris	12
Cerdocyon thous	27
Conepatus chinga	4
Dasyprocta punctata	43
Didelphis albiventris	1
Eira barbara	20
Equus caballus	33
Homo sapiens	9
Leopardus pardalis	39
Leopardus tigrinus	4
Leopardus wiedii	13
Leopardus sp	21
Mazama americana	13
Subulo gouazoubira	33
Mazama/Subulo sp	23
Nasua nasua	6
Panthera onca	23
Pecari tajacu	8
Procyon cancrivorus	17
Puma concolor	27
Puma yagouaroundi	10
Notosciurus pucheranii	22
Sylvilagus brasiliensis	186
Tamandua tetradactyla	1
Tapirus terrestris	109

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Table 1. Frequency of independent detections of medium-large mammals recorded during the suty.

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