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Estimates of jaguar (*Panthera onca*) population density in the South American Greater Madidi-Tambopata Landscape

Estimaciones de la densidad poblacional del jaguar (*Panthera onca*) en el Gran paisaje de Madidi-Tambopata en Suramérica

Guido Marcos Ayala[1], María Estela Viscarra[2], Carlos Fonseca[3], Robert Benedict Wallace[4]

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Abstract

[**Introduction**]**:** The jaguar (*Panthera onca*) is the largest cat in the Americas, and due to vast connected forests, the Amazon currently holds the largest jaguar populations. [**Objective**]**:** We present jaguar population density estimates for seven sites in the Great Madidi-Tambopata Landscape in northwestern Bolivia and southeastern Peru. [**Methodology**]**:** Data collection occurred from 2001 to 2008, using between 26 to 118 camera trap stations distributed in polygons between 37 to 355 km^2 in extent, active from 29 to 75 days at each study site. [**Results**]**:** We identified a total of 63 individuals across all sampling sites. The estimated capture rate for each sampling site ranged from 0.18 to 2.81 independent events / 100 trap nights. The jaguar density estimates with SCR models ranged from of 0.1 to 2.39 individuals / 100 km^2, and derived CAPTURE (MMDM) population density estimates using a regional buffer (5.76 km, n = 19), were between 0.52 and 2.86 individuals / 100 km^2. [**Conclusions**]**:** These results are especially relevant for the development of conservation strategies and evaluations for this threatened species, and also underline the importance of the transboundary Greater Madidi-Tambopata Landscape as a population stronghold for jaguars in the region.

Keywords: Bolivia; camera traps; capture-recapture; mean distance; Peru.

Resumen

[**Introducción**] El jaguar (*Panthera onca*) es el felino más grande de América y debido a los vastos bosques conectados en la Amazonía tiene actualmente las mayores poblaciones de esta especie. [**Objetivos**]**:** Estimamos la densidad de jaguares para 7 sitios en el Gran Paisaje Madidi-Tambopata en el noroeste de Bolivia y el sureste de Perú. [**Metodología**] La toma de datos fue desde el 2001 al 2008, utilizando entre 26 y 118 estaciones de cámaras trampa distribuidas en polígonos entre 37 y 355 km^2 de área muestreada, activas durante 29 a 75 días en cada sitio de estudio. [**Resultados**]**:** Identificamos un total de 63 individuos entre todos los sitios de muestreo. La tasa de captura estimada para cada sitio de muestreo osciló entre 0.18 y 2.81 eventos independientes / 100 trampas noche. Las

1 Scientific Research Coordinator, Wildlife Conservation Society, Greater Madidi-Tambopata Landscape, Bolivia; Department of Biology & Centre Environmental and Marine Studies (CESAM), University of Aveiro, Portugal. gayala@wcs.org; http://orcid.org/0000-0002-7968-7460
2 Head of Biodiversity Surveys Wildlife Conservation Society, Greater Madidi-Tambopata Landscape, Bolivia. mviscarra@wcs.org; http://orcid.org/0000-0003-4992-504X
3 Researcher and Professor, Department of Biology & Centre Environmental and Marine Studies (CESAM); University of Aveiro, Portugal. cfonseca@ua.pt; https://orcid.org/0000-0001-6559-7133
4 Senior Conservation Scientist, Bolivia & Andes-Amazon-Orinoquía, Wildlife Conservation Society, Bolivia; Wildlife Conservation Society, United States. rwallace@wcs.org; https://orcid.org/0000-0001-7411-6338

estimaciones de densidad de jaguar con modelos SCR variaron de 0.1 a 2.39 individuos / 100 km^2 y las estimaciones de densidad de población calculados con CAPTURE (MMDM) utilizando una zona de amortiguamiento regional (5.76 km, n = 19), estuvieron entre 0.52 y 2.86 individuos / 100 km^2. **[Conclusiones]:** Estos resultados son especialmente relevantes para el desarrollo de estrategias de conservación y evaluaciones para esta especie que actualmente está siendo amenazada, también subrayan la importancia del paisaje transfronterizo del Gran Madidi-Tambopata como un bastión poblacional de jaguares en la región.

Palabras clave: Bolivia; cámaras trampa; captura-recaptura; distancia media máxima; Perú.

1. Introduction

The jaguar (*Panthera onca*) is the largest felid in the Neotropics and, for many, it is the most powerful conservation symbol of the Amazon (Sunquist & Sunquist, 2002). Due to its individually large spatial requirements and key ecological role as the principal predator of the Neotropics, the jaguar is also considered an umbrella species (Thornton *et al.*, 2016; Jędrzejewski *et al.*,2018), and its absence would cause trophic cascades, impacting prey populations, and affect the overall ecosystem dynamics (Cavalcanti & Gese, 2009). Historically, the jaguar was present from the southeastern United States, through Central America and South America, as far south as the Argentine Patagonia, covering an area of 19 921 440 km^2 (Rabinowitz & Nottingham, 1986; Cuyckens *et al.*, 2017). However, it currently occupies approximately 57 % of the historical distribution area (Jędrzejewski *et al.*, 2018).

Globally, the jaguar is categorized as Near Threatened (NT) by the International Union for the Conservation of Nature (IUCN: Quigley *et al.*, 2017), however, if conservation actions do not minimize threats, jaguars could move to the threatened category in the near future.

Currently, jaguars are considered regionally threatened in a large part of their range, mainly due to: a) habitat destruction, b) reduction in abundance of their main prey, c) persecution due to human-wildlife conflicts, and since 2014, d) hunting for illegal wildlife trafficking of jaguar body parts, especially fangs, but also claws, skin and others, for international markets (Morcatty *et al.*, 2020; Negrões *et al.*, 2017; Nuñez & Aliaga-Rossel, 2017; Porfirio *et al.*, 2016).

The Amazon region is considered the primary jaguar population stronghold across its range, because it retains a large, continuous block of habitat with a high probability of long-term survival (Sanderson *et al.*, 2002). The tropical rainforest lowlands are the largest ecoregion within the Amazon, spanning five countries including Brazil, Bolivia, Colombia, Ecuador and Peru (Tobler *et al.*, 2013). The Greater Madidi-Tambopata Landscape lies in northwestern Bolivia and southeastern Peru, contains some of the most biodiverse protected areas in the world, and as a transboundary area expands opportunities to protect species with large spatial requirements such as the jaguar.

Population density estimates are a fundamental requirement for conservation management evaluation, as they provide an idea of population size, ballpark estimates to assess the need for conservation interventions (Jędrzejewski *et al.*, 2018; Maffei *et al.*, 2004). The camera trap

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methodology and satellite telemetry technology have dramatically improved knowledge about the jaguar in the last years contributing with studies that have estimated population densities, and shed more light on different ecology and behavior aspects in some of the most important ecosystems within the jaguar's range including the tropical forests of Central America (Moreira *et al*., 2008), the Pantanal wetlands (Silveira *et al*., 2010; Soisalo & Cavalcanti, 2006), the tropical dry forests of the Gran Chaco (Maffei *et al*., 2004), and the Atlantic forest of Brazil (Cullen *et al*., 2005). However, to date there are surprisingly few studies for the vast humid tropical forests of the Amazon which is by far the largest habitat for the jaguar (Silver *et al*., 2004; Tobler *et al*., 2013; Wallace *et al*., 2003).

Therefore, in this article, we present camera trap derived jaguar population density estimates from seven study sites in northwestern Bolivia and south-eastern Peru in one of the largest continuously protected regions in the Amazon: the transboundary Madidi-Tambopata Landscape. This study is one of the first on jaguar population densities in the western Amazon.

2. Methodology

2.1 Study sites

The research was carried out at 7 sites, 6 in Bolivia and 1 in Peru within the Greater Madidi-Tambopata Landscape, a transboundary landscape in the Andean Mountain range, between northwestern Bolivia and southeastern Peru. This area covers approximately 142 530 km^2 (Bolivia 106 810 km^2, Peru 35 720 km^2), and is characterized by an impressive altitudinal range (180 to 6 044 m a.s.l.), varied topography and climate that have resulted in diverse plant and animal communities and a high number of endemic species. Historically, diverse cultural groups settled in the Amazonian portion of the Tropical Andes, among them the Leco, Tacana, Araona, Ese Ejja, T'simane and Mosetene peoples. Together, these indigenous areas cover 42 000 km^2. The conservation value of this landscape is particularly important as a transboundary area, ensuring the connectivity of ecosystems and the binational coordination of conservation efforts.

In Bolivia, sampling was carried out along some of most important rivers of the region: Tuichi, Hondo, Quendeque, Madidi, Heath, Undumo and Tequeje. All 6 Bolivian study sites were within the Abel Iturralde Province of the La Paz Department, 5 within the Madidi National Park and Natural Area of Integrated Management (PN ANMI Madidi), while the sixth site within the Tacana Indigenous Territory or TCO (Community Land of Origin). In Peru, sampling occurred along the Heath, Tambopata, Malinowski and Chuncho rivers, within the Tambopata Province, Madre de Dios Region, and within the Tambopata National Reserve and Bahuaja Sonene National Park (**Figure 1**).

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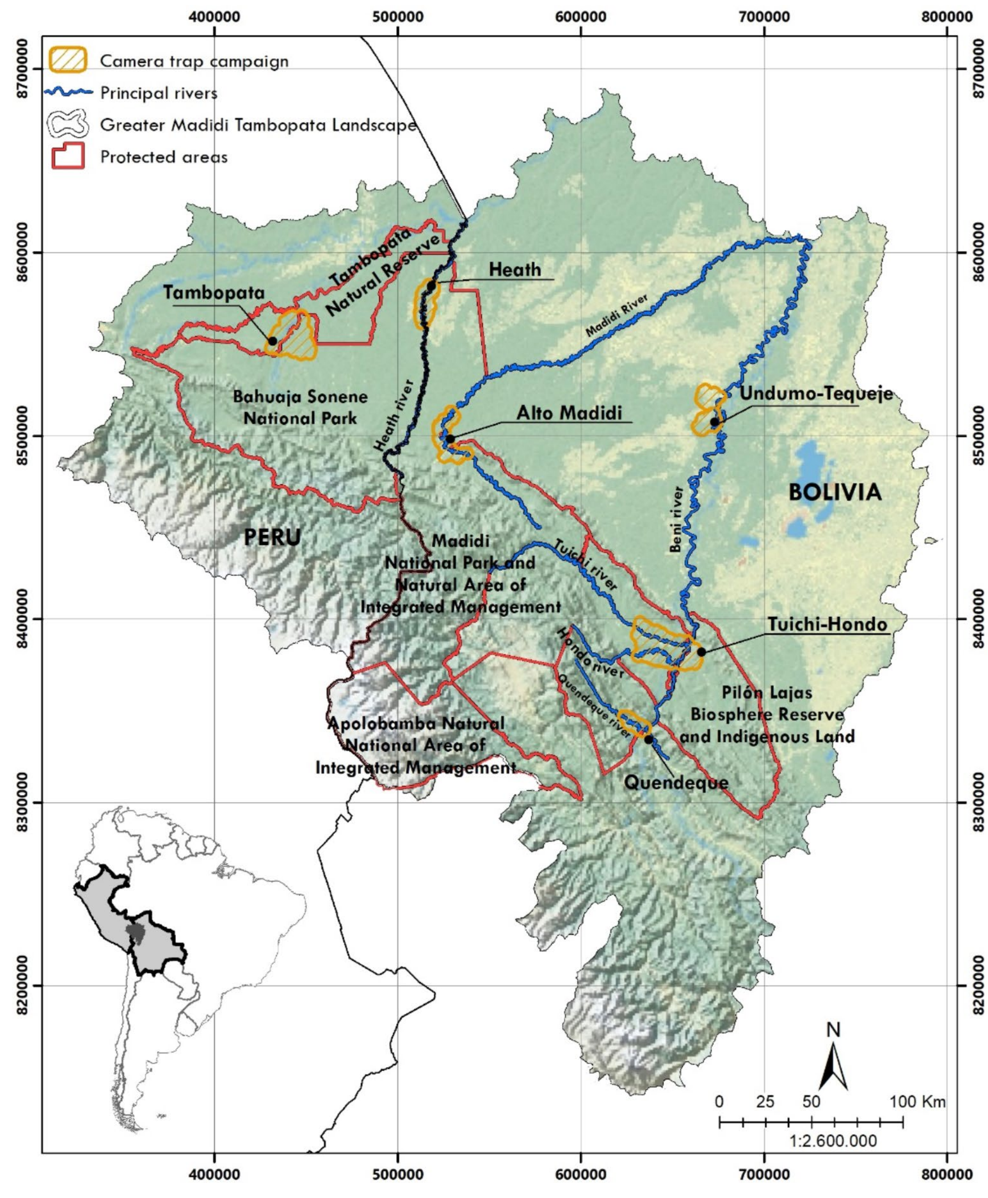

Figure 1. Location of 7 study sites with camera trap polygons in the Greater Madidi–Tambopata Landscape in northwestern Bolivia and southeastern Peru.
Figura 1. Ubicación de 7 sitios de estudio con polígonos de cámaras trampa en el Gran Paisaje Madidi-Tambopata en el noroeste de Bolivia y sureste de Perú.

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The Amazonian study sites are mainly found in the sub-Andean foothill ecoregion, except for the Tequeje-Undumo site found in the pre-Andean Amazon forest and Moxos flooded savanna ecoregions, and the Heath site found in the Pando Amazon flooded forests and Moxos flooded savanna ecoregions (Ibisch *et al.*, 2003).

The Tuichi and Hondo rivers are tributaries of the Beni River located in valleys adjacent to the final foothills of the Andes. The tropical forest vegetation is similar to those of the Beni floodplain (Fuentes, 2005). The Quendeque River is a smaller tributary further upstream on the Beni. These three sites lie completely within the Madidi protected area.

Alto Madidi is located on the Madidi River, a major tributary of the Beni River, at the very base of the final steep slopes of the Andean foothills. The forest is slightly taller than the Tuichi, Hondo and Quendeque, although the species composition is similar (De la Quintana, 2005; Fuentes, 2005). At Alto Madidi, one side of the river is within the Madidi protected area and the other side is within the Ixiamas Muncipal Protected Area.

The Heath River is in the extreme north of the Madidi protected area and represents the border between Bolivia and Peru, therefore, one side of the river is within Madidi and the other side in Bahuaja Sonene National Park in Peru. This site has various vegetation types including natural Amazonian savannas, Amazon terra firme rainforests with good drainage, riparian vegetation, and flooded forests with poor drainage that are strongly marked by recurrent floods. The forests are generally tall, with emergent trees reaching 45 m and a 25-35 m canopy (Fuentes, 2005).

The Tequeje and Undumo study site encompasses the rivers of the same name that flow into the Beni River further downstream within the Tacana Indigenous Land. This area has four vegetation types: Amazonian seasonal humid forest, riparian forest, seasonal flood savanna and wooded savanna (Ribera, 1992).

The Tambopata sampling site in Peru focused along the Tambopata, Malinowski, and Chuncho rivers between 200 and 500 meters above sea level. The Madre de Dios region is characterized by humid tropical forests with large trees exceeding 50 m in height and 5 m in diameter (CI-Perú, 1999).

2.2 Field surveys

Between 2001 to 2008, a total of 15 camera trap surveys were implemented, with a sampling design specifically aiming for jaguars (Cavalcanti & Gese, 2009; Maffei *et al.*, 2011; Silver *et al.*, 2004; Soisalo & Cavalcanti, 2006; Tobler *et al.*, 2013; Wallace *et al.*, 2003). All camera trap efforts were carried out during the dry season between July and October (**Table 1**). A variable number of camera trap stations (n = 26 - 118) (**Table 1**), were placed 1.6 to 2 km apart from each other, based on the minimum home range for a female jaguar of 10 km^2 estimated by Rabinowitz & Nottingham (1986). Each station consisted of two cameras placed face to face so as to photograph jaguars from both sides, each set at 50 - 70 cm from the ground, with at least 3 - 4 m between the two cameras at each camera station (Noss *et al.*, 2013).

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Table 1. Detail of the jaguar camera trap study efforts for 7 sites in the Greater Madidi-Tambopata Landscape.
Cuadro 1. Detalle de los esfuerzos aplicados con trampas cámara para estudios de jaguar en 7 sitios de estudio en el Gran Paisaje Madidi-Tambopata.

Year	Survey site	Dates	GPS local UTM	N° Trap stations	N° Effective days	Camera trap nights	Sampled polygon (km^2)
2001	Tuichi	Aug - Nov	636283 8391747	47	30	1 513	52.56
2002	Tuichi-Hondo	Jul - Oct	637226 8387900	66	56	2 116	213.49
2003	Quendeque	Aug - Sep	629584 8342331	32	29	1 108	37.09
2004	Upper Madidi	Aug - Oct	523814 8500612	26	34	1 138	110.55
2005	Heath	Jul - Oct	514756 8572464	63	50	1 813	103.09
2006	Undumo-Tequeje	Aug - Oct	672042 8514868	59	50	1 640	122.5
2007	Tambopata	Jul - Nov	436491 8550644	118	75	3 420	292.04
2008	Tuichi-Hondo	Jul - Sep	637599 8383253	77	50	2 123	354.87

Throughout the sampling years, three camera trap models were used: Camtrakker ® (Camtrakker, Watkinsville, Georgia, USA), DeerCam ® (DeerCam, Park Falls, Wisconsin, USA) and TRAILMASTER ® (TRAILMASTER, Kansas, USA), film cameras. The cameras were operating continuously for a period of 25 to 34 effective sampling days in the field with a minimum interval of three minutes between photographic events.

The camera trap stations were placed in the predominant habitats of each study area: a) beach, open areas along the main and secondary rivers; b) forest, located within the forest, often along animal trails, and on small streams within the forest; and c) pampa, open grassland locations.

2.3 Density estimation

Jaguar individuals were identified based on differences in spot and rosette patterns, and by sex when possible (Noss *et al*., 2013; Wallace *et al*., 2003). If a photo could not be clearly assigned to an individual, it was excluded from the density analysis.

To estimate jaguar population densities at the study sites, we applied the spatial capture-recapture (SCR) method using the SECR package in R version 3.6.3 (Royle *et al*., 2013). SCR models use spatial information from detections to estimate parameters with a half-normal detection function (probability of detection at the center of the home range g0 and motion parameter σ) (Tobler *et al*., 2013). Although spatially explicit models have been proven to be the best estimators, they tend to underestimate densities if they lack sufficient recaptures of jaguar individuals (Noss *et al*., 2012; Tobler & Powell, 2013). Thus, for comparative purposes with other studies and for sites with few individuals and recaptures, we also report population density estimates with non-spatial capture-recapture methods that estimate density by applying a buffer (Paviolo *et al*., 2008; Silver *et al*., 2004) using the CAPTURE program (Otis *et al*., 1978; Rexstad & Burnham, 1992).

As all study sites were sampling the same overall jaguar population and yet some individual study sites had few jaguar individuals with multiple captures, we calculated a regional buffer using the mean of all the maximum distances traveled (MMDM) by jaguars in different campaigns between 2001 and 2008 (n = 19) when estimating jaguar density using CAPTURE.

We also report the jaguar camera trap relative abundance indices (RAI), considering only independent events, namely records for the same individual separated by at least 24 hours. The indices were calculated following the recommendations of O'Brien *et al*., (2003). The Relative abundance index (RAI) was calculated through the capture rate expressed as the number of independent events per total number of traps night during the study and multiplied by 100 (O'Brien *et al.* 2003). The traps night are the days that the camera traps were active during the study.

We performed Spearman correlations (Rs) between the CAPTURE and SECR population density estimates to analyze the relationship between these estimators.

3. Results

A total of 488 camera trap stations were placed on the ground, generating an effort of between 1 107 and 3 419.29 trap nights per sample site, and covering polygons of between 37.09 to 354.87 km^2 (**Table 1**).

A total of 195 jaguar photographs representing 151 events and 113 independent events were obtained across the seven study sites. The relative abundance index (RAI) for the different study sites varied between 0.18 to 2.81 independent events / 100 trap nights (**Table 2**).

A total of 63 jaguars were identified: 27 adult males, 15 adult females, 1 juvenile male and 1 juvenile female, and 19 adults of unidentified sex. Tuichi-Hondo and Alto Madidi were the sampled sites with the highest number of captured individuals (12 and 15 individuals, respectively) (**Table 2**).

Table 2. Details of the number of photographs, independent events, individuals captured, recaptures, sex and relative abundance indices (RAI) of jaguars recorded with camera traps at 7 study sites in the Greater Madidi-Tambopata Landscape.

Cuadro 2. Detalle del número de fotografías, eventos independientes, individuos capturados, recapturas, sexo e índices de abundancia relativa (RAI) de jaguares registrados con cámaras trampa en 7 sitios de estudio en el Gran Paisaje Madidi-Tambopata.

Year	Survey site	Nº Photos	Independent events	Total individuals	Re-captures	Adult males	Adult females	Unidentified sex	Juveniles	RAI
2001	Tuichi	7	6	2	4	2	0	0	0	0.38
2002	Tuichi-Hondo	37	20	12	7	6	2	3	1	0.94
2003	Quendeque	12	7	4	3	3	0	1	0	0.62
2004	Upper Madidi	54	32	14	17	7	5	2	0	2.81
2005	Heath	14	8	6	2	1	3	1	1	0.44
2006	Undumo-Tequeje	12	3	3	0	0	1	2	0	0.18
2007	Tambopata	28	18	9	2	3	3	3	0	0.53
2008	Tuichi-Hondo	31	19	12	3	5	1	6	0	0.91
Total		195	113	63	37	27	15	19	2	

The SCR density estimates were calculated with the null model (M0), and varied between 0.1 to 2.39 individuals / 100 km^2 (**Figure 2a**). The SCR density for Undumo-Tequeje was not

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estimated due to a lack of recaptures. In Tambopata and Heath, the SCR density estimates were overestimated with high confidence limits, due to scarce recaptures (**Table 3**).

Table 3. SCR derived jaguar population estimates at 7 sites across the Greater Madidi-Tambopata Landscape.
Cuadro 3. Estimaciones de población de jaguar obtenidos con SCR en siete sitios en el Gran Paisaje Madidi-Tambopata.

Year	Sampling Site	Individuals	g0	Sigma	Density/100 km^2	95% Confidence Limits
2001	Tuichi	2	0.008	1 436	0.10 ± 0.05	0.01 - 3.27
2002	Tuichi-Hondo	9	0.003	5 550	1.56 ± 1.15	0.43 - 5.68
2003	Quendeque	4	0.004	1 120	0.27 ± 0.04	0.03 - 2.50
2004	Upper Madidi	14	0.014	4 263	2.22 ± 0.86	1.08 - 4.61
2005*	Heath	6	0.006	1 131	9.16 ± 7.47	2.26 - 37.10
2007*	Tambopata	9	0.002	2 475	6.16 ± 4.97	1.55 - 24.6
2008	Tuichi-Hondo	8	0.004	3 219	2.39 ± 1.53	0.76 - 7.56

* Overestimated density due to low number of re-captures.

* Densidad sobreestimada debido al bajo número de recapturas.

The CAPTURE (MMDM) density estimates with the regional buffer varied between 0.52 to 2.34 individuals / 100 km^2 (**Figure 2b**). **Table 4** compares density estimates using site-specific buffers versus the regional buffer, with the latter reducing confidence limits density estimates for most sites.

Table 4. Jaguar density estimates obtained with CAPTURE (MMDM) at 7 sites across the Great Madidi-Tambopata Landscape using the specific buffer of each sampling site versus the regional buffer obtained from the mean maximum distance traveled (2001 - 2008).
Cuadro 4. Estimaciones de la densidad de jaguares obtenidas con CAPTURE (MMDM) en 7 sitios en el Gran Paisaje Madidi-Tambopata utilizando el buffer específico de cada sitio de muestreo versus el buffer regional obtenida de la distancia media máxima recorrida (2001 - 2008).

		Sample specific MMDM			Regional MMDM		
Year	**Sampling site**	**Sample specific buffer (km)**	**Area sampled (km^2)**	**Density/100 km^2**	**Regional buffer (km)**	**Area sampled (km^2)**	**Density/100 km^2**
2001	Tuichi	11.84	935.47	0.21 ± 0.046	5.76	379.15	0.52 ± 0.14
2002	Tuichi-Hondo	9.51	1085.63	1.11 ± 0.58	5.76	671.23	1.78 ± 0.50
2003	Quendeque	9.55	600.37	0.83 ± 0.34	5.76	305.16	1.63 ± 0.92
2004	Upper Madidi	4.54	465.66	3.65 ± 3.33	5.76	593.2	2.86 ± 0.82
2005	Heath	1.92	191.64	3.65 ± 1.54	5.76	471.92	1.48 ± 0.83
2007	Tambopata	4.16	635.01	2.52 ± 1.25	5.76	801.15	1.99 ± 1.09
2008	Tuichi-Hondo	5.24	835.97	1.32 ± 0.1	5.76	897.25	2.34 ± 1.05

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The SCR and CAPTURE density estimates were significantly correlated (Rs = 0.90, p = 0.037), and at sites with larger numbers of captured and recaptured individuals, such as Tuichi-Hondo (2002 and 2008) and the Upper Madidi, the density estimates using both methods were relatively similar (**Figure 2**).

Tuichi-Hondo had the highest calculated densities with both estimation programs, and there was an increase from 0.52 to 2.34 jaguars / 100 km^2 between 2002 and 2008.

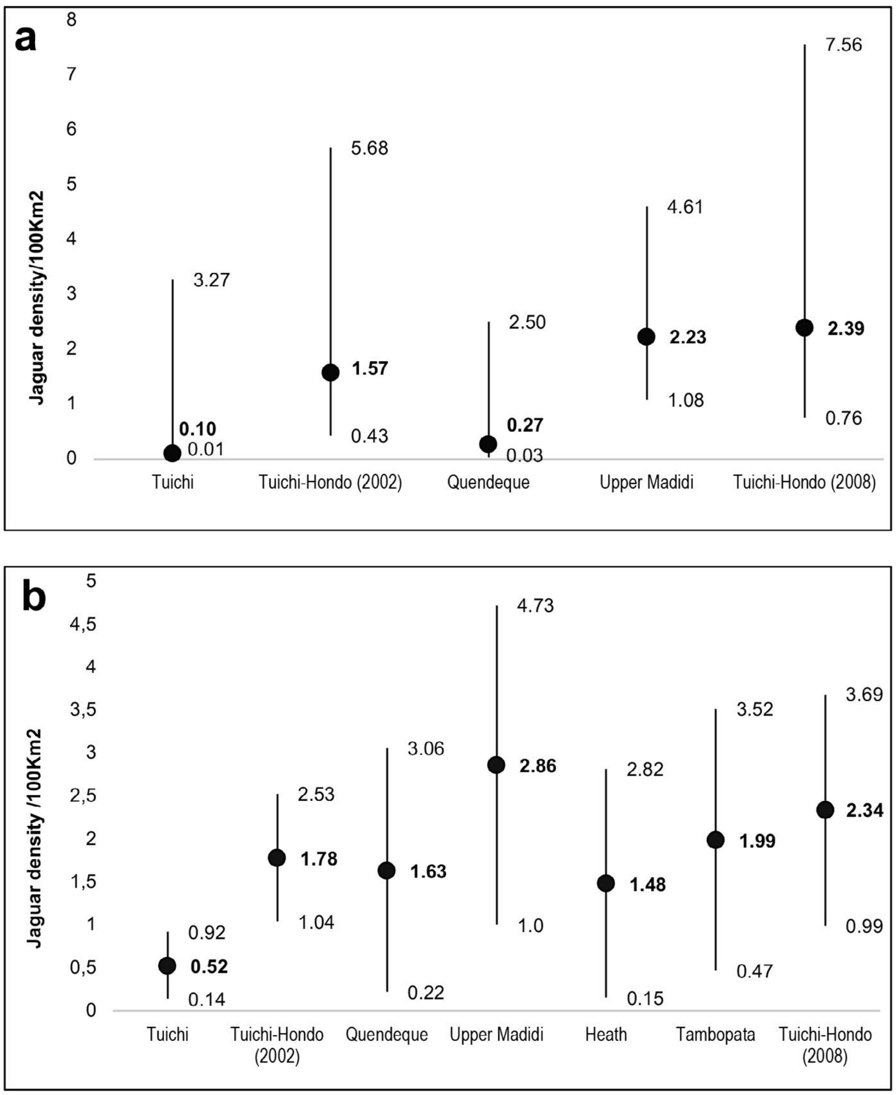

Figure 2. Jaguar density estimates using SCR (a) and CAPTURE (MMDM) (b) at the Greater Madidi-Tambopata Landscape.
Figura 2. Estimaciones de la densidad de jaguar obtenidas con SCR (a) y CAPTURE (MMDM) (b) en el Gran Paisaje Madidi-Tambopata.

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4. Discussion

4.1 Jaguar density

Both estimation methods produced similar density estimate ranges, with SCR estimating 0.10 - 2.39 jaguars / 100 km^2 versus 0.52 - 2.86 jaguars / 100 km^2 for CAPTURE (MMDM). These estimates are higher than those reported nearby in the Bolivian Chaco (0.31 - 1.82 jaguars / 100 km^2; Noss *et al*., 2012), and it is half the density reported in neighboring southeastern Perú (4.4 jaguars / 100 km^2; Tobler *et al*., 2013).

Our density estimates are higher than in Atlantic Forest in Argentina (0.49 - 0.93 jaguars / 100 km^2; Paviolo *et al*., 2008), and northeastern Brazil (1.28 jaguars / 100 km^2; Silveira *et al.* 2010), but lower than estimates for Guatemala (6.1 jaguars / 100 km^2; Moreira, 2008), the Brazilian Pantanal (5.5 jaguars / 100 km^2; Soisalo & Cavalcanti, 2006) and Belize (4.4 jaguars / 100 km^2; Miller & Miller, 2005). However, it should be noted that many of the latter studies were calculated using HMDM and also sampled relatively small areas, both of which can lead to density overestimation (Noss *et al*., 2012; Tobler & Powell, 2013). Although our estimates are not the highest for the jaguar's range, they are valuable because they provide population data from one of the most unknown regions for the species.

4.2 Comparison of SCR vs MMMD estimates

SCR models are increasingly popular in ecology because they address some important criticisms of traditional capture-recapture methods related to heterogeneity in detectability, as well as the emergence of new technologies such as camera traps and non-invasive genetics (Sutherland *et al*., 2019). However, sparse data usually leads to imprecise estimates (Noss *et al*., 2012; Tobler & Powell, 2013), because SCR analyses require multiple detections of the same individuals at different locations in order to estimate the location of latent activity centers and generate a more accurate estimate. A common way to increase the size of the dataset is to prolong the sampling period, thus increasing both the proportion of individuals detected and the number of detections per individual (Noss *et al*., 2012). Thus, the main reason why SCR densities could not be calculated for all study sites was the relatively short sampling extension, which resulted in large confidence intervals, due to low recaptures and detection rates. Other factors, such as the size of the sampling area at some study sites and the use of film cameras, may have also influenced density estimates.

We observed that when using the MMDM, CAPTURE densities are closer to those calculated with SCR. For example, Alto Madidi has the highest MMDM density with CAPTURE (2.86 ± 0.8 jaguars / 100 km^2) and the highest number of recaptures, and SCR produced very similar density estimates: 2.2 ± 0.8 jaguars / 100 km^2 (**Figure 2**). These results suggest that sites with enough recaptures, produce similar density estimates for both analytical methods. However, in places where there are not enough recaptures, spatially explicit estimators tend to produce population densities with very high confidence limits. For example, at Heath and Tambopata,

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SCR derived density estimates of 9.16 ± 7.5 and 6.2 ± 4.9 jaguars / 100 km^2, as compared to CAPTURE estimates of 1.48 ± 0.8 and 1.9 ± 1.1 jaguars / 100 km^2 (**Table 3**). We believe that the regional buffer employed by us, permitted more robust density estimates when comparing with the ones that use a polygon buffer obtained within the specific trapping campaign, procedure followed by the majority of published CAPTURE density estimates (Maffei *et al*., 2004).

However, both density estimation methods have limitations and errors and only by comparing with other data such as radio-tracking and genetic, could we confirm an overestimation of the estimated densities. These results highlight that based on the data obtained, we should carefully look at the sampling design and data when choosing the density calculation method, and when reporting density estimates using different analytical methods.

4.3 Sex difference

In our study, we identified 63 individuals, of which 28 were male, 16 females and 19 unidentifiable (due to photographs with bad angles, and partial and blurred photographs).

We calculated the sex ratio of the proportion of jaguars where the sex could be differentiated, obtaining a sex ratio of 1.8:1 of males relative to females. Similar results were reported in several studies (Maffei *et al*., 2004; Silver *et al*., 2004). Females have smaller territories than males, and when with cubs they exhibit protective maternal behavior by selecting safer areas and reducing the use of exposed areas, thereby decreasing the probability of being photographed (Jędrzejewski *et al*., 2018; Moreira, 2008; Tobler *et al*., 2013).

In this study, due to the insufficient number of recaptures of male and female individuals, it was not possible to estimate density for the different sexes (**Table 2**), even with a pooled data from different years at the same site (e.g. Tuichi-Hondo 2002 and 2008).

4.4 Conservation implications

The jaguar is threatened by high deforestation rates stimulated by the growing demand for beef, soybean and other products, as well as extensive fires, increasing human population, and the recent demand for jaguar parts in an emerging illegal international trade (Morcatty *et al*., 2020; Nuñez & Aliaga-Rossel, 2017; Romero-Muñoz *et al*., 2020). These problems imply the need for transboundary actions for the conservation of this species, an approach that must go beyond geopolitical boundaries to maintain population connectivity (Mena *et al*., 2020; Thompson *et al*., 2020). In this context, our study reveals an important population of jaguars in the Greater Madidi-Tambopata Landscape, representing a stronghold jaguar population within the Amazon. Thanks to a transboundary conservation effort, and the combination of different neighboring and overlapping management systems such as national protected areas, municipal protected areas and indigenous territories, a very large percentage (ca. 60 %) of the 140 000 km^2 landscape is protected, which will be essential for the survival of jaguars and the record-breaking biodiversity that coexists in this region. These characteristics favor conservation actions at the binational level that will also ensure connectivity to safeguard ecological processes and ecosystem services.

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5. Conclusions

Our study reveals conservation relevant jaguar density estimates for the Bolivian and Peruvian Amazon rainforest, where there are few previously reported data. In addition, this study provides key information that can aid in the development of jaguar conservation strategies and monitor jaguar populations and that, at the longer term, will help us better understand their population dynamics and their interaction with other species.

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7. Ethics and conflict of interest

The authors declare having fulfilled all relevant legal and ethical requirements during the study, as well as during the preparation of the manuscript. They also declare that there are no conflicts of interest of any nature, that all financial sources are fully and clearly mentioned in the acknowledgments section, and that they fully agree with the final edited version of the article.

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