

Habitat destruction threatens jaguars in a mixed land use region of eastern Bolivia

Rene Meißner^{1,*}, Moritz Blumer^{2,*}, Merlin Weiß³, Maya Beukes², Gabriel Aramayo-Ledezma^{4,5}, Yannet Condori^{5,6}, José Luis Aramayo-Bejarano^{5,7,8} & Martin Jansen^{2,8}

¹ University of Veterinary Medicine, Research Institute of Wildlife Ecology, Vienna, Savoyenstraße 1, 1160 Vienna, Austria

² Senckenberg Research Institute and Nature Museum, Terrestrial Zoology, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

³ Van Hall Larenstein University of Applied Sciences, Department of Wildlife Management, Agora 1, 8934 CJ, Leeuwarden, Netherlands

⁴ Universidad Autónoma Gabriel René Moreno, Facultad de Ciencias Exactas y Tecnología, Ciudad Universitaria, Av. Busch, Módulo 242, Santa Cruz de la Sierra, Bolivia

⁵ Centro de Investigaciones Ecológicas Chiquitos, Departamento Santa Cruz, Bolivia.

⁶ Universidad Autónoma Gabriel René Moreno, Facultad de Ciencias Agrícolas, km 8 1/2 Carretera al Norte, Santa Cruz de la Sierra, Bolivia

⁷ Universidad Autónoma Gabriel René Moreno, Facultad Cs, Farmacéuticas y Bioquímicas & Facultad de Cs Exactas y Tecnología. Ciudad Universitaria, Av. Busch Santa Cruz de la Sierra, Bolivia

⁸ Museo de Historia Natural Noel Kempff Mercado, Av. Irala 565, Santa Cruz de la Sierra, Bolivia

***Contributed equally.**

Abstract

Large carnivores such as the jaguar (*Panthera onca*) are particularly susceptible to population decline and local extinction as a result of habitat loss. Here, we report on the long-term monitoring of a local jaguar population in a mixed land use area in the eastern lowlands of Bolivia from March 2017 to December 2019. We recorded 15 jaguar individuals and four reproduction events (five offspring from three females), suggesting that our study area harbors a resident breeding population. Seven iterations of spatially explicit capture-recapture models provided density estimates ranging from 1.32 to 3.57 jaguars per 100 km². Jaguar capture rates were highest in forested areas, with few to no jaguar captures occurring in pastures used for livestock. Massive deforestation after the survey period reduced the proportion of dense forest cover by 33%, shrinking the availability of suitable jaguar habitat and placing the resident jaguar population at risk. We use the jaguar as an indicator species to highlight the threat of habitat destruction in the Chiquitano region and to emphasize the importance of intact forest patches for jaguar conservation.

Introduction

Neotropical biodiversity is acutely threatened by habitat degradation as a consequence of human population growth, climate change, and human-caused fires (Ibisch & Mérida, 2004; Kosydar et al., 2014; Peñaranda & Simonetti, 2015). In Bolivia, the continued expansion of the livestock industry was the main contributor to deforestation over the past decades (Müller et al., 2012). This is especially true for the diverse ecosystems of the Chiquitano region in eastern Bolivia (Ibisch & Mérida, 2004; Killeen et al., 2006; Navarro, 2011). The endemic Chiquitano Dry Forest represents the largest block of tropical broad-leaf dry forest in South America (Miles et al., 2006; Power et al., 2016). From 2001 to 2006 approximately 15% of the original extent of the Chiquitano Dry Forest was deforested at a mean rate of 1,080 km² per year (Killeen et al., 2006). In addition, recent widespread, human-caused wildfires have destroyed 12% of the Chiquitano Dry Forest with dramatic consequences for biodiversity (Devisscher et al., 2016; Romero-Muñoz et al., 2019). While many of its small-sized vertebrate species were only recently described (Caminer et al., 2017; Jansen et al., 2019; Pansonato et al., 2020), a large portion remains unknown (Jansen et al., 2011; Gehara et al., 2014), and only few ecological studies have investigated the mammalian fauna (Anderson, 1997; Brooks et al., 2002). Long-term biodiversity monitoring programs are particularly scarce in this region, restricting the documentation and understanding of anthropogenic biodiversity loss, such as the effects of land use change.

Our study focuses on the jaguar (*Panthera onca*, Plate 1), the Neotropical apex predator. Jaguars are considered a wildlife indicator species (Thornton et al., 2016) and suffer

dramatically from illegal hunting, habitat destruction, and forest fragmentation (Wolf & Ripple, 2017; Tucker et al., 2018; Romero-Muñoz et al., 2020). Moreover, poaching has intensified as a result of negative attitudes towards jaguars determined by socioeconomic factors (Caruso et al., 2022), local human-jaguar-conflicts (Wallace et al., 2010, Plates S-1 and S-2), and wildlife trafficking of skulls, claws, and fangs to satisfy the Asian traditional medicine market (Nuñez & Aliaga-Rossel, 2017; Fraser, 2018). At an ecoregional scale (Chaco region of Paraguay, Argentina, and Bolivia) the jaguar distribution has already decreased by 33 % between 1985 and 2013, mainly due to illegal hunting and habitat loss (Romero-Muñoz et al., 2018), while at the national scale, the natural vegetation in central-eastern Bolivia decreased by more than 40 % between 1976 and 2005 (Zemanova et al., 2017). As a consequence, the Bolivian jaguar population has declined considerably from occupying approximately 75% to 50% of the country's area (Maffei et al., 2010). In the department of Santa Cruz, deforestation is identified as a major threat to the jaguar, and its habitat (263,000 km²) is predicted to be reduced by 50 % (to 137,000 km²) by the year 2046 (Maillard et al., 2020). Maillard et al. (2020) identified 39 connecting corridors of 58,000 km² between protected areas involving around 5,700 cattle properties, mainly in the central Chiquitano region. Thus, cattle ranches with suitable habitats should gain more attention in the context of conservation.

The protection of jaguars is system-relevant, as they are a keystone species that play a crucial role in sustaining balanced ecosystems by regulating prey populations.

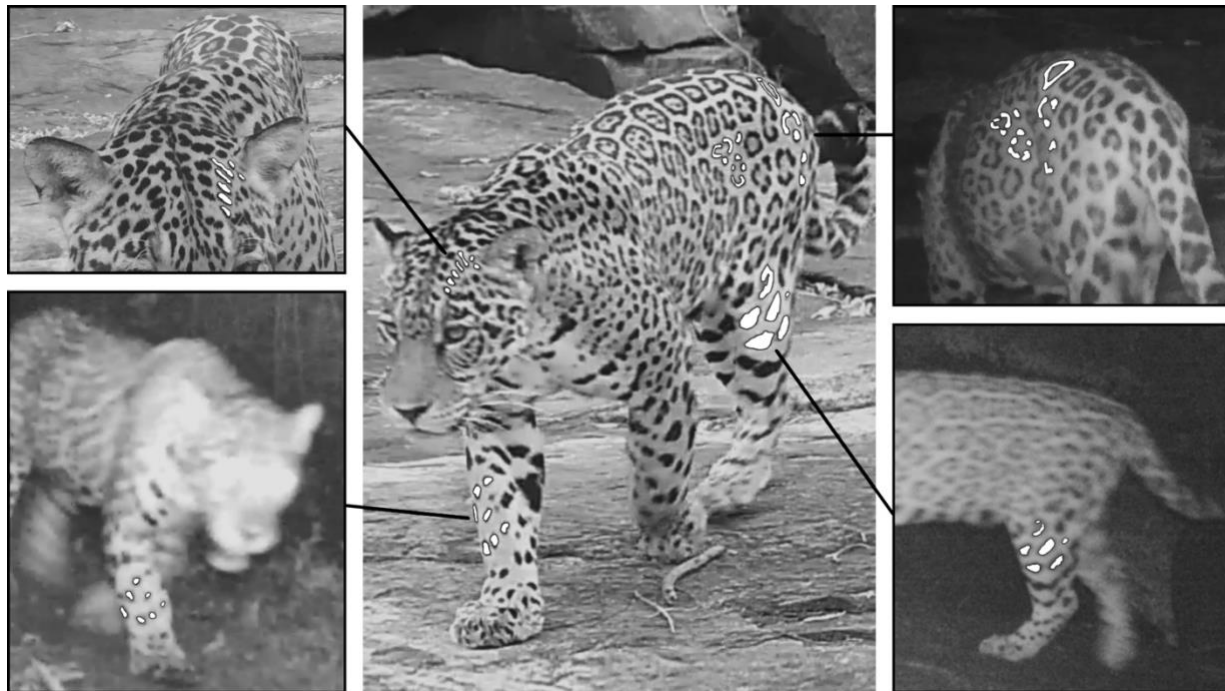


Plate 1 Recognition of jaguar individuals based on unique coat color patterning. All five images are from different capture events and display the same jaguar individual (female F-03) from different angles of varying image quality to demonstrate how unique coat patterning was used to repeatedly identify the same specimen.

Camera traps allow for constant, non-invasive, long-term biomonitoring of jaguars to measure shifts in population structure, or to estimate population sizes (Silver et al., 2004). Previous studies imply that the Chiquitano Dry Forest harbors a substantial but widely understudied population of jaguars and their prey (Rumiz et al., 2002; Arispe et al., 2007; Venegas et al., 2010; Polisar et al., 2016). Here, we report on an ongoing camera trapping survey established in 2017 (Jansen et al., 2020). We

provide rare insights into a healthy jaguar population in a South American dry forest habitat by characterizing complex life history trajectories and by estimating density and relative abundance in relation to land use. Furthermore, we highlight an alarming rate of deforestation by tracking changes in the forest cover of our study area over a five-year period. The scientific evidence we have gathered should be used to motivate against further deforestation in order to preserve the region's faunal and floral diversity.

Study area

Our study area (Fig. 1) covers 133 km² and comprises nine cattle ranches located in the Chiquitano region of the eastern Bolivian lowlands. Approximately 70 % of the area was covered by dense forest vegetation at the beginning of the study period in 2017. Extensive livestock farming is practiced in open areas, but no commercial crops are grown. The area is at an altitude of 500 meters above sea level and falls within a climatic and biogeographic transition zone between the Amazon rainforest, the Gran Chaco Dry Forest, and the Cerrado Savanna of Brazil. Temperatures vary marginally throughout the year with a mean daily

temperature of 24.4 °C (Killeen et al., 2006). Mean annual precipitation is around 1,200 mm (Schulze et al. 2009) with a dry season occurring between July and November (Killeen et al., 2006). The Chiquitano Dry Forest is the primary vegetation type and is characterized by relatively open forests with semi-deciduous trees interspersed with grasses and shrubs of the woody savanna (Killeen et al., 2006). In September 2020 a land conversion project aiming to convert ca. 15 km² of partially protected private forest to pasture was initiated in the core study area, and land use change is likely to progress.

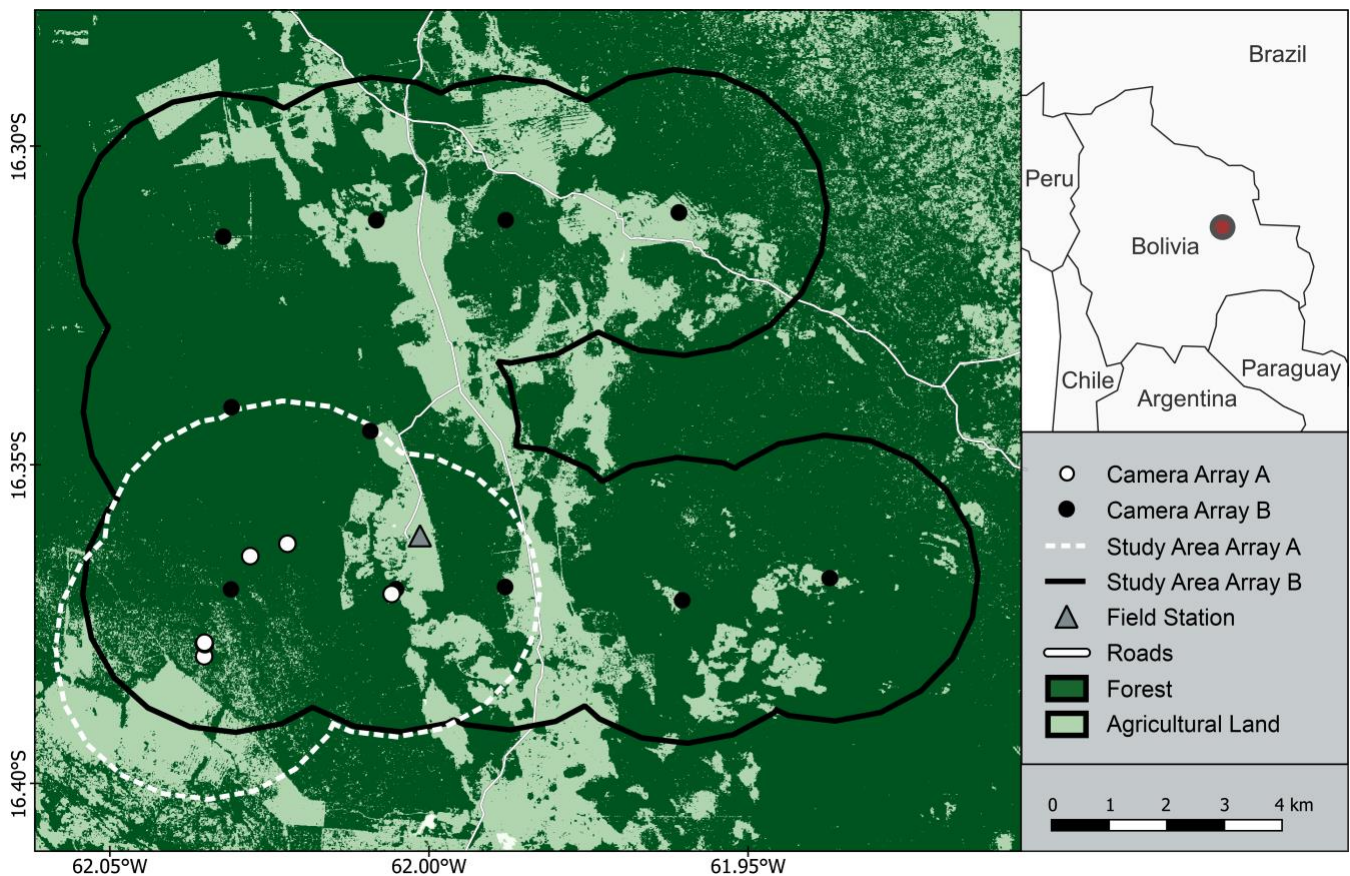


Figure 1 Location of the study area in the Chiquitano region of Bolivia showing the layout of the two camera trap arrays used over the study period from 2017 to 2019. A buffer of 2.5 km around each camera station was used to delineate study plot boundaries. The spacing between camera stations in Array B was approximately 2.5 km accounting for the home range size of jaguars as the focal species. The land use classification was derived from August 2019 imagery.

Methods

Study Design

We conducted two camera trap surveys between March 2017 and December 2019 using two partially overlapping camera trap arrays (Fig. 1). Array A, comprising 13 stations, was active from March 2017 (Jansen et al., 2020) to December 2019. Cameras in Array A were opportunistically placed across a 40 km² area along dirt roads, stream beds, and game trails to increase the probability of detecting species (Fig. 1). Cameras in Array A were mostly set to “photo mode”, or to “video mode” where the frequency of jaguar captures was high, and cameras collected data from 16,104 trap nights. Array B, comprising 11 stations (each with paired cameras), was set up in March 2019, and data collected until December 2019 was considered in this study. Cameras in Array B are laid out as a symmetric grid, covering 133 km² (Fig. 1). The spacing between camera stations in Array B is set to approximately 2.5 km to account for the home range size of jaguars as the focal species (Maffei et al., 2011). Camera traps in Array B were set to “photo mode” with a burst of three images per trigger event, and a minimum delay of 5 seconds between events. Cameras in Array B were active for 4,247 trap nights. A buffer of 2.5 km around each camera station was used to delineate study plot boundaries in Array A and Array B (Fig. 1).

Camera models included Bushnell Trophy Camera Brown Model 119437 (n = 26), Reconyx XR6 UltraFire (n = 3), and Cuddeback G-series Double Barrel Strobe (n = 18). All camera stations were placed in suited microsites, e.g. observed animal trails, and attached to trees 30-40 cm above ground. We visited each camera trap approximately every two weeks to change batteries and to secure data. Not all camera traps were consecutively active due to occasional battery problems or failures caused by humidity. For camera station operation times see Fig. S-1 and S-2. All subsequent analyses were carried out in R (v. 3.6.1) if not specified otherwise. All software and associated version numbers with references are listed in Supplementary Table S-1.

Image processing

To integrate videos into the processing workflow, we extracted three frames per video (t = 0 sec, t = 2 sec, t = 4 sec) using a custom python script (ExtractFramesFromVideo.py, settings --frameTimeLimit 4 -f 0.51). We uploaded all images and extracted frames to Labelbox (Labelbox, 2021), a web-based labeling platform frequently used to create training data sets for machine learning applications. We involved 251 citizen scientists in the online classification of the images (project “WildLIVE! - Entdecke die wilden Tiere Boliviens”, <https://wildlive.sgn.one>) from 5th April 2020 to 25th June 2021. For the initial pass (Step 1: Species assignment), citizen scientists processed the entirety of the camera trap image dataset (N=92,917) recorded by the camera trapping

setup and assigned them to categories: either as empty or as containing any of the defined target species. We (RM, MJ & MB) subsequently reviewed and revised all jaguar classifications made by citizen scientists (Step 2: Expert review) and further identified the remaining records to individual level based on unique coat color patterns (Step 3: Jaguar individualization; Plate 1). In some cases, individual identification was not possible due to insufficient image quality, and we excluded these records from the population structure and population abundance analyses. We assigned maturity as either “adult” (large, single individuals), or “juvenile” (small body size, and/or if accompanied by an adult) and sex according to visible genitalia, or repeated sightings of an adult individual with juvenile(s), which we took as evidence for a female. Offspring was assigned to a specific female if recorded in the same capture event.

Camera trapping data analysis

From a total of 2,869 images labeled by citizen scientists as featuring jaguars, we first discarded 127 images (4.4%) with erroneous timestamps resulting from technical problems. To avoid multiple counting we discarded images with repeated identification of the same individual or a record of an unidentified individual at the same station within 60 minutes and applied temporal autocorrelation (Silveira et al., 2003 ; Foster et al., 2013). The remaining 437 capture events were used to fit an activity curve. To investigate variation in activity relative to sunrise/sunset we used the solar cycle historical data obtained from the R *suncalc* package. Capture events were grouped according to time of day in three categories; day (8h00 to 18h00), night (20h00 to 5h00), and twilight (18h00 to 20h00 and 5h00 to 8h00; Jędrzejewski et al., 2021).

We characterized population composition in terms of sex ratio, kinship, and individual presence after discarding 93 images (3.4%) where unambiguous identification was impossible due to insufficient image quality or photo angle. The adult sex ratio was calculated as the ratio of adult males to adult females in the study area per year. We visualized individual-based capture events (including unidentified individuals) per station in terms of capture frequency relative to sampling effort (number of captures divided by the number of active trapping nights per station * 1000 Botts et al., 2020).

Jaguar density was estimated using maximum likelihood spatially explicit capture recapture (SECR) models using the *secr* package in R. This approach estimates density over a defined space following a hierarchical multi-component model which includes a state-model to describe the spatial distribution of an animal's home range center, and an observation model to describe detections relative to the distance between the home range center and the detector (Borchers & Efford, 2008). Commonly, estimates are calculated for short survey periods as closed capture-recapture models assuming that no births, deaths, or

migration occur during the sampling period (Kendall, 1999). However, extending survey periods from traditional values of e.g. 90 days to 180 days has been shown to improve precision and stability when estimating densities of long-lived mammals across multiple iterations (Dupont et al., 2019; Harmsen et al., 2020). We selected seven overlapping periods of 180 consecutive days in monthly intervals throughout 2019, from the first day of January to July 2019 (Harmsen et al., 2020). Two consecutive sessions had a mean overlap of 83.2% which decreased by a mean of 17% for each session in-between. Every session included temporally independent captures of adult jaguars, as cubs of solitary felids generally have low capture probabilities (Karanth, 1995) and cannot be considered independent of their mother. We generated capture histories of every 180-day session while accounting for potential differences in sampling effort per station (if the cameras per station differed in their activity due to technical problems) and fitted SECR models to every session. Every model was fitted using a half-normal detection function and the default model structure. We defined the area of interest by a buffer size of at least five times the initial estimate of the root pooled spatial variance (Slade & Swihart, 1983), which ranged from 6,588.5 m to 9,642.7 m (mean 8,169.1 \pm 1,486.7 m). We did not include sex as an individual-related covariate as a distinction between sexes drastically reduced the number of captures available to estimate density per session resulting in too poor of a model fit.

Results

Population structure, life history trajectories and activity

We analyzed a total of 20,351 trap nights and assigned individual identifications to all jaguar capture events if image quality was sufficient, and furthermore inferred reproduction, mortality, and activity patterns based on individual occurrence data.

We documented 437 independent capture events (12.85 \pm 9.83 per month) throughout the study period (March 2017 to December 2019, Array A plus Array B) and the detected number of jaguar individuals per month (= minimal estimate) varied between 1 and 5 (2.76 \pm 0.99, Fig. 2). Among 15 identified jaguars we recorded 6 males, 4 females, and 5 juveniles. Four reproduction events (5 cubs) and three deaths were inferred (one adult and two cubs; Fig. 2; Plate S-1). Jaguars in our study area followed a mostly nocturnal and crepuscular activity pattern with 48% of records occurring at night and 40% at twilight (Fig. 3).

Density and spatial distribution

Based on 437 independent jaguar capture events, we estimated population density for both camera arrays using the same SECR model, and inferred spatial distribution based on abundance relative to sampling efforts.

We tested whether jaguar captures of Array B in 2019 differed significantly between land use using Wilcoxon's rank sum test (with $\alpha = 0.05$). Since open landscapes and some forest patches are used as pastures, we classified the type of land-use at each camera station as being either pasture (> 5 livestock capture events) or non-pasture (< 5 livestock capture events) for this analysis.

Vegetation cover analysis

Three cloudless Sentinel-2 images of the study area were acquired from Earthexplorer (USGS) for the years 2017 (early study period), 2019 (late study period), and 2021 (after survey concluded and extensive deforestation took place). All 10 m resolution images were taken between 15th and 20th August to avoid seasonal bias (Coppin et al., 2004). The images were processed to show the Normalized Difference Vegetation Index (NDVI) within a range between -1 and 1 (Aburas et al., 2015) using QGIS. Negative values refer to a lack of vegetation cover, whereas positive values refer to different rates of vegetation density. NDVI for the study area was assigned to five classes ranging from no vegetation to dense vegetation cover. The resulting cover density rasters were used to calculate the decrease of vegetation cover in the study area over a five-year period (Aburas et al., 2015).

Density estimates ranged from 1.32 (SE 1.86) to 3.57 (SE 2.58) jaguars per 100 km² (Fig. 4, Supplementary Table S-2). Jaguar detection frequency in relation to sampling effort and independent jaguar captures was highest in the southwestern, forested section of the study area (Fig. 5). Land use classification based on livestock observations indicates that jaguars occupy forest patches that are not used as pasture significantly more than areas frequently used for livestock grazing ($p = 0.021$, effect size $r = 0.72$, Fig. S-3). Few to no jaguars were recorded in transformed agricultural land (Fig. 5).

Land use change

We created three NDVI maps of our study area to visualize the vegetation change (Fig. 6). Two NDVI maps were made during the survey period (2017-2019) and one NDVI map was made of the area's recent state (2021).

Major deforestation and conversion activities were observed between 2017 and 2021, and the ratio of dense vegetation cover within the study area decreased by 33% between 2017 and 2021 (Fig. 6). In contrast, medium densely vegetated areas increased by 26% and areas with a low vegetation density increased by 7%. We estimate that approximately 46.48 km² of forest within the study area has been cleared or severely degraded over a five-year period.

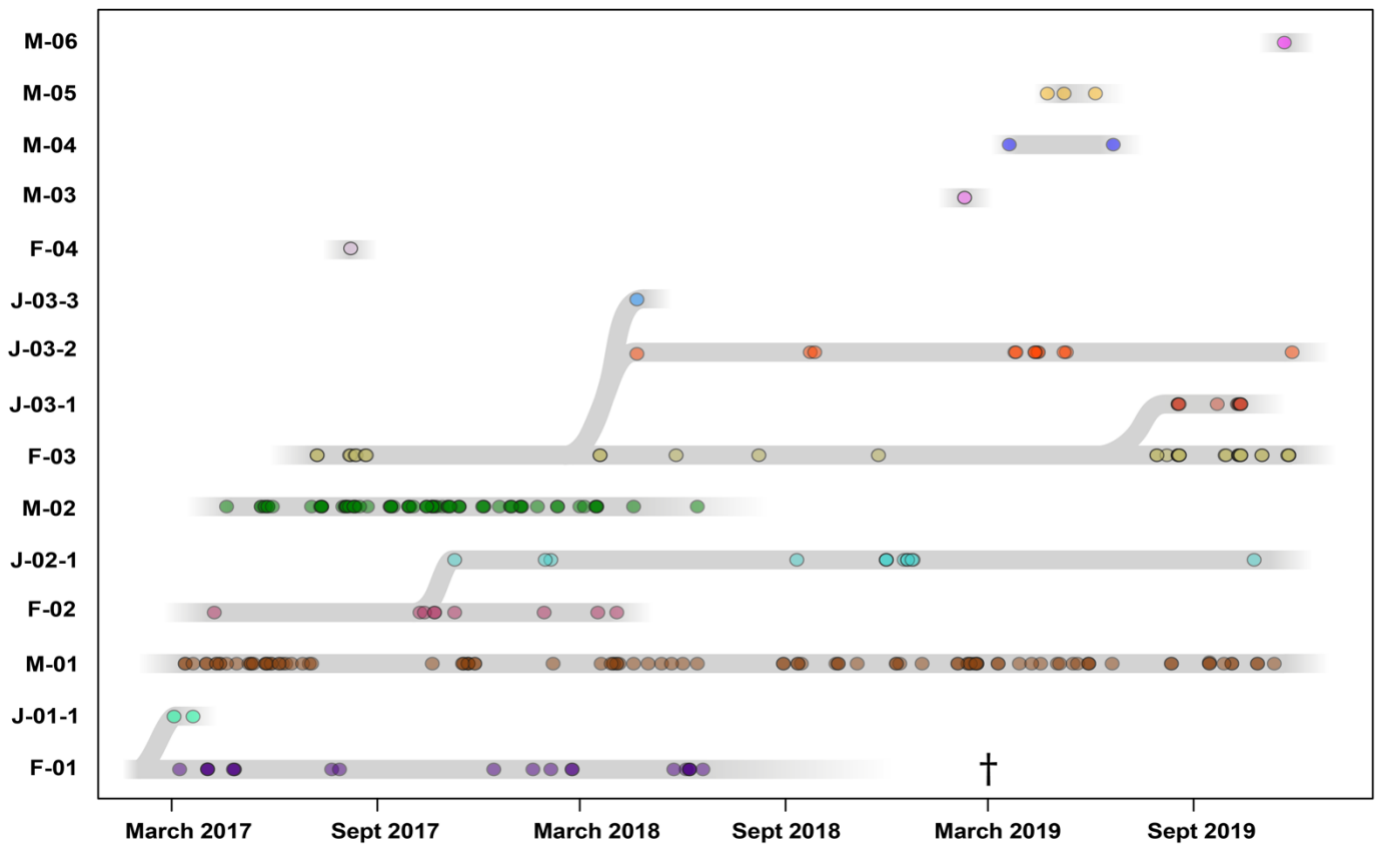


Figure 2 Individual life histories as illustrated by capture histories of jaguars over three years in the Chiquitano Dry Forest. Linked bands depict mother-offspring relationships; F= female, M=male; J=juvenile; cross indicates the confirmed death of an individual.

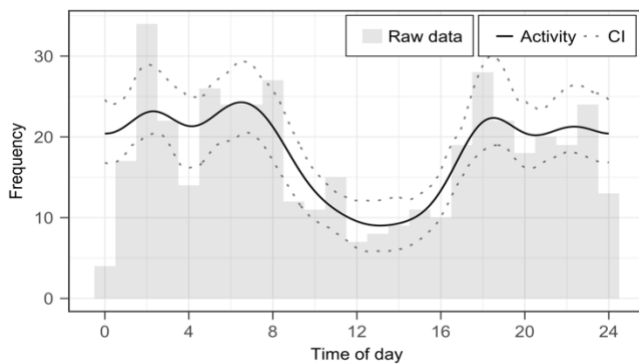


Figure 3 Circadian activity of jaguars in the study area including all capture events from camera Arrays A and B pooled. Solid line: Modeled activity. Dotted lines: upper and lower confidence intervals. Bars: raw data.

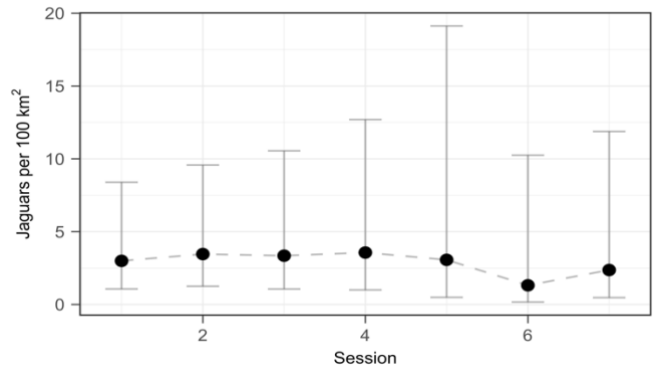


Figure 4 Density estimates (individuals per 100 km²) of all seven sessions (representing consecutive survey periods of 180 days in monthly intervals) in 2019. Black dots: Density estimates, bars: Upper and lower confidence intervals.

Discussion

Our study area harbors a productive jaguar population. Out of the ten recorded adult jaguars, three females and two males appeared to be resident individuals as they were repeatedly captured on the camera traps. At least two out of five cubs deceased before reaching adulthood and only two juveniles were recaptured independent from their mothers in later life stages.

The adult sex ratio (males:females) increased over the study period (first year: 1:2, second year: 1:1.5, third year: 1:0.4). More studies have identified male-biased (Maffei et al., 2004; Soisalo & Cavalcanti, 2006; Salom-Pérez et al., 2007), than female-biased (Moreno et al., 2006; Tobler & Powell, 2013) sex ratios, which we observed only in the final year of our study. However, our observed shift towards

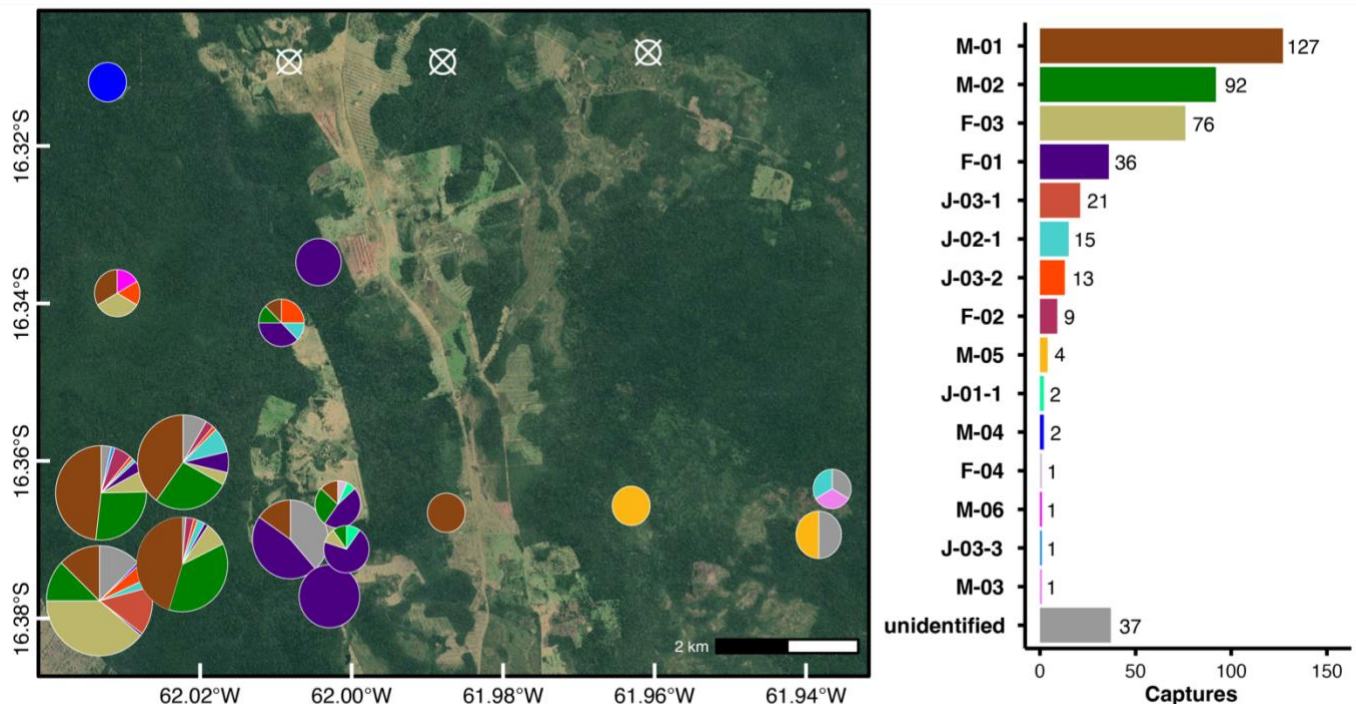


Figure 5 Temporally independent jaguar captures per station (pie chart) integrated over the entire study period (bar chart). Pie chart sizes are scaled by jaguar abundance relative to sampling effort. White points (⊗) resemble stations with no captures. Note that the diameter of the pie charts reflects sampling effort, and that the number of individuals per chart is not directly comparable between stations. Base map was retrieved from Google (2022). (Readers of the printed journal are referred to the online article for a color version of this figure.)

more males in 2019 likely results from extending the surveyed area towards a better representation of the sampled population, rather than documenting an actual sex ratio shift over time. Males and females differ in their spatial use of habitats (Conde et al., 2010; Maffei et al., 2011), which causes spatial heterogeneity of sex ratios within a population, with small survey areas not necessarily being representative of the sampled population. While our initial restricted setup (Camera Array A) covered a core habitat for resident females (as it contained a protected forest particularly suited for females to raise offspring, evidenced by frequent mother-cub captures), the later expansion of the survey area into a larger mixed landscape (more representative for the region, Camera Array B) shifted the observed sex ratio towards males, which are more tolerant to human-modified landscapes (Conde et al., 2010). Because Camera Array A was set up based upon anecdotal reports of frequent jaguar reproduction events it is likely female-biased. On the contrary, Camera Array B uses a systematic grid layout and covers a larger fraction of the sampled population. Yet even the 2019 sex ratio (like any sex ratio estimate using similar methodology) is potentially biased by known sex-specific differences in jaguars. It is assumed that males are more frequently caught in camera traps, as they have larger territories, are more mobile (Crawshaw & Quigley, 1991; McBride & Thompson, 2018), and are more likely to disperse over greater distances

(Kantek et al., 2021), causing a general bias towards capturing male jaguars.

Little is known about reproduction in wild jaguars, but our survey provides some insights. Between March 2017 and December 2019 we evidenced four reproduction events involving three females. Three litters consisted of single cubs, and one of two cubs. Geographically diverse studies documented similarly sized litters and attributed them to low conception rates or high infant mortality (Cavalcanti & Gese, 2009; Carrillo et al., 2009; Cuéllar et al., 2012). One female reproduced twice with approximately 16 months between the first records of the first and second litter. The results from a radiotelemetry based study estimated a 22-24 month breeding interval for wild jaguars (Carrillo et al., 2009).

Our data indicates no mating season in jaguars, which is consistent with previous studies (Cavalcanti & Gese, 2009; Beisiegel et al., 2012; Cavalcanti et al., 2012; Harmsen et al., 2020). The occurrence of females and cubs was concentrated in forested areas, suggesting that these patches provide better conditions to raise offspring than a more disturbed and fragmented environment. This is in line with previous studies and has been associated with higher prey abundances compared to open landscapes (Weckel et al., 2006; Conde et al., 2010). We found no evidence for seasonal spatial avoidance between females as suggested by Cavalcanti & Gese (2009), but some evidence for the avoidance between males: During the first survey year, an

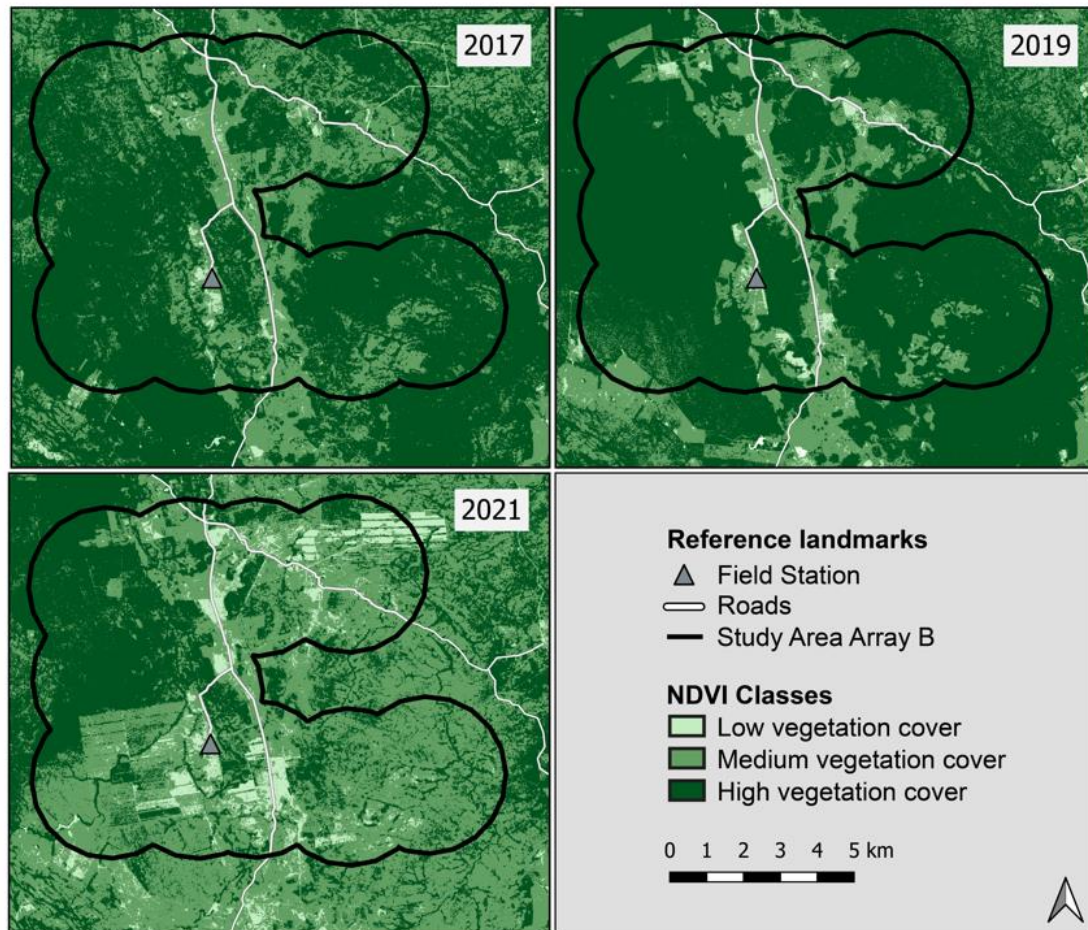


Figure 6 NDVI vegetation cover classes for August 2017, August 2019, and August 2021. Major fires and deforestation took place between September and December 2019. Study Area Array B was used as the reference to calculate vegetation cover change.

increased capture frequency of a known resident male (M-02) corresponded with fewer sightings of a second known male (M-01), and the disappearance of the first male (July 2018) resulted in higher capture frequencies of the second male.

Jaguars exhibited primarily nocturnal and crepuscular activity periods with peaks in activity around dusk/dawn, and 2/3 am. While several studies found similar activity patterns in Bolivia (Maffei et al., 2011), others report deviating patterns throughout the distribution range of the jaguar, supporting flexibility in the species' circadian activity (Botts et al., 2020). This variation in jaguar activity patterns might be correlated with habitats, prey, and competition (Harmsen et al., 2011; Botts et al., 2020). Additionally, sex and reproductivity could further affect jaguar activity with reproductive females showing higher daytime activity levels than adult males, non-reproductive females, and cubs (Jędrzejewski et al., 2021).

Our estimated jaguar densities coincide with similar studies from the Chiquitano Dry Forest (Supplementary Table S-3). These results provide further support that unprotected areas with intact natural habitats, especially cattle ranches, represent crucial habitats for jaguars (Arispe et al., 2003; Rumiz et al., 2003; Maffei et al., 2011; Jędrzejewski et al., 2018). Ecological research on jaguars to date has focused

on protected areas and only one fifth (27/131) of the available density estimates are derived from unprotected areas (Foster et al., 2020). Density estimates with SECR in small study areas over short time frames require cautious interpretation. However, the reliability of density estimates can be strengthened by providing estimates acquired over multiple survey sessions throughout a year (Harmsen et al., 2020). We provide a range of density estimates using a 180-day sample period taken over 12 months, instead of the commonly used, single, 50 to 70-day survey period (Jędrzejewski et al., 2021). So far, population closure in jaguars is poorly understood and by extending the survey period to 180 days the data gained is thought to outweigh the risk of closure violation (Tobler & Powell, 2013).

We recorded no capture events in deforested agricultural land indicating that jaguars avoid agricultural areas. However, jaguars are able to persist within agricultural regions that maintain intact forested areas and where hunting of both jaguar and prey is limited (Boron et al., 2016). Jaguar activity depends on forest coverage and prey availability which is likely linked to jaguars' opportunistic foraging behavior (Weckel et al., 2006; Thompson et al., 2018).

Deforestation and the number of large wildfires in the Brazilian Amazon have dramatic consequences on

biodiversity and displace hundreds of jaguars per year (Menezes et al., 2021). Widespread wildfires in 2019 burned 20,000 km² of Chiquitano Dry Forest, killing an estimated 5.9 million mammals (Pacheco et al., 2021). These fires affected our study area in August 2019, coinciding with the second lowest density estimation of jaguars afterwards. While we note this coincidence, we refrain from interpreting it at this point due to residual statistical uncertainty. Protected areas serve as important refuges for large carnivores, but they may not be large enough to sustain viable populations (Rabinowitz & Zeller, 2010; Boron et al., 2016). The jaguar in particular is at risk of displacement, population decline, and local extinction (Menezes et al., 2021). Previous studies documented healthy and rich ecosystems in the Chiquitano Dry Forest (Rumiz et al., 2002; Arispe et al., 2007; Venegas et al., 2010; Polisar et al., 2016; Jansen et al., 2020). Our results give further support that the Chiquitano Dry Forest in Bolivia, often embedded in a mixed land use area, harbors a significant, but still largely understudied population of jaguars.

Our investigation reports on a productive jaguar site on privately owned lands, just before the destruction of much of this habitat through massive deforestation. Of the 263,000 km² potential jaguar habitats in the Department of Santa Cruz, a large portion (55%) occurs on privately owned properties that potentially harbor productive jaguar sites (Maillard et al., 2020). Therefore, it seems exceedingly important to involve private landowners in actions to

address nature conservation to counteract biodiversity loss. Future regional landscape management should focus on the connectivity between conservation units in order to preserve wildlife in fragmented areas (Hess & Fischer, 2001; Petracca et al., 2014). Due to the specific situation in the Chiquitano region, where around 5,700 cattle properties consist mainly of potential jaguar habitat (Maillard et al. 2020), private landowners are in the position to make significant contributions to the protection of the Chiquitano Dry Forest. Therefore, local institutions and NGOs should explore ways to include and integrate landowners in conservation actions accompanied by education and open discussions. For example, bringing all landscape stakeholders (farmers, indigenous communities, conservationists) together in participatory and co-creational processes could increase local knowledge and awareness of nature and its threats. This could contribute to strengthening the socio-cultural identity of indigenous communities towards nature and the landowners' capacity for sustainable land use management. Incentives for ranchers such as green labeling and biodiversity credits, should be developed (Amit & Jacobson, 2018; Hyde et al., 2022), and ecotourism in the region should be promoted. These efforts could use projects like the San Miguelito ranch as a model to approach the human-jaguar conflict in Bolivia (Rumiz et al., 2002, 2003; Arispe et al., 2005). Furthermore, efforts in environmental information and education should be increased to improve how biodiversity is perceived locally (Marchini & Macdonald, 2020).

Author contributions

Study management and supervision: MJ, study design: MBI, MJ, RM. Raw data management: JL. Data collection in the field: YC, JL, GA, RM, MBI, MJ. Jaguar individual identification: RM, MBI, MJ. Data analysis: MW, MBe, MBI, MJ, RM. Writing: MJ, RM, MBI, MBe, MW. Figures: MW, MBe, MBI, RM, MJ, GA. External funding: MJ.

Acknowledgements

We want to thank especially the owners of the involved cattle ranches: Domingo Nazer, Roger Alejandro Parada Ortiz, Ángel Belaunde, María E. Suarez de la Belaunde, Eduardo Jordán and Miguel Antelo, as well as our collaborators in the field: Israel Costaleito, Leidy Chamu, Mario Cerón Altamirano, Lenor Guayacuma, Wilber Daza Humaza, Corcino Ramos, Eugenio Mallco, Eunice Copa, Emanuel Crespo, Sissy Suarez and Martha Córdova. Analysis of camera trap data was only possible because of the enormous engagement of many citizen scientists (see Tab. S-4). We especially thank Anja Czoelder, Jan Göpel, Alexandra König, Carmen Spalke, Alexandra Ottong, and Peter Zehner. We thank the editor and two anonymous reviewers for their constructive critique and positive review of our paper. Alfredo Romero-Muñoz provided useful comments on a previous version of the manuscript, and Oswaldo Maillard contributed additional information. This study was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – 437771903, and by BIOPAT e.V., Darmstadt, Germany. The study was performed under the agreement between the Museo Historia Natural Noel Kempff Mercado, Santa Cruz, and the Senckenberg Research Institute and Nature Museum approved by the Directorate of Biodiversity, Ministry of Environment and Water, Plurinational State of Bolivia.

Conflicts of interest

None

Ethical standards

Our handling and use of camera trap data was aligned with the ethical code of conduct framework as described by Sharma et al. (2020)”

References

- Aburas, M.M., Abdullah, S.H., Ramli, M.F. & Ash'aari, Z.H. (2015) Measuring land cover change in Seremban, Malaysia using NDVI index. *Procedia Environmental Sciences*, 30, 238–243.
- Amit, R. & Jacobson, S.K. (2018) Participatory development of incentives to coexist with jaguars and pumas. *Conservation Biology*, 32, 938–948.
- Anderson, S. (1997) Mammals of Bolivia: taxonomy and distribution. *Bulletin of the American Museum of Natural History* 231, 1–652.
- Arispe, R., Rumiz, D.I. & Venegas, C. (2005) *Second camera-trap Survey for jaguars (Panthera onca) and other mammals at San Miguelito Ranch*. Wildlife Conservation Society, Bolivia.
- Arispe, R., Rumiz, D.I. & Noss, A.J. (2007) Six species of cats registered by camera trap surveys of tropical dry forest in Bolivia. *Cat News*, 46, 36–38.
- Beisiegel, B., Sana, D. & Moraes, E. (2012) The jaguar in the Atlantic Forest. *Cat News*, Special Issue 7, 14–18.
- Borchers, D.L. & Efford, M. (2008) Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics*, 64, 377–385.
- Boron, V., Tzanopoulos, J., Gallo, J., Barragan, J., Jaimes-Rodriguez, L., Schaller, G., et al. (2016) Jaguar densities across human-dominated landscapes in Colombia: the contribution of unprotected areas to long term conservation. *PLoS ONE*, 11, e0153973.
- Botts, R. T., Eppert, A.A., Wiegman, T.J., Rodriguez, A., Blankenship, S.R., Asselin, E.M., et al. (2020) Circadian activity patterns of mammalian predators and prey in Costa Rica. *Journal of mammalogy*, 101, 1313–1331.
- Brooks, D.M., Rojas, J.M., Aranibar, H., Vargas, R.J. & Tarifa, T. (2002) A preliminary assessment of mammalian fauna of the Eastern Bolivian Panhandle. *Mammalia*, 65, 509–520.
- Caminer M.A., Milá, B., Jansen, M., Fouquet, A., Venegas, P.J., Chávez, G., Chek, A., Ron, S.R. (2017) Systematics of the *Dendropsophus leucophyllatus* species complex (Anura: Hylidae): Cryptic diversity and the description of two new species. *PLoS ONE*, 12, e0176902
- Carrillo, E., Saenz, J. & Fuller, T. (2009) Interbirth interval of a free-ranging jaguar. *Mammalian Biology*, 74, 319–320.
- Caruso, F., Perovic, P., Talamo, A., Sillero-Zubiri, C., Altrichter, M. (2022) Human-jaguars coexistence: social factors influencing jaguar conservation in Southern Bolivia. *Kempffiana*, 17, 1–17.
- Cavalcanti, S.M. & Gese, E.M. (2009) Spatial ecology and social interactions of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. *Journal of Mammalogy*, 90, 935–945.
- Cavalcanti, S.M., Azevedo, F.D., Tomás, W.M., Boulhosa, R.L. & Crawshaw Jr, P.G. (2012) The status of the jaguar in the Pantanal. *Cat News*, 7, 29–34.
- Conde, D.A., Colchero, F., Zarza, H., Christensen Jr, N.L., Sexton, J.O., Manterola, C., Chávez, C., et al. (2010) Sex matters: Modeling male and female habitat differences for jaguar conservation. *Biological Conservation*, 143, 1980–1988.

- Coppin, P., Jonckheere, I., Nackaerts, K., Muys, B. & Lambin, E. (2004) Review Article Digital change detection methods in ecosystem monitoring: a review. *International journal of remote sensing*, 25, 1565–1596.
- Crawshaw Jr, P.G. & Quigley, H.B. (1991) Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. *Journal of Zoology*, 223, 357–370.
- Cuéllar, R.L., Alarcón, D., Peña, F., Méndez, C., Romero-Muñoz, A., Maffei, L., et al. (2012) Kaaiyana: a jaguar with cubs in the Kaa-lya del Gran Chaco National Park, Bolivia. *Cat News*, 57, 4–6.
- De Souza, J.C., da Silva, R.M., Gonçalves, M.P.R., Jardim, R.J. & Markwith, S.H. (2018) Habitat use, ranching, and human wildlife conflict within a fragmented landscape in the Pantanal, Brazil. *Biological Conservation*, 217, 349–357.
- Devisscher, T., Anderson, L.O., Aragão, L.E., Galván, L. & Malhi Y. (2016) Increased wildfire risk driven by climate and development interactions in the Bolivian Chiquitania, Southern Amazonia. *PLoS ONE*, 11, p.e0161323.
- Dupont, P., Milleret, C., Gimenez, O. & Bischof, R. (2019) Population closure and the bias-precision trade-off in spatial capture–recapture. *Methods in Ecology and Evolution*, 10, 661–672.
- Efford, M. G., & Schofield, M. R. (2020) A spatial open-population capture-recapture model. *Biometrics*, 76, 392-402.
- Fraser, B. (2018) China's lust for jaguar fangs imperils big cats. *Nature*, 555, 13–14.
- Foster, V.C., Sarmiento, P., Sollmann, R., Tôrres, N., Jácomo, A.T.A., Negrões, N., et al. (2013) Jaguar and puma activity patterns and predator-prey interactions in four Brazilian biomes. *Biotropica*, 45, 373–379.
- Foster, R.J., Harmsen, B.J., Urbina, Y.L., Wooldridge, R.L., Doncaster, C.P., Quigley, H., et al. (2020) Jaguar (*Panthera onca*) density and tenure in a critical biological corridor. *Journal of mammalogy*, 101, 1622-1637.
- Gehara, M., Crawford, A.J., Orrico, V.G., Rodriguez, A., Loetters, S., Fouquet, A., et al. (2014) High levels of diversity uncovered in a widespread nominal taxon: continental phylogeography of the Neotropical tree frog *Dendropsophus minutus*. *PLoS ONE*, 9, e103958.
- Google (2022) Static map. <https://maps.googleapis.com/maps/api/staticmap?center=-16.345,-61.9865&zoom=13&size=640x640&scale=2&mapttype=satellite&language=en-EN&key=xxx> [accessed 01 December 2022].
- Hess, G.R. & Fischer, R.A. (2001) Communicating clearly about conservation corridors. *Landscape Urban Plan*, 55, 195–208.
- Hyde, M., Boron, V., Rincon, S., Passos Viana, D. F., Larcher, L., Reginato, G. A., & Payán, E. (2022) Refining carbon credits to contribute to large carnivore conservation: The jaguar as a case study. *Conservation Letters*, 2022, 15:e12880.
- Ibisch, P.L. & Mérida, G. (2004) *Biodiversity: The richness of Bolivia*. Editorial FAN, Santa Cruz, Bolivia.
- Jansen, M., Bloch, R., Schulze, A. & Pfenninger, M. (2011) Integrative inventory of Bolivia's lowland frogs reveals hidden diversity. *Zoologica Scripta*, 40, 567–583.
- Jansen, M., Engler, M., Blumer, L.M., Rumiz, D.I., Aramayo, J.L. & Krone, O. (2020) A camera trapping survey of mammals in the mixed landscape of Bolivia's Chiquitano region with a special focus on the jaguar. *CheckList*, 16, 323–335.
- Jansen, M., Santana, D., Teixeira, B.F.D. & Köhler, G. (2019) A new striped species of *Dendropsophus* (Anura: Hylidae) with a composite advertisement call and comments on the *D. rubicundulus* group. *Vertebrate Zoology*, 69, 227–246.
- Jędrzejewski, W., Robinson, H.S., Abarca, M., Zeller, K.A., Velasquez, G., Paemelaere, E.A.D., et al. (2018) Estimating large carnivore populations at global scale based on spatial predictions of density and distribution - Application to the jaguar (*Panthera onca*). *Plos ONE*, 13, e0194719.

- Jędrzejewski, W., Vivas, I., Abarca, M., Lampo, M., Morales, L.G., Gamarra, G., et al. (2021) Effect of sex, age, and reproductive status on daily activity levels and activity patterns in jaguars (*Panthera onca*). *Mammal Research*, 66, 531–539.
- Kantek, D.L.Z., Trinca, C.S., Tortato, F., Devlin, A. L., de Azevedo, F.C.C., Cavalcanti, S., et al. (2021) Jaguars from the Brazilian Pantanal: Low genetic structure, male-biased dispersal, and implications for long-term conservation. *Biological Conservation*, 259, 109153.
- Karanth, K.U. (1995) Estimating tiger *Panthera tigris* populations from camera-trap data using capture-recapture models. *Biological Conservation*, 71, 333-338.
- Kendall, W.L. (1999) Robustness of closed capture-recapture methods to violations of the closure assumption. *Ecology*, 80, 2517–2525.
- Killeen, T.J., Chavez, E., Pena-Claros, M., Toledo, M., Arroyo, L., Caballero, J., et al. (2006) The Chiquitano dry forest, the transition between humid and dry forest in eastern lowland Bolivia. In *Neotropical Savannas and Seasonally Dry Forests: Plant Diversity, Biogeography and Conservation* (eds R.T. Pennington, G.P. Lewis & J.A. Ratter), pp. 213–223. CRC Press, Boca Raton, USA.
- Kosydar, A.J., Rumiz, D.I., Conquest, L.L. & Tewksbury, J.J. (2014) Effects of hunting and fragmentation on terrestrial mammals in the Chiquitano Forests of Bolivia. *Tropical Conservation Science*, 7, 288–307.
- Labelbox (2021) [Online]. Available: <https://labelbox.com>, [accessed on 22 August 2022].
- Maffei, L., Cuéllar, E. & Noss, A.J. (2004) One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera trapping in the Kaa-lyá National Park. *Journal of Zoology*, 262, 295–304
- Maffei, L., Rumiz, D., Arispe, R., Cuellar, E. & Noss, A. (2010) Situación del jaguar en Bolivia. In *El Jaguar en el Siglo XXI: La Perspectiva Continental* (eds R.A. Medellín, J.A. de la Torre, H. Zarza, C. Chávez & G. Ceballos), pp. 353–366. Fondo de Cultura Económica, Universidad Nacional Autónoma de México, México City.
- Maffei, L., Noss, A.J., Silver, S.C. & Kelly, M.J. (2011) Abundance/density case study: Jaguars in the Americas. In *Camera traps in Animal Ecology*, (eds A.F. O'Connell, J.D. Nichols & K.U. Karanth), pp. 119–144. Springer, Tokyo, Japan.
- Maillard, O., Angulo, S., Vides-Almonacid, R., Rumiz, D., Vogt, P., Monroy-Vilchis, O., et al. (2020) Integridad del paisaje y riesgos de degradación del hábitat del jaguar (*Panthera onca*) en áreas ganaderas de las tierras bajas de Santa Cruz, Bolivia. *Ecología en Bolivia*, 55, 94–110.
- Marchini, S. & Macdonald, D.W. (2020) Can school children influence adults' behavior toward jaguars? Evidence of intergenerational learning in education for conservation. *Ambio*, 49, 912–925.
- Masubuchi, S., Watanabe, E., Seo, Y., Okazaki, S., Sasagawa T., Watanabe, K., et al. (2020) Deep-learning-based image segmentation integrated with optical microscopy for automatically searching for two-dimensional materials. *npj 2D Materials and Applications*, 4, 1–9.
- McBride, R.T. & Thompson, J.J. (2018) Space use and movement of jaguar (*Panthera onca*) in western Paraguay. *Mammalia*, 82, 540–549.
- Menezes, J.F., Tortato, F.R., Oliveira-Santos, L.G., Roque, F.O. & Morato, R.G. (2021) Deforestation, fires, and lack of governance are displacing thousands of jaguars in Brazilian Amazon. *Conservation Science and Practice*, 3, e477.
- Miles, L., Newton, A.C. & DeFries, R.S. (2006) A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, 33, 491–505.
- Moreno, R.S., Kays, R.W. & Samudio, R. (2006) Competitive release in diets of ocelot (*Leopardus pardalis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. *Journal of Mammalogy*, 87, 808–816.
- Müller, R., Müller, D., Schierhorn, F., Gerold, G. & Pacheco, P. (2012) Proximate causes of deforestation in the Bolivian lowlands: an analysis of spatial dynamics. *Regional Environmental Change*, 12, 445–459.

- Navarro, G. (2011) *Clasificación de la vegetación de Bolivia*. Centro de Ecología Simón I. Patiño, Santa Cruz, Bolivia.
- Núñez, A. & Aliaga-Rossel, E. (2017) Jaguar fang trafficking by Chinese in Bolivia. *Cat News*, 65, 50–51.
- Pacheco, L.F., Quispe-Calle, L.C., Suárez-Guzmán F.A., Ocampo, M. & Claire-Herrera, Á.J. (2021) Muerte de mamíferos por los incendios de 2019 en la Chiquitania. *Ecología en Bolivia*, 56, 4–16.
- Pansonato, A., Motta, A., Cacciali, P., Haddad, C.F.B., Strüssmann, C. & Jansen, M. (2020) On the identity of species of *Oreobates* (Anura: Craugastoridae) from central South America, with the description of a new species from Bolivia. *Journal of Herpetology*, 54, 393–412.
- Peñaranda, D.A. & Simonetti, J.A. (2014) Predicting and setting conservation priorities for Bolivian mammals based on biological correlates of risk of decline. *Conservation Biology*, 29, 834–843.
- Petracca, L.S., Hernández-Potosme, S., Obando-Sampson, L., Salom-Pérez, R., Quigley, H. & Robinson, H.S. (2014) Agricultural encroachment and lack of enforcement threaten connectivity of range-wide jaguar (*Panthera onca*) corridor. *Journal for Nature Conservation*, 22, 436–444.
- Polisar, J., de Thoisy, B., Rumiz, D.I., Díaz Santos, F., McNab R.B, Garcia-Anleu R, et al. (2016) Using certified timber extraction to benefit jaguar and ecosystem conservation. *Ambio*, 46, 588–603.
- Power, M.J., Whitney, B.S., Mayle, F.E., Neves, D.M., de Boer, E.J. & Maclean, K.S. (2016) Fire, climate and vegetation linkages in the Bolivian Chiquitano seasonally dry tropical forest. *Philosophical transactions of the Royal Society of London, Series B, Biological sciences* 371, 20150165.
- R Core Team (2018) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Vienna, Austria. <https://www.R-project.org/>. Accessed on 22.08.2022.
- Rabinowitz, A. & Zeller, K.A. (2010) A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. *Biological Conservation*, 143, 939–945.
- Romero-Muñoz, A., Torres, R., Noss, A. J., Giordano, A. J., Quiroga, V., Thompson, J. J., et al. (2019) Habitat loss and overhunting synergistically drive the extirpation of jaguars from the Gran Chaco. *Diversity and Distributions*, 25, 176-19
- Romero-Muñoz, A., Jansen, M., Núñez, A.M., Almonacid, R.V. & Kummerle, T. (2019) Fires scorching Bolivia's Chiquitano forest. *Science*, 366, 6469, 1089.
- Romero-Muñoz, A., Benítez-López, A., Zurell, D., Baumann, M., Camino, M., Decarre, J., et al. (2020) Increasing synergistic effects of habitat destruction and hunting on mammals over three decades in the Gran Chaco. *Ecography*, 43, 954–966.
- Rumiz, D.I., Fuentes, A.F., Rivero, K., Santiváñez, J.L., Cuéllar, E., Miserendino, R., et al. (2002) La biodiversidad de la Estancia San Miguelito, Santa Cruz - Bolivia: Una justificación para establecer reservas privadas de conservación. *Ecología en Bolivia*, Documentos, Serie Biodiversidad N° 1, 1–37.
- Rumiz, D.I., Arispe, R., Noss, A.J. & Rivero, K. (2003) *Censo de jaguares (Panthera onca) y otros mamíferos con trampas-cámara en la Estancia San Miguelito, Santa Cruz, Bolivia*. Wildlife Conservation Society, Technical Report 143, Bolivia.
- Salom-Pérez, R., Carrillo, E., Sáenz, J.C. & Mora, J.M. (2007) Critical condition of the jaguar *Panthera onca* population in Corcovado National Park, Costa Rica. *Oryx*, 41, 51–56.
- Schulze, A., Jansen, M., Köhler, G. (2009) Diversity and ecology of an anuran community in San Sebastián, Bolivia. *Salamandra*, 45, 75–90.
- Sharma, K., Fiechter, M., George, T., Young, J., Alexander, J.S., Bijoor, A., et al. (2020) Conservation and people: Towards an ethical code of conduct for the use of camera traps in wildlife research. *Ecological Solutions and Evidence*, 1. e12033.
- Silveira, L., Jácomo, A.T., & Diniz-Filho, J.A.F. (2003) Camera trap, line transect census and track surveys: a comparative evaluation. *Biological conservation*, 114, 351–355.

- Silver, S.C., Ostro, L.E., Marsh, L.K., Maffei, L., Noss, A.J., Kelly, M.J., et al. (2004) The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx*, 38, 148–154.
- Slade, N.A. & Swihart, R.K. (1983) Home range indices for the hispid cotton rat (*Sigmodon hispidus*) in northeastern Kansas. *Journal of Mammalogy*, 64, 580–590.
- Soisalo, M.K. & Cavalcanti, S.M. (2006) Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. *Biological Conservation*, 129, 487–496.
- Thornton, D., Zeller, K., Rondinini, C., Boitani, L., Crooks, K., Burdett, C., et al. (2016) Assessing the umbrella value of a range-wide conservation network for jaguars (*Panthera onca*). *Ecological Applications* 26, 1112–1124.
- Tobler, M.W. & Powell, G.V. (2013) Estimating jaguar densities with camera traps: problems with current designs and recommendations for future studies. *Biological conservation*, 159, 109–118.
- Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S.C., et al. (2018) Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science* 359, 466–469.
- Venegas, C., Rumiz, D.I., Angulo, S. & Rivero, K. (2010) Censo de jaguares (*Panthera onca*) y otros mamíferos con trampas cámara en la propiedad Alta Vista del Bosque Seco Chiquitano. *Informe Técnico WCS-FCBC-Museo NKM, Santa Cruz*.
- Wallace, R.B., Gomez, H., Zulia, R.P. & Rumiz, D. (2010) *Distribución, ecología y conservación de los mamíferos medianos y grandes de Bolivia*. Centro de Ecología Difusión Simón I. Patiño, Santa Cruz, Bolivia.
- WildLIVE (2021) *Project WildLIVE! - Entdecke die wilden Tiere Boliviens*. Wildlive.sgn.one [accessed 03 August 2021].
- Weckel, M., Giuliano, W. & Silver, S. (2006) Jaguar (*Panthera onca*) feeding ecology: distribution of predator and prey through time and space. *Journal of zoology*, 270, 25–30.
- Wolf, C. & Ripple, W.J. (2017) Range contractions of the world's large carnivores. *Royal Society open science*, 4, 170052.
- Zemanova, M.A., Perotto-Baldivieso, H.L., Dickins, E.L., Gill, A.B., Leonard, J.P. & Wester, D.B. (2017) Impact of deforestation on habitat connectivity thresholds for large carnivores in tropical forests. *Ecological Processes*, 6, 1-11.