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

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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](image_url) 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
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 ± 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 ± 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. 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.
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...
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
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


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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)"

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