CrossMark

ORIGINAL PAPER

Density and population structure of the jaguar (*Panthera onca*) in a protected area of Los Llanos, Venezuela, from 1 year of camera trap monitoring

Włodzimierz Jędrzejewski[1] · Maria F. Puerto[1] · Joshua F. Goldberg[2] ·
Mark Hebblewhite[3] · María Abarca[1] · Gertrudis Gamarra[4] · Luis E. Calderón[4] ·
José F. Romero[4] · Ángel L. Viloria[1] · Rafael Carreño[1] · Hugh S. Robinson[5,6] ·
Margarita Lampo[1] · Ernesto O. Boede[7] · Alejandro Biganzoli[8] · Izabela Stachowicz[1] ·
Grisel Velásquez[1] · Krzysztof Schmidt[9]

Abstract Density is crucial for understanding large carnivore ecology and conservation, but estimating it has proven methodologically difficult. We conducted 1 year of camera trapping to estimate jaguar (*Panthera onca*) density and population structure in the Los Llanos region of Venezuela on the Hato Piñero ranch, where hunting is prohibited and livestock are excluded from half of ranch lands. We identified 42 different jaguars and determined their sex, age class, and reproductive status. We estimated adult jaguar densities with spatial capture-recapture models, using sex/reproductive state and session as covariates. Models without temporal variation received more support than models that allowed variation between sessions. Males, reproductive females, and nonreproductive females differed in their density, baseline detectability, and movement. The best estimate of total adult jaguar population density was 4.44 individuals/100 km^2. Based on reproductive female density and mean number of offspring per female, we estimated cub density at 3.23 individuals/100 km^2 and an overall density of 7.67 jaguars/100 km^2. Estimated jaguar population structure was 21% males, 11% nonreproductive females, 26% reproductive females, and 42% cubs. We conclude that extending the sampling period to 1 year increases the detectability of females and cubs and makes density estimates more robust as compared to the more common short studies. Our results demonstrate that the Venezuelan Llanos represent important jaguar habitat, and further, they emphasize the importance of protected areas and hunting restrictions for carnivore conservation.

Keywords Carnivore conservation · Felid ecology · Hato Piñero · Jaguar breeding · Population density estimate · Spatial capture-recapture

---

Communicated by: Karol Zub

✉ Krzysztof Schmidt
kschmidt@ibs.bialowieza.pl

[1] Centro de Ecología, Instituto Venezolano de Investigaciones Científicas (IVIC), Carretera Panamericana km 11, Caracas 1020-A, Venezuela

[2] Evolution, Ecology and Organismal Biology Program, University of California, Riverside, CA 92521, USA

[3] Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, MT 59812, USA

[4] Hato Piñero–UPSAT Piñero, El Baúl, Cojedes 2213, Venezuela

[5] Panthera, New York, NY 10018, USA

[6] College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA

[7] Fundación para el Desarrollo de las Ciencias, Físicas, Matemáticas y Naturales–FUDECI, Caracas 1010-A, Venezuela

[8] Departamento de Biología, Facultad de Ciencias, Universidad de Los Andes ULA, Mérida 5101, Venezuela

[9] Mammal Research Institute, Polish Academy of Sciences, 17-230 Białowieża, Poland

🕊 Springer

Introduction

Population density is central to understanding the ecology, spatial distribution, and abundance of all organisms (Krebs 2001), yet estimating density reliably remains a challenging problem in applied ecology. This issue remains especially persistent for ecologically important large carnivores. Carnivore population density is one of the major components that determines the impacts of predation on prey populations (Holling 1959; Messier 1994; Jędrzejewska and Jędrzejewski 1998). Accurate density estimates are also critical to evaluate population size and trends of large carnivores, an increasingly important aim given worldwide declines of many of these species (Gros et al. 1996; Treves and Karanth 2003; Ripple et al. 2014).

For large carnivores, like other threatened and endangered species, the knowledge of population structure and demography can help predict population trends and long-term persistence (Shaffer 1981; Coulson et al. 2001; Cooley et al. 2009). Demographic parameters may depend upon species biology but also reflect the breeding performance of a population. A high proportion of breeding females and cubs suggests a high reproduction rate and potentially a growing population. Conversely, carnivore populations with few breeding individuals may have a higher extinction risk. Thus, integrating methods to estimate large carnivore population breeding structure with density could improve population trend predictions and promote effective conservation (Woodroffe 2011; Rosenblatt et al. 2014).

As the top predator in the Neotropics, the jaguar (*Panthera onca*) may have large impacts on prey populations, and an important role in trophic cascades and ecosystem regulation (Terborgh et al. 2001; Cavalcanti and Gese 2010; Estes et al. 2011). Like many large carnivores, the jaguar has experienced a rapid contraction of its natural range due to anthropogenic influences, especially habitat alteration and fragmentation (Quigley and Crawshaw 1992; Nowell and Jackson 1996; Sanderson et al. 2002a; Zeller 2007). Moreover, the reported densities of the jaguar vary substantially across its present distribution, but the factors that shape this variation are poorly understood (see Maffei et al. 2011 and Tobler and Powell 2013 for review).

A variety of field and statistical methods have been used to estimate large carnivore population densities (e.g., Gros et al. 1996; Karanth and Nichols 1998; Stander 1998; Wilson and Delahay 2001). Initial attempts at estimating jaguar density were based on radio-tracking (Schaller and Crawshaw 1980; Crawshaw 1995; Ceballos et al. 2002). In the last decade, camera trapping combined with capture-recapture statistical methods has become common (Maffei et al. 2011). The recent development of spatially explicit capture-recapture (SCR) methods has further improved the quality of density estimates

(Borchers and Efford 2008; Noss et al. 2012; Royle et al. 2014). However, application of these methods may still present unresolved issues, such as the large differences among estimates from consecutive seasons within the same study area (e.g., de la Torre and Medellin 2011; Foster and Harmsen 2012; Tobler et al. 2013). This variation among estimates may result not only from study areas of insufficient size but also from low detectability, especially of females and juveniles. The low number of detections may be partially attributable to short study periods (1–3 months), which are commonly used to address the assumption of population closure in capture-recapture models (Karanth and Nichols 1998; Silver et al. 2004; Maffei et al. 2011). In theory, prolonged study periods may allow for immigration, emigration, births, and deaths in the study area and lead to overestimates or underestimates of abundance by the closed population models applied in SCR packages (White et al. 1982; Kendall et al. 1997; Efford and Fewster 2013; Royle et al. 2014). However, extending study duration may bring important benefits, such as an increased number of detections. For example, better detectability of all sex/age groups would allow estimating population breeding structure and would broaden the applicability of camera trapping to an array of other ecological and conservation questions (du Preez et al. 2014). While the open population models are still less established and have been rarely applied to density estimates (e.g., Gardner et al. 2010; Whittington and Sawaya 2015), it would be practical to find solutions for applying the commonly used SCR methods based on closed population models to long-term camera trapping data.

Here, we study a jaguar population in Los Llanos, a region of vast plains interspersed with numerous rivers, marshes, open grasslands, and forests, extending through large parts of Venezuela and Colombia. This unique region constitutes an important habitat for jaguar in northern South America (Hoogesteijn and Mondolfi 1992; Sanderson et al. 2002b; Rabinowitz and Zeller 2010); however, human-jaguar conflicts related to frequent jaguar attacks on cattle threaten populations of this carnivore in the area (Hoogesteijn et al. 1993). Conservation measures implemented on cattle ranches can improve the prospects of jaguar persistence in this region (Hoogesteijn and Chapman 1997).

In this work, we assessed the impact of study design on the estimates of jaguar density and population structure in the partially protected Hato Piñero ranch in the Venezuelan Los Llanos. First, we examined the impact of sampling period on population density estimates with SCR methods. To fulfill the assumptions of the closed population model, we divided our long study to shorter sessions and used these sessions as a covariate in our SCR models. We tested whether increased study duration leads to increased detectability, especially of

females and cubs, and if it improves robustness of the density estimates. We further estimated basic reproductive parameters and structure of the jaguar population to assess the status of this species in our study area and the efficacy of the protection measures applied in Hato Piñero. Based upon our findings, we made recommendations for conservation and future studies of jaguars and other large carnivores.

Methods

Study area

Hato Piñero ranch encompasses a total area of 800 km^2 in the south-eastern part of Cojedes state of Venezuela. It includes the hills of Macizo de El Baúl and vast plains between the rivers Cojedes, Portuguesa, Chirgua, and Pao. We conducted the study in the north-central portion of Hato Piñero, between 68.0334° W, 8.9827° N and 68.2148° W, 8.8562° N (Fig. A1). The landscape is dominated by a mosaic of open lowland savanna, partially converted to pastures, open marshes, deciduous and dry forests, and chaparral on the hillsides (Huber et al. 2006). Precipitation drives the seasonal climate with most rain occurring between June and November. Average annual rainfall is approximately 1400 mm (Polisar et al. 2003); however, there is profound variation between years (data of the meteorological station of El Baúl). The main rivers are located on the borders of the ranch, but a network of small streams, channels, and artificial ponds and lakes is well developed inside these borders. Between July and October, large parts of the ranch are normally flooded, and in the driest period—between February and May—only the largest rivers and a small number of artificial ponds retain water.

Until 2009, Hato Piñero was a private cattle ranch with approximately 50% of its area maintained as a nature reserve that strived to preserve the jaguar and its prey communities. Hunting was prohibited within ranch boundaries. In 2010, the Venezuelan government expropriated Hato Piñero as a state farm but retained the conservation protections of the ranch. However, after expropriation, the number of cattle increased from about 11,000 in 2009 to approximately 13,000 in 2014. In recent years, the number of domestic buffalo has also increased, reaching approximately 2000 in 2014. In addition to livestock, common prey species include peccaries (*Pecari tajacu* and *Tayassu pecari*), capybaras (*Hydrochoerus hydrochaeris*), white-tailed deer (*Odocoileus virginianus*), tapir (*Tapirus terrestris*), caimans (*Crocodilus crocodilus*), and giant anteater (*Myrmecophaga tridactyla*) (Polisar et al. 2003; Scognamillo et al. 2003; Jędrzejewski et al. 2014). Sympatric carnivores include puma (*Puma concolor*), ocelot (*Leopardus pardalis*), jaguarundi (*Puma yagouaroundi*), and crab-eating fox (*Cerdocyon thous*).

Camera trapping

From July 2013 to July 2014 (376 days), we conducted a continuous camera trapping effort in the study area (Table 1, Fig. A1). We used 27–56 camera-traps at any given time, mostly HC 500 (Reconyx Inc., Holmen, WI, USA) and TrophyCam HD Max (Bushnell, Overland Park, MI, USA). We aimed to distribute the cameras in a regular grid of 2 km by 2 km; however, we adjusted camera positions in response to local topography, site accessibility, and the presence of jaguar trails indicated by track records (Fig. A1). Normally, we placed cameras along small dirt roads, animal trails, and water-bodies, one camera per site. The total area of the polygon encompassing all camera stations was 168.1 km^2. To improve the quality of imagery for individual identification, we placed a small piece of carpet (10 cm × 10 cm) soaked with a beaver castoreum/catnip oil lure in front of the cameras (usually at a distance of 3–4 m) (Schmidt and Kowalczyk 2006; Schlexer 2008). Placing lures does not bias density estimates but may improve individual identifications or detectability (Gerber et al. 2012; du Preez et al. 2014).

Table 1 Summary of camera-trapping effort for jaguar (*Panthera onca*) study conducted in Hato Piñero, Venezuela, over six sessions during July 2013–July 2014

Session	N days	N trap sites	Polygon size	Photos identifiable	N adult jaguars identified	Captures	Recaptures
1	47	48	142.7	252	20	215	195
2	40	56	135.3	175	22	152	130
3	65	27	114.5	171	20	138	118
4	69	42	157.4	315	23	264	241
5	57	32	146.1	168	21	148	127
6	98	31	113.7	288	23	230	207
mean	62.7	39.3	134.9	228.2	21.5	191	170
Total	376	194	168.1	1369	28	1147	1018

The following parameters are presented: the numbers of trapping days, camera trap sites, and all photos with identifiable individuals (taken with at least 10-min difference), numbers of jaguar captures and recaptures, and minimum convex polygon of all cameras during each session. The number of captures and recaptures per session has been defined using one capture per occasion (day)

We divided our sampling period into six sessions that corresponded with camera maintenance and data download. Mean session duration was 63 days (range 47–99 days, Table 1). During each site visit, we inspected the cameras to adjust camera settings and, if required, the spatial location of cameras due to landscape changes (i.e., flooding, droughts, fires, etc.), observation of jaguar tracks, or technical problems. We also refreshed the lure when servicing each camera.

We identified individual jaguars based on unique spot patterns (Silver et al. 2004). We distinguished four sex/age groups: males, nonreproductive females, reproductive females, and cubs. Cubs included obviously young and immature individuals recorded with adult females. Sex of adult individuals was determined by the presence/absence of testicles or nipples and other reproductive signs. We classified females as reproductive if they were recorded with cubs at any point during the study year, and as nonreproductive, if they were never recorded with cubs. We treated presence of cubs as an objective criterion for evidence of breeding. Classification of breeding or non was held constant for the entire study period. Although simplified, we believe this classification justified by the long reproductive cycle of female jaguars (i.e., 3 months gestation and 17 months care of cubs) and long (3–4 years) time to first reproduction (Crawshaw and Quigley 1991; De Paula et al. 2013). We make the assumption that reproductive females maintain their territories for long periods (i.e., years) and any short-term event (i.e., losing cubs) would not change their territory size. Furthermore, we generally recorded older cubs (>3 months old), which would have survived the presumed very early peak in juvenile mortality documented in other large carnivores (Jędrzejewska et al. 1996; Palomares et al. 2005). The identification process was performed by two authors independently (MFP and MA) and verified by a third (WJ). Unidentifiable captures were excluded from subsequent analyses. For capture-recapture models, we defined daily sampling occasions such that we considered only one capture per day per trap, i.e., binomial detection histories (Royle et al. 2009; Goldberg et al. 2015).

Population density estimation for adult jaguars

We applied maximum likelihood SCR models within the secr 2.10.3 R package (Efford et al. 2004, 2009; Borchers and Efford 2008; Efford 2016) to estimate jaguar densities. These hierarchical models define (1) a spatial model of the distribution of animal activity centers and (2) a spatial observation model relating the probability of detecting an individual at a particular trap to the distance from the animal's activity center (Efford 2004). For the observation model, we used a hazard half-normal detection function:

$$\lambda(d) = 1 - \exp\left[-\lambda_0 \exp\left(\frac{-d^2}{2\sigma^2}\right)\right] \quad (1)$$

where λ_0 represents the baseline detection probability at an individual's activity center, σ defines the shape of the decline in detection away from the activity center and can be interpreted in terms of the animal movement distribution, and d specifies the distance between a detector (camera trap) and the activity center (Efford et al. 2009; Efford 2016). This detection model implies a Binomial distribution of detections of an individual at a particular detector (Efford and Fewster 2013; Royle et al. 2014). We used a 15-km buffer around the study area to include the activity centers of any individuals that may have been exposed to sampling. We checked the adequacy of the buffer size by examining likelihoods and estimates from models with larger buffers. We applied full likelihood models with three sex/reproductive status groups (adult males, adult reproductive females, and adult nonreproductive females) and six shorter sessions as covariates (Borchers and Efford 2008). By doing this, we also fulfilled the assumptions of the closed population model in analyzing our long dataset. We fit models with all possible additive combinations of sex/reproductive status groups and sessions as covariates on density (D), λ_0, and σ. For density, we always used sex/female reproductive state as a covariate to provide an estimate of population structure and did not consider intercept-only models. We assessed how D, λ_0, and σ differed across sessions and sex/reproductive status groups and how this variation influenced the overall density estimate. We evaluated models with AICc (corrected Akaike information criterion) and AICc weights (Hurvich and Tsai 1989; Wagenmakers and Farrell 2004). To test the effect of study duration on estimates of all parameters, we compared models that included session covariates in the parameters D, λ_0, and σ (corresponding to the situation when model parameters were estimated based on separate sessions, as in short-term studies) with the best model that did not include any session covariates.

The spatial scale parameter, σ, implies an estimate of individual space use and the scale of movement about an activity center. These estimates provide another means of addressing the reliability of our model results through comparison to telemetry-derived home range sizes. We transformed the σ values for each sex/reproductive state into the radius of an individual activity range, encompassing 95% of animal locations during the observation period. We made this conversion using the hra function in the R package SCRbook (Royle et al. 2013; https://sites.google.com/site/spatialcapturerecapture/scrbook-r-package), since an analytical solution with the hazard half-normal detection function is not readily available. The hra function approximates the 95% activity range of an individual, given parameter values, using a discrete meshwork of points about the activity center. We calculated 95% activity range size for our best model and compared them to home range size estimates from radio-tracking.

To allow comparisons with earlier studies, we also applied nonspatial capture-recapture methods to estimate adult jaguar density (see Appendix B for methods and results).

Estimating cub density and population structure

We estimated densities separately for males, reproductive females, and nonreproductive females. We attempted to fit models directly to observations of cubs, but their sparse capture histories did not provide sufficient data for a maximum likelihood analysis. To estimate cub density, we multiplied the reproductive female density from our best model by mean number of cubs per reproductive female. These estimates allowed calculation of total jaguar density and population structure for males, nonreproductive females, reproductive females, and cubs.

Results

Camera trapping and detection numbers for sex/age groups

Our total sampling effort was 12,302 camera trap-nights. We obtained 1465 captures, including 1369 with identifiable individuals (Table 1). In total, we identified 42 jaguars, including 14 adult males, 14 adult females, and 14 cubs. Of the 14 photographed adult females, 7 were actively reproducing and photographed with cubs (Photos D1, D2). Although we registered equal numbers of males, females, and cubs in the study area, the capture frequency of each group differed: 58% of identified photos were those of males (798 captures), 33% of identifiable captures were those of females (452), and only 9% were those of cubs (119). On average, males were captured 56 times each, females 32 times, and cubs only 9 times. Reproductive females had slightly higher total number of captures than nonreproductive females (257 versus 195, respectively) and higher average number of captures per individual (38 versus 28). Reproductive females were more frequently captured alone (109 times) than accompanied by cubs (69 captures) during the period of known offspring dependency. Conversely, cubs were recorded more frequently with their mothers (83 individual captures) than alone (36 captures).

Density estimates of adult jaguars

Of the 32 models analyzed with the secr package with sex/reproductive status and sessions as covariates, those which did not allow density to vary across sessions obtained the lowest AICc values. In contrast, models assuming density variation across sessions received less support (Tables 2, C1). The top secr model for adult jaguars included an effect of sex/female reproductive status on D, λ_0, and σ and between session variation in λ_0. All three parameters differed significantly between sex/reproductive status groups (Table 3). Baseline detection probability was lowest for reproductive females (0.04 on average), whereas nonreproductive females had the greatest baseline detectability (0.13 on average) and males intermediate (0.08 on average) to the two female reproductive classes. Males had the largest values of estimated movement distribution ($\sigma = 2.97 \pm 0.09$ km), while reproductive and nonreproductive females obtained smaller σ values (2.04 ± 0.11 and 2.32 ± 0.19 km, respectively). Estimated densities were higher for reproductive females and males (1.97 ± 0.33 and 1.62 ± 0.22 individuals/ 100 km^2, respectively) than for nonreproductive females (0.85 ± 0.19 individuals/ 100 km^2). In total, the best model estimated 4.44 ± 1.16 adult jaguars/100 km^2 (Table 3).

Cub density and jaguar population structure

From observations of the seven reproductive females with offspring during the study period, we estimated 1.64 cubs per reproductive female on average. Additionally, one cub was recorded alone on a single occasion and had an unknown mother. We excluded this lone observation from further analysis. On the basis of reproductive female density from the top model, we estimated 3.23 cubs/100 km^2 in the study area. Thus, we estimated a total density of 7.67 jaguars/100 km^2. Jaguar population structure was 21% adult males, 11% nonreproductive females, 26% reproductive females, and 42% cubs (Table 3).

Table 2 Model selection results for selected models analyzed in secr 2.10.3, with six sessions and three sex/reproductive state groups as covariates

Model	AIC$_c$	ΔAIC$_c$	w_i
$D \sim$ sexg $\lambda_0 \sim$ sexg + session $\sigma \sim$ sexg	11,485.0	0.0	0.68
$D \sim$ sexg $\lambda_0 \sim$ sexg $\sigma \sim$ sexg	11,487.8	2.8	0.17
$D \sim$ sexg $\lambda_0 \sim$ sexg $\sigma \sim$ session + sexg	11,489.1	4.0	0.09
$D \sim$ sexg $\lambda_0 \sim$ sexg + session $\sigma \sim$ sexg + session	11,490.0	5.0	0.06
$D \sim$ sexg + session $\lambda_0 \sim$ sexg + session $\sigma \sim$ sexg + session	11,502.2	17.2	0.00

Selection parameters for all 32 analyzed models are presented in Table C1 (Supplementary materials)

D density, λ_0 baseline detection probability, σ movement distribution parameter, *sexg* sex/reproductive state group

Table 3 Parameter estimates from the top model of jaguar density

Model/parameter	Session 1	Session 2	Session 3	Session 4	Session 5	Session 6	Mean
$D \sim$ sexg $\lambda_0 \sim$ sexg + session $\sigma \sim$ sexg (ΔAICc = 0)							
λ_0 males (SE)	0.09 (0.01)	0.06 0.01	0.10 (0.02)	0.09 (0.01)	0.06 (0.01)	0.10 (0.01)	0.08
λ_0 reproductive females (SE)	0.04 (0.01)	0.03 (0.00)	0.04 (0.01)	0.04 (0.01)	0.02 (0.00)	0.04 (0.01)	0.04
λ_0 nonreproductive females (SE)	0.14 (0.03)	0.10 (0.02)	0.16 (0.05)	0.14 (0.02)	0.09 (0.02)	0.16 (0.04)	0.13
σ males (SE)	2.97 (0.09)	2.97 (0.09)	2.97 (0.09)	2.97 (0.09)	2.97 (0.09)	2.97 (0.09)	2.97
σ reproductive females (SE)	2.04 (0.11)	2.04 (0.11)	2.04 (0.11)	2.04 (0.11)	2.04 (0.11)	2.04 (0.11)	2.04
σ nonreproductive females (SE)	2.32 (0.21)	2.32 (0.21)	2.32 (0.21)	2.32 (0.21)	2.32 (0.21)	2.32 (0.21)	2.32
D males (SE)	1.62 (0.22)	1.62 (0.22)	1.62 (0.22)	1.62 (0.22)	1.62 (0.22)	1.62 (0.22)	1.62
D reproductive females (SE)	1.97 (0.33)	1.97 (0.33)	1.97 (0.33)	1.97 (0.33)	1.97 (0.33)	1.97 (0.33)	1.97
D nonreproductive females (SE)	0.85 (0.19)	0.85 (0.19)	0.85 (0.19)	0.85 (0.19)	0.85 (0.19)	0.85 (0.19)	0.85
D adult jaguars total (SE)	4.44 (1.16)	4.44 (1.16)	4.44 (1.16)	4.44 (1.16)	4.44 (1.16)	4.44 (1.16)	4.44
D cubs	3.23	3.23	3.23	3.23	3.23	3.23	3.23
95% home range males (km^2)	167	167	168	167	167	168	167
95% home range reproductive females (km^2)	79	79	79	79	79	79	79
95% home range nonreproductive females (km^2)	103	102	103	103	102	103	103

For each sex/reproductive state group, values of λ_0, σ, and D for the top models are presented. Cub density was calculated by multiplying reproductive female density by mean number of cubs/per female. Home range sizes were estimated from σ and λ_0 values (see "Methods")

D density (individuals/100 km^2), λ_0 baseline detection probability, σ movement distribution parameter, *sexg* sex/reproductive state group, *SE* standard error

Estimates of home range sizes

Based on the detection and movement parameter values, we estimated 95% home range sizes. Males had the largest ranges (167 km^2), while nonreproductive females and reproductive females moved in smaller ranges (103 and 79 km^2, respectively, Table 3).

Study duration and density estimates

The best secr model included seasonal variation in the baseline detection probability, but not in density or the movement distribution parameter. The top model that excluded seasonal variation in all parameters had the second overall rank order in our model set (ΔAIC$_c$ = 2.8, w_i = 0.17, Table 2) and produced similar overall density estimates (D_{total} = 4.47 ± 1.06 jaguars/100 km^2). In contrast, the model assuming between session variation in all three parameters gave highly variable results: from 3.65 to 5.62 jaguars/100 km^2 in different sessions (Fig. 1, Table C2). This model received no support from our model selection criterion (ΔAIC$_c$ = 17.2).

Discussion

Our study provides a robust estimate of jaguar density from a large, long-term photographic capture-recapture dataset. This scope allowed us to address the concerns of many previous jaguar studies, including small sample sizes, low detectability of females and cubs, and limited spatial and temporal extent to provide a more complete description of the jaguar population in our study area. We estimate breeding and nonbreeding female density as well as cub density and total population structure for jaguars in Hato Piñero. We record high jaguar densities in the Venezuelan Llanos, providing evidence of the importance of this habitat for conservation. Moreover, our approach to spatial and temporal study design may offer useful guidance for future capture-recapture studies of jaguars and other large carnivores.

Jaguar population density in Hato Piñero and implications for conservation

Our estimates of jaguar density in Hato Piñero of 4.4 adults/100 km^2 and 7.6 total jaguars/100 km^2 (including cubs) are among the highest documented in South and Central America. Comparable density estimates have been reported only in the tropical forests of Peru, Belize, and Guatemala (Moreira et al. 2008; Harmsen et al. 2010; Tobler et al. 2013; Kelly and Rowe 2014) and in the wetlands of the Brazilian Pantanal (Soisalo and Cavalcanti 2006). This high jaguar density most likely results from high prey availability and productivity in our study area. Karanth et al. (2004) demonstrated a similar relationship for tigers in India. Polisar et al. (2003) estimated that the biomass of potential jaguar prey in Hato Piñero was about 750 kg/km^2 of wild prey and about 7700 kg/km^2 of livestock. These estimates place Hato Piñero in a class of biomass availability and productivity with Manu National Park, Peru (270 kg/km^2 of wild prey),
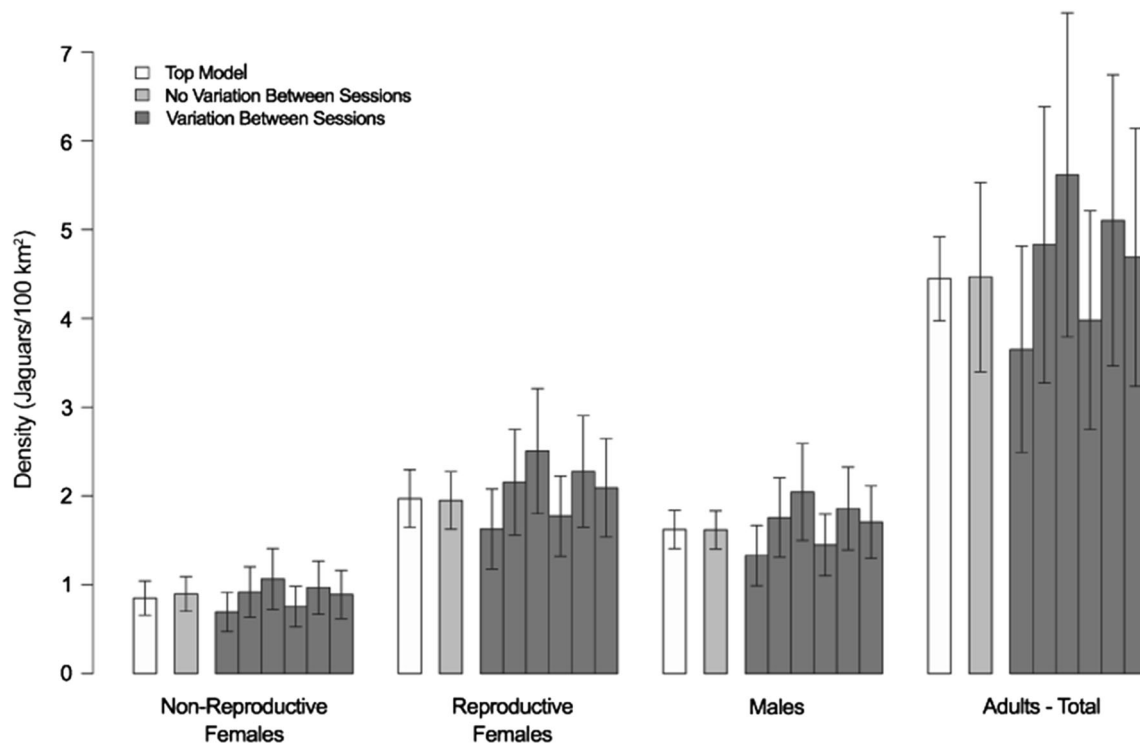
Fig. 1 Comparison of jaguar total densities in Hato Piñero, Venezuela, during July 2013–July 2014 estimated with three different models: (1) the top model selected with AICc, (2) the model with all parameters constant across sessions (corresponding to a long-term study), and (3) for the model with all parameters free to vary between sessions (corresponding to short-term studies). *Error bars* denote ±1 SE

and the Pantanal, Brazil (380 kg/km²), two famous jaguar hotspots (Schaller 1983; Emmons 1987).

The wet parts of Los Llanos, with mosaics of seasonally flooded savannahs, marshes, dry or wet forests, and numerous rivers and streams, may provide exceptionally good conditions for jaguars. However, cattle breeding, human-jaguar conflicts, and hunting likely limit jaguar population growth outside the few protected areas in Los Llanos (Hoogesteijn et al. 1993; González Fernández 1995; Hoogesteijn and Hoogesteijn 2008). Boron et al. (2016) conducted camera-trapping study in an unprotected part of the Colombian Los Llanos and documented much lower adult jaguar density (2.2 jaguars/100 km²) than in Hato Piñero, despite the similarities in primary productivity, forest cover, and human population density between the two study areas. However, in the Colombian study site, hunting of jaguars and its prey is common, as well as retaliatory killing of jaguars due to their attacks on cattle (Boron et al. 2016). This contrast strongly supports the efficacy of the jaguar conservation measures adopted in Hato Piñero, including prohibition of hunting, 50% land excluded from cattle grazing, and development of eco-tourism. Similar protections have benefitted jaguar conservation in the Pantanal of Brazil (Zimmermann et al. 2005b; Greve 2014; Hoogesteijn et al. 2016).

Protected areas and other refuges play a crucial role for maintaining other large carnivore populations in landscapes with large human impacts (Mills 1991; Thapar 1999; Naughton-Treves et al. 2005; Carroll and Miquelle 2006). Our data confirm the importance of protected areas for jaguar conservation. We show that large protected areas, like Hato Piñero, can maintain robust jaguar populations at high density and high reproductive output. As such, they may be a source of dispersing individuals, supporting the persistence of jaguar populations in the surrounding areas.

Differences between sex/reproductive groups

Consistent with previous studies accounting for sex differences, we found higher detection and movement parameter estimates for males than females (Sollmann et al. 2011; Tobler et al. 2013). Our decision to discriminate between reproductive and nonreproductive females further refined the differences among females, based upon whether we observed them caring for cubs. The low detection probability of reproductive females may result from protective maternal behavior. Females with cubs may select the safest areas and reduce use of exposed movement corridors, such as roads and trails, to avoid male jaguars and pumas that may threaten young. Infanticide by unrelated males is common in other felids (e.g., Packer and Pusey 1983; Balme et al. 2013). The higher detectability, larger movement ranges, and lower

density of nonreproducing females may result from young individuals using transient territories and moving large distances in search of a territory (Beier 1995; Schmidt 1998; Zimmermann et al. 2005a).

Length of study duration

The capture-recapture literature frequently emphasizes the importance of the closed population (no birth, immigration, death, or emigration) assumption of capture-recapture models (White et al. 1982; Kendall et al. 1997). To address this concern, most researchers have adopted the recommendation that study periods should not exceed 3 months (Karanth and Nichols 1998; Silver et al. 2004). Although the closed population assumption is important, meeting this requirement does not require such stringent limits on study period. In the analysis of our long-term data, we introduced sessions as a covariate to act as a surrogate for the shorter time frames typically employed by camera trapping studies. The best model allowed for seasonal variation in one of the parameters (baseline detection probability), but not in the other two (density and movement distribution). Furthermore, the model that ignored seasonal variation provided similar parameter estimates and received some statistical support. In contrast, the model assuming variation between sessions in all parameters (corresponding to short-term studies) received no statistical support and produced much less precise density estimates.

Seasonal fluctuations in activity and density estimates have been shown in other jaguar studies (de la Torre and Medellin 2011; Harmsen et al. 2011; Kelly and Rowe 2014; Tobler et al. 2013). This variation may be attributable to poor camera site selection, camera failures, stolen cameras, local fires, or due to seasonal changes in jaguar spatial activity patterns. Changes in jaguar distribution may depend upon the availability of water sources. During the dry season, only a few artificial ponds, lakes, and streams persisted in our study area. Alternatively, the spatial distribution of jaguars may depend upon jaguar reproductive cycles. Scognamillo et al. (2002) reported that the two jaguar females they radio-tracked in Hato Piñero drastically reduced their activity ranges for about 2 months after giving birth to cubs. Comparable patterns of seasonal activity changes related to reproductive cycles have been demonstrated for other felids, e.g., for lynx in Białowieża Primeval Forest (Schmidt 1998). Thus, seasonal changes in activity patterns and territory use may have some impact on detection probability and population assessments, as shown by our results. Density estimates from data with a limited temporal extent may have a greater stochastic component and be less precise than those obtained in long-term studies.

The increased sampling duration in our study did not lead to any obvious overestimates of population density and produced several key benefits. Most importantly, the long-term monitoring increased detection numbers and led to better parameter estimates for the most elusive groups within the jaguar population. We could estimate densities separately for each sex, age, and reproductive group to provide a more complete description of jaguar population structure. Our estimate of population structure with reproductive females and cubs comprising 26 and 42%, respectively, of all individuals indicates a healthy, productive jaguar population. Similar high share of reproducing females and cubs has been observed in radio-tracking studies of other large felid populations, e.g., lynx in partially protected Białowieża Forest in Poland (Jędrzejewski et al. 1996).

In sum, the advantages of long-term studies suggest that extended camera trap monitoring in combination with spatial capture-recapture models may offer significant insights into the population biology of target species.

Home range size estimates

Our estimates of year-round home range sizes (79 km^2 for reproducing females, 103 km^2 for nonreproducing females, and 167 km^2 for males) show, in general, a similar pattern to estimates obtained with telemetry studies and further corroborate our density estimates. Previous radio-telemetry research, conducted on two male and two female jaguars in Hato Piñero during 1996–1998, estimated average seasonal home range sizes of 65 km^2 for females and 100 km^2 for males (Polisar et al. 2003; Scognamillo et al. 2002, 2003). In a GPS telemetry study of jaguars conducted by Cavalcanti and Gese (2009) in Pantanal, Brazil, a habitat similar to Hato Piñero, seasonal female home ranges varied from 34 to 101 km^2 (average: 63 km^2) and seasonal male home ranges varied from 58 to 263 km^2 (average: 156 km^2). Slightly higher average estimates obtained with SCR methods may result from the fact that this technique assumes circular home ranges, while telemetry captures actual space use, which is rarely circular (e.g., Cavalcanti and Gese 2009). However, the higher estimates of home range sizes of nonreproductive females can result from their transient character which can cause a bias in movement estimates (Royle et al. 2016).

Conclusions

Our study demonstrates that protected areas in Los Llanos are potentially important jaguar habitat and that jaguar populations in this region may reach some of the highest densities recorded for South America. Jaguar conservation plans and actions should pay more attention to this region and promote increasing the number of protected areas in Los Llanos. Although today, Hato Piñero is an unquestionable jaguar hotspot in northern South America, it needs more international concern to maintain its good state of conservation, especially in the context of the political instability, growing environmental risks, and uncertain future of this region.

Our study also suggests new perspectives on future research. Spatial capture-recapture studies of jaguars and similar species, with camera traps, may benefit from extended monitoring not limited to 3 months. Based upon our experience, we recommend large study areas with dense trap stations to maximize the number of individuals captured and number of detections. Although we did not quantify the effect of lures, we found them to increase picture quality and thus detectability. Long-term camera trapping can provide additional insights into carnivore population biology.

References

Balme GA, Batchelor A, Woronin Britz N, Seymour G, Grover M, Hes L, Macdonald DW, Hunter LT (2013) Reproductive success of female leopards *Panthera pardus*: the importance of top-down processes. Mammal Rev 43:221–237

Beier P (1995) Dispersal of juvenile cougars in fragmented habitat. J Wildlife Manage 59:228–237

Borchers DL, Efford M (2008) Spatially explicit maximum likelihood methods for capture–recapture studies. Biometrics 64:377–385. doi:10.1111/j.1541-0420.2007.00927.x

Boron V, Tzanopoulos J, Gallo J, Barragan J, Jaimes-Rodriguez L, Schaller G, Payán E (2016) Jaguar densities across human-dominated landscapes in Colombia: the contribution of unprotected areas to long term conservation. PLoS One 11:e0153973. doi:10.1371/journal.pone.0153973

Carroll C, Miquelle DG (2006) Spatial viability analysis of Amur tiger *Panthera tigris altaica* in the Russian far east: the role of protected areas and landscape matrix in population persistence. J Appl Ecol 43:1056–1068

Cavalcanti SMC, Gese EM (2009) Spatial ecology and social interactions of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. J Mammal 90:935–945. doi:10.1644/08-MAMM-A-188.1

Cavalcanti SMC, Gese EM (2010) Kill rates and predation patterns of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. J Mammal 91:722–736. doi:10.1644/09-MAMM-A-171.1

Ceballos G, Chávez C, Rivera A, Manterola C (2002) Tamaño poblacional y conservación del jaguar en la reserva de la biosfera de Calakmul, Campeche, México. In: Medellín RA, Equihua CA, Chetkiewicz CL, Crawshaw P, Rabinowitz A, Redford KH, Robinson JG, Sanderson EW, Taber A (eds) El jaguar en el nuevo milenio. Fondo de cultura económica FCE-Universidad nacional autónoma de México UNAM-Wildlife Conservation Society, México. UNAM-Wildlife Conservation Society, México, pp. 403–417

Cooley HS, Wielgus RB, Koehler G, Maletzke B (2009) Source populations in carnivore management: cougar demography and emigration in a lightly hunted population. Anim Conserv 12:321–328

Coulson T, Catchpole EA, Albon SD, Morgan BJT, Pemberton JM, Clutton-Brock TH, Crawley MJ, Grenfell BT (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:1528–1531. doi:10.1126/science.292.5521.1528

Crawshaw PG Jr (1995) Comparative ecology of ocelot *Felis pardalis* and jaguar *Panthera onca* in a protected subtropical forest in Brazil and Argentina. PhD thesis, University of Florida, Gainesville, USA

Crawshaw PG, Quigley HB (1991) Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. J Zool 223:357–370

de la Torre JA, Medellin RA (2011) Jaguars *Panthera onca* in the greater Lacandona ecosystem, Chiapas, Mexico: population estimates and future prospects. Oryx 45:546–553

De Paula RC, Desbiez A, Cavalcanti SMC (2013) Plano de ação nacional para conservação da onça-pintada. Instituto Chico Mendes de Conservação da Biodiversidade, ICMBio, Brasilia, p 384. http://www.icmbio.gov.br/portal/biodiversidade/fauna-brasileira/plano-de-acao/1344-plano-de-acao-para-conservacao-da-onca-pintada.html

du Preez BD, Loveridge AJ, Macdonald DW (2014) To bait or not to bait: a comparison of camera-trapping methods for estimating leopard *Panthera pardus* density. Biol Conserv 176:153–161

Efford M (2004) Density estimation in live-trapping studies. Oikos 106:598–610

Efford M (2016) SECR 2.10- spatially explicit capture–recapture in R Available at https://cran.r-project.org/web/packages/secr/vignettes/secr-overview.pdf

Efford MG, Fewster RM (2013) Estimating population size by spatially explicit capture–recapture. Oikos 122:918–928

Efford MG, Dawson DK, Robbins CS (2004) DENSITY: software for analysing capture-recapture data from passive detector arrays. Anim Biodivers Conserv 27:217–228

Efford MG, Dawson DK, Borchers DL (2009) Population density estimated from locations of individuals on a passive detector array. Ecology 90:2676–2682

Emmons LH (1987) Comparative feeding ecology of felids in a Neotropical rain-Forest. Behav Ecol and Sociobiol 20:271–283

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JBC, Marquis RJ, Oksanen L, Oksanen T, Paine RT, Pikitch EK, Ripple WJ, Sandin SA, Scheffer M, Schoener TW, Shurin JB, Sinclair ARE, Soulé ME, Virtanen R, Wardle DA (2011) Trophic downgrading of planet earth. Science 333:301–306

Foster RJ, Harmsen BJ (2012) A critique of density estimation from camera-trap data. J Wildlife Manage 76:224–236

Gardner B, Reppucci J, Lucherini M, Royle JA (2010) Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies. Ecology 91:3376–3383

Gerber BD, Karpanty SM, Kelly MJ (2012) Evaluating the potential biases in carnivore capture–recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. Popul Ecol 54:43–54

Goldberg JF, Tempa T, Norbu N, Hebblewhite M, Mills LS, Wangchuk TR, Lukacs P (2015) Examining temporal sample scale and model choice with spatial capture-recapture models in the common leopard *Panthera pardus*. PLoS One 10:e0140757

González Fernández A (1995) Livestock predation in the Venezuelan Llanos. Cat News 22:14–15

Greve S (2014) Ecotourism: an opportunity for Jaguar conservation at Fazenda Barranco Alto Lodge, In: ISCONTOUR 2014-Tourism Research Perspectives: Proceedings of the International Student Conference in Tourism Research, p 191. BoD–Books on Demand

Gros PM, Kelly MJ, Caro TM (1996) Estimating carnivore densities for conservation purposes: indirect methods compared to baseline demographic data. Oikos 77:197–206

Harmsen BJ, Foster RJ, Silver SC, Ostro LE, Doncaster CP (2010) The ecology of jaguars in the Cockscomb Basin wildlife sanctuary, Belize. In: MacDonald DW, Loveridge A (eds) The biology and conservation of wild felids. Oxford University Press, Oxford, pp. 403–416

Harmsen BJ, Foster RJ, Doncaster CP (2011) Heterogeneous capture rates in low density populations and consequences for capture-recapture analysis of camera-trap data. Popul Ecol 53:253–259

Holling CS (1959) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. The Canadian Entomologist 91:293–320

Hoogesteijn R, Chapman C (1997) Large ranches as conservation tools in the Venezuelan Llanos. Oryx 31:274–284

Hoogesteijn R, Hoogesteijn A (2008) Conflicts between cattle ranching and large predators in Venezuela: could use of water buffalo facilitate felid conservation? Oryx 42:132–138

Hoogesteijn R, Mondolfi E (1992) El jaguar: Tigre americano. Armitano, Caracas, Venezuela, p 182

Hoogesteijn R, Hoogesteijn A, Mondolfi E (1993) Jaguar predation and conservation: cattle mortality caused by felines on three ranches in the Venezuelan Llanos. Symposium of the Zoological Society of London 65:391–407

Hoogesteijn R, Hoogesteijn A, Tortato FR, Rampin LE, Vilas Boas-Concone H, May-Junior JA, Sartorello L (2016) Conservación de jaguares (*Panthera onca*) fuera de áreas protegidas: turismo de observación de jaguares en propiedades privadas del Pantanal, Brasil. In: Payán-Garrido E, Lasso-Alcalá C, Castaño-Uribe C (eds) Conservación de grandes vertebrados en áreas no protegidas de Colombia, Venezuela y Brasil. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH), Bogota, pp. 259–274

Huber O, de Stefano RD, Aymard G, Riina R (2006) Flora and Vegetation of the Venezuelan Llanos: a review. In: Pennington T, Lewis GP, Ratter JA (eds) Neotropical savannas and seasonally dry forests: plant diversity, biogeography, and conservation. Taylor & Francis, Florida, pp. 95–120

Hurvich CM, Tsai CL (1989) Regression and time series model selection in small samples. Biometrika 76:297–307

Jędrzejewska B, Jędrzejewski W (1998) Predation in vertebrate communities: the Bialowieza primeval Forest as a case study. In: Ecological studies 135 Germany. Springer, Berlin Heidelberg, p. 443

Jędrzejewska B, Jędrzejewski W, Bunevich AN, Miłkowski L, Okarma H (1996) Population dynamics of wolves *Canis lupus* in Białowieża primeval Forest (Poland and Belarus) in relation to hunting by humans, 1847–1993. Mammal Rev 26:103–126

Jędrzejewski W, Jędrzejewska B, Okarma H, Schmidt K, Bunevich A, Miłkowski L (1996) Population dynamics (1869-1994),

demography, and home ranges of the lynx in Białowieża primeval Forest (Poland and Belarus). Ecography 19:122–138

Jędrzejewski W, Cerda H, Viloria A, Gamarra JG, Schmidt K (2014) Predatory behavior and kill rate of a female jaguar (*Panthera onca*) on cattle. Mammalia 78:235–238

Karanth KU, Nichols JD (1998) Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852–2862

Karanth KU, Nichols JD, Kumar NS, Link WA, Hines JE (2004) Tigers and their prey: predicting carnivore densities from prey abundance. P Natl Acad Sci USA 101:4854–4858

Kelly MJ, Rowe C (2014) Analysis of 5-years of data from Rio Bravo Conservation and Management Area (RBCMA) and one year of data from Gallon Jug/Yalbac Ranch, on trap rates and occupancy for predators and prey, including jaguar density estimates in unlogged versus sustainably logged areas. Progress Report for: Rio Bravo Conservation and Management Area, Programme for Belize. May 10, 2014

Kendall WL, Nichols JD, Hines JE (1997) Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology 78:563–578

Krebs CJ (2001) Ecology. In: The experimental analysis of distribution and abundance. Benjamin Cummings-Addison Wesley Longman Inc, San Francisco, p. 801

Maffei L, Noss AJ, Silver SC, Kelly MJ (2011) Abundance/density case study: jaguars in the Americas. In: O'Connell AF, Nichols JD, Karanth KU (eds) Camera traps in animal ecology: methods and analyses. Springer, Tokyo, pp. 119–144

Messier F (1994) Ungulate population models with predation: a case study with the north American moose. Ecology 75:478–488

Mills MGL (1991) Conservation management of large carnivores in Africa. Koedoe 34:81–90

Moreira J, McNab R, García R, Méndez V, Ponce-Santizo G, Córdova M, Tun S, Caal T, Corado J (2008) Densidad de jaguares en el Biotopo Protegido Dos Lagunas, Parque Nacional Mirador Río Azul, Petén, Guatemala. Informe Interno WCS-Programa para Guatemala, p 21

Naughton-Treves L, Holland MB, Brandon K (2005) The role of protected areas in conserving biodiversity and sustaining local livelihoods. Annu Rev Environ Resour 30:219–252

Noss AJ, Gardner B, Maffei L, Cuéllar E, Montaño R, Romero-Muñoz A, Sollman R, O'Connell AF (2012) Comparison of density estimation methods for mammal populations with camera traps in the Kaa-Iya del gran Chaco landscape. Anim Conserv 15:527–535

Nowell K, Jackson P (1996) Status survey and conservation action plan wild cats. IUCN/SSC Cat Specialist Group, Burlington, Cambridge, p 421

Packer C, Pusey AE (1983) Adaptations of female lions to infanticide by incoming males. Am Nat 121:716–728

Palomares F, Revilla E, Calzada J, Fernández N, Delibes M (2005) Reproduction and pre-dispersal survival of Iberian lynx in a subpopulation of the Doñana National Park. Biol Conserv 122:53–59

Polisar J, Maxit I, Scognamillo D, Farrell L, Sunquist ME, Eisenberg JF (2003) Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem. Biol Conserv 109:297–310

Quigley HB, Crawshaw PG Jr (1992) A conservation plan for the jaguar *Panthera onca* in the Pantanal region of Brazil. Biol Conserv 61:149–157

Rabinowitz A, Zeller KA (2010) A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. Biol Conserv 143:939–945

Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP (2014) Status and ecological effects of the world's largest carnivores. Science 343:1241484. doi:10.1126/science.1241484

Rosenblatt E, Becker MS, Creel S, Droge E, Mweetwa T, Schuette PA, Watson F, Merkle J, Mwape H (2014) Detecting declines of apex

carnivores and evaluating their causes: an example with Zambian lions. Biol Conserv 180:176–186

Royle JA, Chandler RB, Sollmann R, Gardner B (2014) Spatial capture-recapture. Academic Press, Elsevier, New York, p. 569

Royle JA, Chandler RB, Sun CC, Fuller AK (2013) Integrating resource selection information with spatial capture–recapture. Methods Ecol Evol 4:520–530

Royle JA, Fuller AK, Sutherland C (2016) Spatial capture–recapture models allowing Markovian transience or dispersal. Popul Ecol 58:53–62

Royle JA, Karanth KU, Gopalaswamy AM, Kumar NS (2009) Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. Ecology 90:3233–3244

Sanderson EW, Redford KH, Chetkiewicz CLB, Medellin RA, Rabinowitz AR, Robinson JG, Taber AB (2002a) Planning to save a species: the jaguar as a model. Conserv Biol 16:58–72

Sanderson E, Chetkiewicz CL, Medellín R, Rabinowitz A, Redford K, Robinson J, Taber A (2002b) Prioridades geográficas para la conservación del jaguar. In: Medellín RA, Equihua CA, Chetkiewicz CL, Crawshaw P, Rabinowitz A, Redford KH, Robinson JG, Sanderson EW, Taber A (eds) El jaguar en el nuevo milenio, Fondo de cultura económica FCE-Universidad nacional autónoma de México UNAM-Wildlife Conservation Society, México, pp. 629–640

Schaller GB (1983) Mammals and their biomass on a Brazilian ranch. Arquivos de Zoologia 31:1–36

Schaller GB, Crawshaw PG Jr (1980) Movement patterns of jaguar. Biotropica 12:161–168

Schlexer FV (2008) Attracting animals to detection devices. In: Long RA, Mackay P, Zielinski WJ, Ray JC (eds) Noninvasive survey methods for carnivores. Island Press, Washington, pp. 263–292

Schmidt K (1998) Maternal behaviour and juvenile dispersal in the Eurasian lynx. Acta Theriol 43:391–408

Schmidt K, Kowalczyk R (2006) Using scent-marking stations to collect hair samples to monitor Eurasian lynx populations. Wildlife Soc B 34:462–466

Scognamillo D, Maxit I, Sunquist M, Farrell L (2002) Ecología del jaguar y el problema de la depredación de ganado en un hato de los Llanos Venezolanos. In: Medellín RA, Equihua CA, Chetkiewicz CL, Crawshaw P, Rabinowitz A, Redford KH, Robinson JG, Sanderson EW, Taber A (eds) El jaguar en el nuevo milenio, Fondo de cultura económica FCE-Universidad nacional autónoma de México UNAM- Wildlife Conservation Society, México, pp. 139–150

Scognamillo D, Maxit IE, Sunquist M, Polisar J (2003) Coexistence of jaguar (Panthera onca) and puma (Puma concolor) in a mosaic landscape in the Venezuelan llanos. J Zool 259:269–279

Shaffer ML (1981) Minimum population sizes for species conservation. Bioscience 31:131–134

Silver SC, Ostro LET, Marsh LK, Maffei L, Noss AJ, Kelly MJ, Wallace RB, Gomez H, Ayala G (2004) The use of camera traps for estimating jaguar Panthera onca abundance and density using capture/recapture analysis. Oryx 38:148–154

Soisalo MK, Cavalcanti SMC (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. Biol Conserv 129:487–496

Sollmann R, Furtado MM, Gardner B, Hofer H, Jácomo ATA, Tôrres NM, Silveira L (2011) Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in Central Brazil. Biol Conserv 144:1017–1024

Stander PE (1998) Spoor counts as indices of large carnivore populations: the relationship between spoor frequency, sampling effort and true density. J Appl Ecol 35:378–385

Terborgh J, Lopez L, Nunez P, Rao M, Shahabuddin G, Orihuela G, Riveros M, Ascanio R, Adler GH, Lambert TD (2001) Ecological meltdown in predator-free forest fragments. Science 294:1923–1926

Thapar V (1999) The tragedy of the Indian tiger: starting from scratch. In: Seidensticker J, Christie S, Jackson P (eds) Riding the tiger: tiger conservation in human-dominated landscapes. Cambridge University Press, Cambridge, pp. 286–306

Tobler MW, Powell GVN (2013) Estimating jaguar densities with camera traps: problems with current designs and recommendations for future studies. Biol Conserv 159:109–118

Tobler MW, Carrillo-Percastegui SE, Zúñiga Hartley A, Powell GVN (2013) High jaguar densities and large population sizes in the core habitat of the southwestern Amazon. Biol Conserv 159:375–381

Treves A, Karanth KU (2003) Human-carnivore conflict and perspectives on carnivore management worldwide. Conserv Biol 17:1491–1499

Wagenmakers EJ, Farrell S (2004) AIC model selection using Akaike weights. Psychon B Rev 11:192–196

White GC, Anderson DR, Burnham KP, Otis DL (1982) Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, p 235

Whittington J, Sawaya MA (2015) A comparison of grizzly bear demographic parameters estimated from non-spatial and spatial open population capture-recapture models. PLoS One 10:e0134446

Wilson GJ, Delahay RJ (2001) A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. Wildlife Res 28:151–164

Woodroffe R (2011) Demography of a recovering African wild dog (Lycaon pictus) population. J Mammal 92:305–315

Zeller K (2007) Jaguars in the new millennium data set update: the state of the jaguar in 2006. Wildlife Conservation Society, New York, p. 77

Zimmermann A, Walpole MJ, Leader-Williams N (2005b) Cattle ranchers' attitudes to conflicts with jaguar Panthera onca in the Pantanal of Brazil. Oryx 39:406–412

Zimmermann F, Breitenmoser-Würsten C, Breitenmoser U (2005a) Natal dispersal of Eurasian lynx (Lynx lynx) in Switzerland. J Zool 267:381–395