



## Improving density estimates for elusive carnivores: Accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil

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### ABSTRACT

Owing to habitat conversion and conflict with humans, many carnivores are of conservation concern. Because of their elusive nature, camera trapping is a standard tool for studying carnivores. In many vertebrates, sex-specific differences in movements – and therefore detection by cameras – are likely. We used camera trapping data and spatially explicit sex-specific capture–recapture models to estimate jaguar density in Emas National Park in the central Brazilian Cerrado grassland, an ecological hotspot of international importance. Our spatially explicit model considered differences in movements and trap encounter rate between genders and the location of camera traps (on/off road). We compared results with estimates from a sex-specific non-spatial capture–recapture model. The spatial model estimated a density of 0.29 jaguars 100 km<sup>−2</sup> and showed that males moved larger distances and had higher trap encounter rates than females. Encounter rates with off-road traps were one tenth of those for on-road traps. In the non-spatial model, males had a higher capture probability than females; density was estimated at 0.62 individuals 100 km<sup>−2</sup>. The non-spatial model likely overestimated density because it did not adequately account for animal movements. The spatial model probably underestimated density because it assumed a uniform distribution of jaguars within and outside the reserve. Overall, the spatial model is preferable because it explicitly considers animal movements and allows incorporating site-specific and individual covariates. With both methods, jaguar density was lower than reported from most other study sites. For rare species such as grassland jaguars, spatially explicit capture–recapture models present an important advance for informed conservation planning.

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### 1. Introduction

Owing to worldwide, large-scale habitat conversion and direct conflict with humans, many large and wide-ranging carnivores are of conservation concern. Although many charismatic species such as the big cats have received considerable attention through research over the past decade (Brodie, 2009), their populations continue to decrease (IUCN, 2010). Abundance and population

density are key baseline parameters for conservation planning (Lebreton et al., 1992; Reid et al., 2002). Yet reliable estimates are hard to obtain for these species because of their elusive nature and the spatial and temporal scale of their movements that need to be addressed by conservation-oriented studies (Karanth et al., 2006; Karanth and Chellam, 2009).

Camera traps have considerably advanced our ability to study elusive animals (Kays and Slauson, 2008). They have the advantage of being non-intrusive and applicable over large areas with relatively moderate effort (Silveira et al., 2003). Today, camera trapping is used to study a variety of aspects of wildlife ecology, ranging from species presence (Linkie et al., 2007) and behavior (Harmsen et al., 2009) to relative abundance within a species assembly (O'Brien et al., 2003). Particularly for species with individually identifiable coat patterns, data from camera trapping can

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be analyzed within the analytically sound framework of capture–recapture models to estimate population abundance and density (Karanth, 1995; Karanth and Nichols, 1998; Otis et al., 1978; White et al., 1982) or population dynamics (Karanth et al., 2006; Gardner et al., 2010a). These models account for the fact that we do not necessarily observe all animals in the study area, i.e., the issue of imperfect detection. This methodology has been applied to several different species such as common genets (*Genetta genetta* – Sarmiento et al., 2010), maned wolves (*Chrysocyon brachyurus* – Trolle et al., 2007), pumas (*Puma concolor* – Kelly et al., 2008) and is most commonly used to study individually distinctive large cats (e.g., Karanth and Nichols, 1998; Silver, 2004).

Though widespread, the use of camera trapping in combination with capture–recapture models has an important shortcoming that it shares with other methods applied to estimate abundance: the interpretation of abundance, or specifically the estimation of the area to which this abundance refers (e.g., Karanth and Nichols, 1998; Royle et al., 2009). Whereas most models assume geographic closure of the population, i.e., no movement on and off the sampling grid (White et al., 1982), this assumption is generally and widely violated (e.g., Karanth and Nichols, 1998), especially for large mammals. The standard approach is to buffer the grid with half the mean maximum linear distance moved by individuals captured in more than one trap (MMDM, Karanth and Nichols, 1998). Although this approach performed well in simulation studies (Wilson and Anderson, 1985), it is an ad hoc approach with little theoretical justification (Williams et al., 2002). Other approaches have been used to estimate buffer width, for example the full MMDM (twice the MMDM–fMMDM), or the radius of an average home range, both based on telemetry data (Soisalo and Cavalcanti, 2006) and on information from the literature (Wallace et al., 2003). Since density estimates are directly influenced by the chosen buffer width, comparisons of estimates from different methodologies become difficult.

Spatially explicit capture–recapture (SECR) models are a recent advance in the field of density estimation (Efford, 2004; Royle and Young, 2008). These models make use of the spatial location of captures in order to first determine an individual's activity center and then to estimate the density of activity centers across a precisely defined polygon containing the trap array (Gardner et al., 2009; Royle et al., 2009). They thereby circumvent the problem of estimating the effective area sampled. SECR models can be implemented within a Bayesian framework and therefore provide valid inferences even with small sample sizes. The 'pseudo-code' used by the freely available software WinBUGS (Gilks et al., 1994) provides an easy-to-use and flexible framework for fitting Bayesian SECR models.

The flexibility of these models also allows for the incorporation of other factors of interest, for example sex as an individual covariate (Gardner et al., 2010b). Differences between the sexes in their behavior and space use are typical for vertebrate social organizations, particularly for most felids, for which the home range or territory of a single male or a group of males may partially or completely overlap the generally smaller home ranges or territories of one to several females (Sandell, 1989). The resulting differences in space use and movement between the sexes will be reflected in differences in encounter probability with camera traps and should be taken into account when estimating population density and abundance.

The jaguar *Panthera onca* (Linnaeus, 1758) is the largest American felid and the third-largest big cat. It occurs from the south-western United States and Mexico to northern Argentina. Over the last century, the species' range has contracted to approximately 55% of its original extent (Zeller, 2007) because of loss of natural habitat and persecution (Sanderson et al., 2002). The IUCN classifies the jaguar as Near Threatened (IUCN, 2010). In spite of its

wide distribution and conservation concern, the species remains less studied than most other large cats (Brodie, 2009).

Here, we used SECR models to estimate jaguar abundance and density in Emas National Park (ENP), which holds one of the last jaguar populations in the Cerrado savanna of central Brazil. The Cerrado was identified as one of the earth's 25 ecological hotspots (Myers et al., 2000) and is threatened by rapid and large-scale habitat loss. The biome has been neglected by conservation oriented research and few studies have previously investigated jaguar ecology and conservation status in this biome. We therefore deployed 119 camera trap stations across the entire 1320 km<sup>2</sup> of ENP – the largest single-site camera trapping study implemented for jaguars. Considering the sex-specific differences in behavior outlined above and the fact that differential space use between sexes has recently been documented in jaguars (Conde et al., 2010), we incorporated sex-specific parameters into the SECR model. We compared its results with those from a sex-specific but non-spatial approach. Our study not only provides novel information about jaguar ecology in the Cerrado, but has general implications for estimating population densities of large carnivores and other elusive species for most sampling designs.

## 2. Material and methods

### 2.1. Study area

Emas National Park, listed as a Human Heritage Reserve by UNESCO, is located in south-western Goiás state (18°19'S, 52°45'W; Fig. 1) in the Cerrado savanna of central Brazil. The park has 1320 km<sup>2</sup> and protects large tracts of grassland plains (97%), small patches of *cerrado* shrub fields (1%), marshes, and riparian forest (2%). During the wet season (October–March), rainfall averages 1500 mm. There is very little precipitation during the rest of the year, when daytime temperatures can reach 40 °C and nighttime temperatures may drop to –1.5 °C (IBDF/FBCN, 1981). ENP is situated in a highly productive agricultural area. Large-scale soybean, corn and sugar cane plantations dominate and fragment the regional landscape. This situation is typical of the Cerrado: Brazil's second largest biome covers 21% of the country's area but over the last 35 years more than half of it has been transformed into cultivated land (Klink and Machado, 2005). Today, only 1.9% is strictly protected and 80% is considered degraded (Cavalcanti and Joly, 2002).

### 2.2. Camera trapping and data preparation

We deployed 119 camera trap stations on a park-wide 3.5 × 3.5 km grid (Fig. 1). A maximum distance of 3.5 km between traps was recommended on the basis of the smallest jaguar home range recorded to date to ensure that all animals in the study area are exposed to traps and thus, in theory have a capture probability >0. This is a prerequisite for the non-spatial capture–recapture models (Karanth and Nichols, 1998; Silver, 2004) but not for the SECR models. We adjusted the locations of the trap stations to maximize the number of traps along park roads for logistic reasons and to maximize capture probability (Karanth and Nichols, 1998, 2002). At off-road locations, we installed cameras along game trails. Each station consisted of two camera traps (the 35-mm Leaf-River C1-BU, Vibrashine Inc., Taylorsville, MS 3968, USA) facing each other with a lateral offset of approximately 30 cm to avoid flash interference. Camera traps were strapped to trees or stakes approximately 40–50 cm above ground, as recommended by Silver (2004).

Since cameras were easily triggered by sunlight in the predominantly open habitat of ENP, we programmed cameras to work

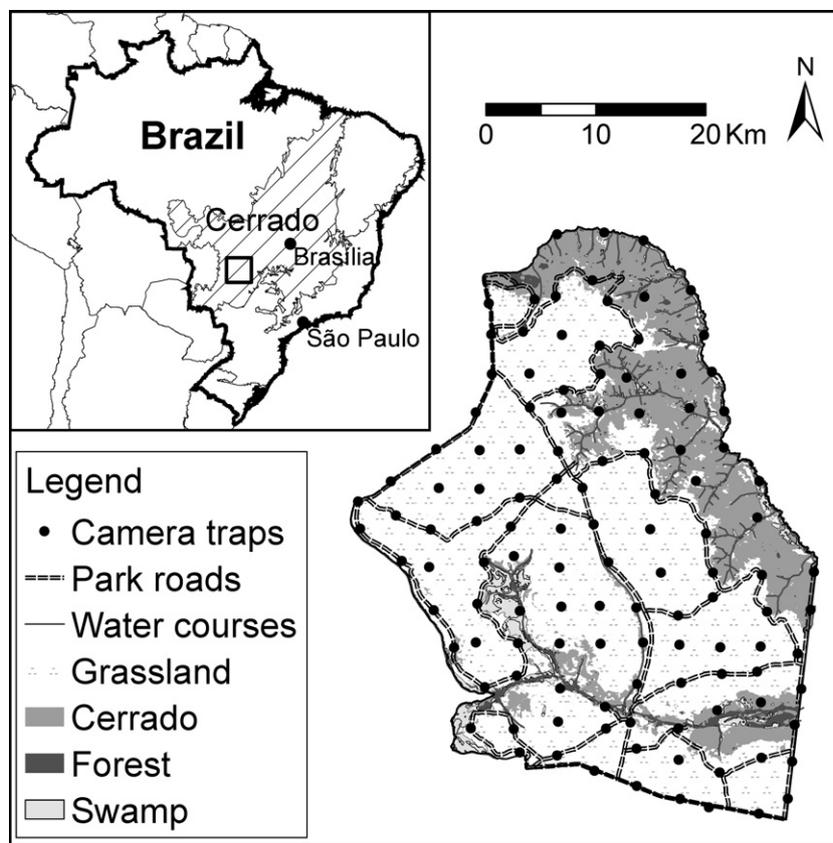


Fig. 1. Location of Emas National Park in Brazil (square in inset) and map of the study area with camera trap locations (dots).

throughout day and night in shady locations and only during the night in locations exposed to sunlight. For analyses, we only considered jaguar photographs taken at night. We installed camera traps in March 2008, kept them in the field for 85 consecutive days and checked them at 10–14-day intervals to replace film rolls and batteries.

We identified jaguar individuals in photographs based on their unique spot patterns and identified gender by secondary sexual traits. We divided our sample period into 17 5-day trapping occasions. For the non-spatial capture–recapture models we noted whether an individual had been photographed during each occasion (the binary detection history of each individual). For the SECR approach, we noted how often an individual was photographed at each trap during each occasion (the count history of each individual).

### 2.3. Spatial model

Since jaguars in ENP are known to move beyond the park borders (Silveira, 2004) and thus, beyond our trapping grid, SECR models are ideal tools to account for these movements in density estimation. SECR models are essentially generalized linear mixed models (GLMM) that assume an unobserved activity center  $\mathbf{s}_i$  for each individual  $i$ , which remains constant over the survey (the random effect). The encounter rate of an individual with a given trap is a monotonically decreasing function of the distance from the activity center to that trap.  $y_{ij}$ , the number of times animal  $i$  is caught by trap  $j$  during a sampling occasion, is a random variable following a Poisson distribution,

$$\lambda_{ij} \sim \text{Poisson}(\lambda_{ij})$$

Here, we model variation in  $\lambda_{ij}$  by allowing for sex-specific encounter rates and a sex-specific movement parameter  $\sigma$ . Assuming that

the Poisson mean  $\lambda_{ij}$  decreases according to a normal probability density function,

$$\lambda_{ij} = \lambda_0 * \exp(-d_{ij}^2/\sigma^2),$$

the complete model in its log-linear form (Royle and Gardner, 2011) is as follows:

$$\log(\lambda_{ij}) = \log(\lambda_0[k_i]) + \log(\rho[r_j]) - (1/\sigma^2[k_i]) * d_{ij}^2$$

Here,  $\lambda_0$  is the baseline encounter rate, i.e., the expected number of captures of individual  $i$  at trap  $j$  during a sampling occasion when an individual's activity center  $\mathbf{s}_i$  is located precisely at trap  $j$ , and  $k$  is a binary vector that indicates the sex of individual  $i$  (i.e.,  $k_i = 1$  for males, 0 otherwise).  $\rho$  is a road effect where  $\mathbf{r}$  is a binary vector that indicates whether trap  $j$  is on or off a road ( $r_j = 1$  if the trap is located on a road, and 0 otherwise). Particularly in the more open habitats of the ENP roads provide clearer landscape structures that “channel” animals towards camera traps than game trails, thus we expect higher trap encounter rates at on-road locations. Lastly,  $d_{ij} = |\mathbf{x}_j - \mathbf{s}_i|$  is the distance from individual  $i$ 's activity center ( $\mathbf{s}_i$ ) to trap  $j$  located at  $\mathbf{x}_j$  ( $\mathbf{x}_j$  being a pair of UTM latitude and longitude coordinates), and  $\sigma$  (units of the trapping grid, here km) is the parameter that controls the shape of the distance function. We can translate  $\sigma$  into a 95% home range radius by assuming a circular bivariate normal model for movement.

Density ( $D$ ) is a derived parameter that we calculate by dividing  $N$  by the area of  $S$ , where  $N$  is the number of activity centers in  $S$ , an arbitrarily large area that includes the trap polygon. We used a 40 km buffer from the outermost  $x$  and  $y$  coordinates of the trapping grid, corresponding to an area  $S$  of 15,832 km<sup>2</sup>.

To estimate the latent parameters including  $N$  and  $\mathbf{s}_i$  – the number of individuals and their activity centers – we used a Bayesian analysis by data augmentation of the model (Royle et al., 2007),

which was implemented in the program WinBUGS (Gilks et al., 1994), accessed through the program R, version 2.10.1 (R Core Development Team, 2009) using the package R2WinBUGS (Sturtz et al., 2005). In data augmentation, we let  $M$  be a number that is larger than the largest possible population size (i.e., the number of activity centers  $N$ ) in  $S$ , and  $n$  be the number of detected individuals. We assume a prior distribution for  $N$  that is uniform over the interval  $(0, M)$  and augment the observed data set with an arbitrarily large number  $(M - n)$  of individuals whose photographic encounter histories are all 0. This reformulation of the model based on data augmentation is a zero-inflated binomial mixture and the number of activity centers  $N$  in  $S$  is then estimated as a fraction of  $M$ .

For model analysis, WinBUGS uses Gibbs sampling, a Markov chain Monte Carlo (MCMC) method simulating samples from the joint posterior distribution of the unknown quantities in a statistical model (Casella and George, 1992). MCMC chains are started at arbitrary parameter values and since successive iterations depend on the outcome of the previous iteration, the start value will be reflected in a number of initial iterations that should be discarded (the burn-in). This characteristic can also lead to autocorrelation of successive iterations. To reduce autocorrelation, a thinning rate is specified as every  $i$ th iteration used in the characterization of the posterior distribution of the parameters. We ran three MCMC chains with 10,000 iterations, a burn-in of 5000 and a thinning rate of three. This combination of values ensured an adequate number of iterations to characterize the posterior distributions, that MCMC chains showed no indications of autocorrelation or effects of the initial values, and that all chains converged (i.e., oscillated around essentially the same mean parameter value). We checked for chain convergence using the Gelman–Rubin statistic (Gelman et al., 2004), R-hat, which compares between and within chain variation. R-hat values below 1.1 indicate convergence (Gelman and Hill, 2006). Values for all estimated parameters were below 1.01. The WinBUGS code is available as electronic [Supplementary material](#). The results below are presented as means  $\pm$  standard errors of the mean (SEM).

#### 2.4. Non-spatial capture–recapture model

To estimate jaguar abundance  $N$  and sex-specific capture probability  $p$  under a non-spatial model, we used the full closed capture–recapture models in program MARK (White and Burnham, 1999). These models allow  $p$  to vary among groups of individuals, in our case between males and females, as well as with time or as a function of a behavioral response to trapping. The model with a sex-specific  $p$  had lower values of the Akaike Information Criterion adjusted for small sample size (AICc, Burnham and Anderson, 2002) than models with equal  $p$  for both sexes, a behavioral response in  $p$  or time variation in  $p$ . The AICc of the best model was at least 2 units lower than any other AICc, a difference sufficient to warrant a clear decision to prefer this model (Burnham and Anderson, 2002). Therefore, and because we are predominantly interested in a comparison with the spatial model with sex-specific parameters, we do not present results from the other non-spatial models.

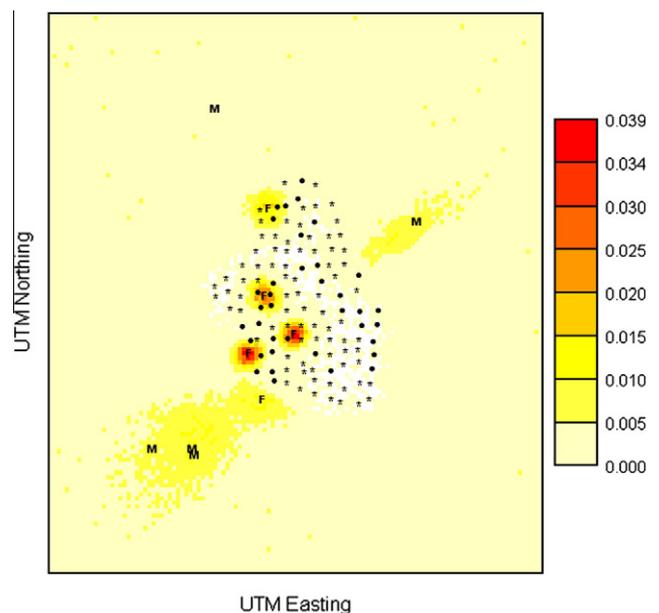
We used the MMDM to buffer the trap polygon and account for jaguar movement beyond the park borders (e.g. Karanth and Nichols, 1998; Silver et al., 2004). Large portions of the park's immediate surroundings are composed of crop plantations and cattle pasture (Fig. 1), habitat types generally avoided by jaguars in the study area (Silveira, 2004) and elsewhere (Cullen, 2006). We therefore subtracted unsuitable habitat from the buffer and added only area covered by native habitat to obtain the effective area sampled. We divided the non-spatial abundance estimate by the size of this area to obtain the final density estimate.

### 3. Results

We obtained 105 jaguar photographs taken at night. All pictures were suitable for individual identification and corresponded to five male and five female individuals. Photographic frequencies were heterogeneous among individuals and sexes: one male accounted for 42 of the records whereas all females were captured by only 15 pictures.

For the SECR models, with  $0.47 \pm 0.48$  photographs occasion<sup>-1</sup>, the male baseline encounter rate at a given camera  $\lambda_0$  was close to 10 times higher than that for females. The movement parameter  $\sigma$  was almost four times larger for males ( $22.10 \pm 3.14$  km) than for females ( $6.18 \pm 1.12$  km). For all jaguars, encounter rates with on-road cameras were 10 times higher than with off-road cameras. The model estimated density at  $0.29 \pm 0.10$  individuals 100 km<sup>-2</sup>. Sex ratio, expressed as the probability of being a male, was  $0.18 \pm 0.09$ . The posterior mean locations of the activity centers of the 10 observed individuals are shown in Fig. 2. Further results of the posterior distributions of parameters are summarized in Table 1.

For the non-spatial model, the estimate of detection probability for males was  $0.49 \pm 0.05$ . Female detection probability was five times lower ( $0.09 \pm 0.04$ ). Estimates of  $N$  were  $5 \pm 0.01$  for males and  $5.59 \pm 1.61$  for females. With  $15.40 \pm 4.97$  km, the MMDM for males was more than three times higher than the MMDM for females ( $4.47 \pm 3.08$  km). After removal of patches of anthropogenic habitat unsuitable for jaguars, which accounted for approximately 50% of the buffer zone surrounding ENP, the effective area sampled was  $2004 \pm 788$  km<sup>2</sup> for males and  $1498 \pm 422$  km<sup>2</sup> for females. Consequently, male density was  $0.25 \pm 0.10$  100 km<sup>-2</sup> and female density was  $0.37 \pm 0.15$  100 km<sup>-2</sup>. The combined density of adult jaguars was then  $0.62 \pm 0.18$  100 km<sup>-2</sup>. For comparison, combined density was  $0.51 \pm 0.19$  100 km<sup>-2</sup> without removal of the area deemed unsuitable from the buffer strip.



**Fig. 2.** Map of posterior density of activity centers of jaguars in Emas National Park, central Brazil. Colors code for the estimated number of activity centers in each  $1 \times 1$  km pixel; letters indicate mean activity center location for identified individuals (M = males, F = females); asterisks indicate camera trap locations; dots indicate locations where jaguars were photographed. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

**Table 1**

Summaries of posterior distributions of sex-specific parameters from spatially explicit capture–recapture models of jaguar camera trapping data from Emas National Park, central Brazil;  $\sigma$  = movement parameter [km],  $\lambda_0$  = baseline encounter rate of on-road cameras [occasion<sup>-1</sup>];  $\rho$  = multiplicative coefficient for  $\lambda_0$  at off-road locations;  $\pi$  = sex ratio, the probability of being a male;  $N$  = number of individuals in the 15,832 km<sup>2</sup> area containing the trapping grid;  $D$  = jaguar density [individuals 100 km<sup>-2</sup>].

| Parameter           | Units                              | Mean  | SE    | 2.5%  | Median | 97.5% |
|---------------------|------------------------------------|-------|-------|-------|--------|-------|
| $\sigma$ males      | km                                 | 22.10 | 3.14  | 16.79 | 21.86  | 28.56 |
| $\sigma$ females    | km                                 | 6.18  | 1.12  | 4.49  | 6.01   | 8.72  |
| $\lambda_0$ males   | Photographs occasion <sup>-1</sup> | 0.47  | 0.48  | 0.12  | 0.31   | 1.81  |
| $\lambda_0$ females | Photographs occasion <sup>-1</sup> | 0.05  | 0.02  | 0.01  | 0.04   | 0.10  |
| $\rho$              | –                                  | 0.11  | 0.04  | 0.04  | 0.10   | 0.20  |
| $\pi$               | –                                  | 0.18  | 0.09  | 0.05  | 0.16   | 0.40  |
| $N$                 | –                                  | 45.94 | 15.68 | 21.00 | 44.00  | 81.00 |
| $D$                 | Individuals 100 km <sup>-2</sup>   | 0.29  | 0.10  | 0.13  | 0.28   | 0.51  |

#### 4. Discussion

Over the last decade, camera trapping in combination with capture–recapture modeling has become a standard tool in research on large felids. Spatially explicit capture–recapture (SECR) models are a recent development in this field and overcome the conceptual problem of interpreting abundance estimates from traditional non-spatial capture–recapture models (Efford, 2004; Royle and Young, 2008). While estimates of abundance alone may be of interest for purely site-specific issues such as management, they do not allow for comparison with other sites without relating it to a known area. Using this flexible class of models, we can also address other issues such as heterogeneity in capture rates owing to trap site-specific covariates (Kéry et al., 2010) or individual covariates such as sex (Gardner et al., 2010b).

##### 4.1. Sex-specific and spatially explicit density models

Although most jaguar camera trapping studies observed a larger number of males than females, and females are generally recaptured less often than males (e.g., Salom-Pérez et al., 2007; Silver et al., 2004; Soisalo and Cavalcanti, 2006; Wallace et al., 2003), this is the first study to quantify the difference between the sexes in detection rates and movements.

Female jaguars generally have smaller home ranges than males (Astete et al., 2008) and consequently are exposed to fewer camera traps. They may also show a lower tendency to walk along roads and well established tracks (Salom-Pérez et al., 2007) where camera traps are preferably set up (Silver, 2004). Non-spatial models reflect these characteristics in an overall lower detection probability of females but do not provide information on the underlying causes. Using the SECR approach permitted us to model these distinct movement patterns explicitly for both sexes, as this framework formalizes the relationship between exposure to the trap array and movements (Gardner et al., 2009; Royle and Young, 2008). The results corroborated what we expected on the basis of observations of previous jaguar camera trapping data and our own raw data: female baseline encounter rate at a given trap was close to one tenth of that for males, which indicates that in addition to having smaller home ranges, females also move less than males. Female home range centers seem to be concentrated in the center region of ENP (Fig. 2), but the calculated estimate of  $\sigma$  of just over 6 km suggests that females used most of the park area during our study. Still,  $\sigma$  for females was barely one-fourth of that for males. Consequently, the estimated sex ratio was extremely skewed towards females (about 1 male to 4 females). It is methodologically intuitive that the model interprets the low female encounter rate as an indication that there are many more females than we actually photographed. For ENP we would be cautious to interpret this sex ratio as an indication that there are 15–20 females in the park. Rather, results indicate that, due to

their wider movements, males exposed to the trapping grid may come from a much larger area than females.

Although the skew initially seems remarkable in ecological terms, it reflects received and published wisdom on the distribution and overlap of male and female home ranges in large felids. For instance, Schaller and Crawshaw (1980) reported the presence of 2–3 female jaguars in the area of one male on a ranch in the Pantanal, and several authors reported male–female ratios of 1 to 3–4 for adult tigers *Panthera tigris* (Sunquist, 1981).

When using the non-spatial approach, female capture probability emerged as five times lower than male capture probability. However, this resulted in similar estimates of abundance for both sexes (5 males vs. 5.6 females). When we transform the count data into the binary format of detection/non-detection for non-spatial capture–recapture models and remove all of that spatial location data, much information about differences between the sexes is lost. The ability to use all data rather than a reduced binary set is an advantage of the SECR models, especially for the small data sets typical for studies of large carnivores.

The marked differences in estimated parameters provide insights into the distinct spatial behavior of male and female jaguars. A model that accounts for such differences is more realistic and informative than a model that ignores them, and this approach can easily be extended to covariates other than sex by incorporating different facets of individual heterogeneity. These considerations are important for any species where males and females differ in their spatial behavior, including all big felids, other carnivores such as bears (Gardner et al., 2010b) and many other mammals.

##### 4.2. Comparing the performance of jaguar density models

The density estimate under the spatial model (0.29 100 km<sup>-2</sup>) was about half of that under the non-spatial model. In the non-spatial model, we applied the MMDM algorithm, used by most jaguar camera trapping studies to estimate the effective area sampled (Maffei et al., 2004; Paviolo et al., 2008; Salom-Pérez et al., 2007; Silver et al., 2004). Estimates of the MMDM are constrained by the size of the sampling grid, as camera traps do not capture any movements beyond it. Thus, this approach likely underestimates movements and hence overestimates density. Even with the supposedly unsuitable habitat included in the buffer area, the combined density of 0.51 individuals 100 km<sup>-2</sup> was still much higher than under the spatial model. Combining camera trapping with GPS telemetry of jaguars, Soisalo and Cavalcanti (2006) showed that the MMDM algorithm underestimated movement and that the fMMDM was more realistic. Controversially, similar studies for leopards (Balme et al., 2009) and ocelots (Maffei and Noss, 2008) reached the opposite conclusion. These inconsistencies raise doubts about the usefulness of buffering approaches based on distance measures derived from the camera trapping grid.

In the present case, MMDM for both males (15.40 km) and females (4.47 km) were much lower than the SECR model estimates

of home range radius (38.25 km for males and 10.69 km for females). The issue of underestimating animal movement is important and applies to virtually all camera trapping surveys which usually sample much smaller areas than the present study, and even for jaguars are limited to areas ranging from 90 (Salom-Pérez et al., 2007) to 550 km<sup>2</sup> (Paviolo et al., 2008).

On the other hand, it is possible that the spatial model may underestimate density. Within the framework of our current model, we assume that all 15,000 km<sup>2</sup> of *S* are homogeneous in terms of habitat suitability for jaguars, i.e., individuals are equally likely to live and move anywhere within this area. This is essentially the same assumption that the MMDM-based approach makes, buffering the trap array by some additional area to account for animal movements. However, the spatial and non-spatial model approach of “buffering” are inherently different: While in the non-spatial model the choice of the buffer width has an immediate effect on the density estimate, in the spatial model the inclusion of the trapping grid into a larger landscape rectangle allows for animal movement beyond the trapping grid to be estimated without truncation. In our study area, we know that habitat suitability does vary, since our sampling grid covered the ENP, a protected area, whereas the rest of *S* is fragmented and converted by about 50% to cultivation, pastures and settlements (MMA, 2007). Subtracting such apparently unsuitable areas from the total buffer area, or from *S* (Royle et al., 2009) corrects for this heterogeneity and can ultimately influence the movement and density estimates in the SECR model. However, this is an ad hoc approach and, thus to some extent, arbitrary, unless we were certain about the areas jaguars do and do not use. True jaguar density within the park is therefore likely underestimated by the spatial model and overestimated by the non-spatial models.

In contrast to our results, Silveira (2004) estimated jaguar density in ENP at an order of magnitude higher at 2 individuals 100 km<sup>-2</sup> for a region of 500 km<sup>2</sup> in the east of the park. Silveira (2004) considered this to be the only region of ENP inhabited by the species, therefore suggesting significant heterogeneity in habitat suitability for jaguars even within the park. Based on the spatial distribution of jaguar encounters in the present study (Fig. 2), we draw the conclusion that jaguar movements are not nearly as restricted and, consequently, density across the entire park is hence much lower. With the increased amount of information on jaguar movements within ENP due to the large scale of the sampling grid and by explicitly modeling movements, the order of magnitude of our density estimates is likely to be more realistic for ENP as a whole.

#### 4.3. Comparison of jaguar densities across the range

Jaguar density in ENP as estimated by this study is lower than most published estimates from across the species range. The population currently still residing in ENP is therefore more likely to go extinct in the medium to long term (Sollmann et al., 2008). At such low densities, most protected areas, when isolated by surrounding cultivated land as ENP, likely only harbor small populations. Much of central Brazil is covered by habitat considered to be very difficult for successful dispersal of jaguars (Rabinowitz and Zeller, 2010) and in areas with cattle ranching, conflict with humans because of livestock predation poses an additional threat to the species.

However, for ENP we also observed indications that the population is somewhat stable: some individuals had already been registered by camera traps in earlier years, occasional records of cubs and juveniles show that reproduction occurs, and sporadic camera trapping in 2009 showed the presence of new adult individuals in the population. The ability of a small population to persist is related to the potential reproductive output of a species, which is generally

high for large felids (e.g., Lindzey et al., 1994; Karanth and Stith, 1999). Karanth and Stith (1999) showed that in a stochastic population model even small tiger populations had a low risk of extinction when simulated over 100 years. Thus, we may also expect some resilience to extinction in small jaguar populations.

There are some apparent trends in jaguar density: higher densities are encountered in tropical forests (up to 8.8 100 km<sup>-2</sup> in Belize; Silver et al., 2004) and prey-rich seasonal flood plains of the Pantanal (6.7 100 km<sup>-2</sup>; Soisalo and Cavalcanti, 2006) than in drier habitats such as the Gran Chaco (2.3–5.4 100 km<sup>-2</sup>; Maffei et al., 2004) or the Caatinga (2.7 100 km<sup>-2</sup>; Silveira et al., 2009), or severely anthropogenically modified and degraded environments such as the Brazilian Atlantic forest (as low as 0.2 100 km<sup>-2</sup>; Paviolo et al., 2008). The present estimates fit into this overall pattern, coming from a severely anthropogenically modified drier region.

However, the density estimates from other studies do not use a spatially explicit Bayesian modeling technique and use some ad hoc rule of defining buffer zones. These non-spatial density estimates are directly influenced by the chosen width of the buffer (e.g., MMDM vs. fMMDM), making them difficult to compare. As our study shows, these buffer widths lead to a substantially smaller effective sampled area than the estimates of home range radius delivered by the Bayesian SECR models, thereby automatically inflating density estimates. Also, other factors such as the size of the effective area sampled (e.g., Smallwood, 1997; Gaston et al., 1999) can confound density estimates. For such purposes, SECR models have the additional advantage over the traditional approach in that they provide a unified and formalized approach to estimate density, thus rendering them comparable.

#### 4.4. Future developments

While we believe that including sex as an individual covariate into both spatial and non-spatial capture–recapture studies is generally better than ignoring its obvious influence, we acknowledge the problem of sample size that becomes more severe with adding such covariates to a density model. Although for the SECR models the Bayesian framework provides valid inference for small sample size, this remains a problem. The standard errors of  $\lambda_0$  and  $\sigma$  reported above show that there is still much residual variation in these parameters. While the model structure can easily be adjusted to account for individual heterogeneity in  $\lambda_0$  and  $\sigma$ , in exploratory analyses (data not shown) our data set did not support the resulting number of parameters and some parameters became non-identifiable. Future work will have to identify whether this is purely an effect of small sample size or whether other properties of the data set are responsible for these difficulties.

Just as with buffer estimation in non-spatial density estimates, SECR models assume jaguar home ranges to be circular. For any situation where an animal is guided in its movements along specific landscape features, this assumption does not hold. In the present case, male jaguars followed the major water courses of the park (Fig. 1), and their home range shape is better described as an ellipse. To reconcile the observed spatial pattern of captures (i.e., equal or similar trap encounter rates in a wide span of traps located along a water course used as travel route and low to 0 encounter rates in traps that are adjacent to but not part of this route) with the assumption of circular home ranges the model “places” the activity centers of males beyond the park border (Fig. 2). Based on the actual habitat conditions in the park’s surrounding area, however, this is – in ecological terms – highly unlikely. Female home ranges are apparently much better described as circular. Relaxing the assumption on home range shape would be an interesting model development with the potential to benefit studies of many different species.

## 5. Conclusion

As for many populations of large cats, there is an urgent need to develop effective conservation strategies for jaguars in the Cerrado, as current conservation efforts are hampered by a persistent lack of knowledge. Occurring at generally low densities, big felids are not only particularly vulnerable to large-scale habitat loss, as is occurring in the Cerrado (Machado et al., 2004) and elsewhere, but despite improved methodologies and equipment they remain difficult to study. SECR models are an analytical step forward from traditional approaches to estimate densities of jaguars and other elusive species, since they overcome the problem of interpreting abundance and make use of the full information obtained by photographic data, including auxiliary spatial information. Nevertheless, these require large financial and logistical efforts in order to obtain sufficient data for reliable inference. Research and conservation efforts should therefore focus on the most pressing issues for the conservation of the species of interest. In the case of the Cerrado jaguar, this issue is where the remaining key populations are located and how a functional landscape connectivity can be created amongst them (Silveira and Jácomo, 2002). A first important step in this direction was undertaken by the effort of the Brazilian non-governmental organization Jaguar Conservation Fund to implement a dispersal corridor along the Araguaia River that starts in the immediate vicinity of ENP. Populations such as the one studied here must avoid becoming isolated and thereby extinction-prone simply owing to stochastic factors that arise from their small size (Shaffer, 1981). The fact that the species has persisted in the ENP over the last decades despite somewhat adverse conditions suggests that the potential is there.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.12.011.

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