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Reserve size, dispersal and population viability of wide ranging carnivores: the case of jaguars in Emas National Park, Brazil

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Keywords
spatially explicit capture recapture model; population viability analysis; large carnivores; protected areas; Panthera onca; reserve size; conservation.

Abstract
Protected areas may be important refuges for large carnivores, but many are not large enough to sustain viable populations. Without sufficient dispersal between protected areas, large carnivore populations inside them are at risk of becoming genetically isolated and demographically vulnerable. In this study, we use the jaguar population in and around Emas National Park in the Brazilian Cerrado as a case study to evaluate the demographic sustainability of a large carnivore population within a small and potentially isolated protected area. We used camera trapping data and spatially explicit capture-recapture models to estimate density and corresponding population size of jaguars in Emas National Park. We then used a matrix-based age and sex structured stochastic population model to evaluate the demographic viability of jaguar populations across a range of population sizes, including those estimated for Emas. We detected 10 individual jaguars during our survey with a total of 74 detections. Our density estimation became unbiased using a buffer width of 30 km and produced a density of 0.17 jaguars per 100 km$^2$. The estimated population sizes of 10–60 animals suffered extinction risks of 70–90% without net immigration. However, only a low number of immigrants were required to suppress extinction risk towards zero. Our density estimate for jaguars was lower than in previous studies, and our simulations suggested that this population may have a substantial extinction risk. Ensuring dispersal and connectivity outside of protected areas, through the implementation of habitat corridors, can greatly reduce this extinction risk, and we suggest that this scenario is potentially applicable to many other large carnivore populations.

Introduction
Large carnivores have suffered historic declines from persecution and habitat loss (Dalerum et al., 2009; Estes et al., 2011). This conflict is ongoing, and despite considerable conservation efforts the future of many large carnivore species is uncertain (Ripple et al., 2014). Conflicts between large carnivores and humans are typically related to livestock damage and expansion of agricultural activities (Treves & Karanth, 2003). However, conflict may also arise from direct risk to human safety and from more subtle causes related to perceived quality of life in rural areas (Thirgood, Woodroffe & Rabinowitz, 2005; Dickman, 2010; Penteriani et al., 2016). Subsequently, protected areas have become important refuges for large carnivores (Woodroffe, 2001), although recent expansions of large carnivores across Europe (Ensersink & Vogel, 2006; Chapron et al., 2014) and India (Athreya et al., 2013) suggest that these species may also exist in a matrix of human-dominated landscapes.

Maintaining large carnivores within protected areas is not without complications. The extensive areas required by these animals make it logistically daunting to create protected
areas of adequate size. Therefore, large carnivores may also suffer substantial extinction risk inside of reserves (Woo
droffe & Ginsberg, 1998; Brashares, Arcese & Sam, 2001). Even with large protected areas, there needs to be adequate
dispersal between them for population exchange to occur
(Somers, Gusset & Dalerum, 2012). In heavily fragmented
landscapes, this may not always be possible (Davies-Mostert,
Mills & Macdonald, 2015). Both carnivore behaviour and
predator-prey dynamics may also be influenced by human
activity within protected areas (Berger, 2007; Belton,
Cameron, & Dalerum, 2018), which may lead to unwanted
or unexpected ecological consequences of predation (Gaston
et al., 2008). Therefore, large carnivores may not always be
useful as proxies for biodiversity conservation inside pro-
tected areas (Linnell, Swenson & Andersen, 2000; Dalerum
et al., 2008; Sergio et al., 2008). As a consequence of these
issues, large carnivore conservation has recently focused on
how to manage large carnivore populations outside of pro-
tected areas, including using spatial models as an aid in
proactive conflict resolution planning (Eriksson & Dalerum,
2018; Zarzo-Arias et al., 2019) and incorporating social and
political aspects in large carnivore management (reviewed in
Hovardas, 2018). This focus follows a general trend in con-
servation biology, which has seen a shift from a utilitarian
view of environmental resources to its current focus on sus-
tainable incorporation of human societies into their ecoloi-
gical realities (Dalerum, 2014).

The jaguar Panthera onca is the third largest extant felid
and is one of the major apex predators of the Americas (Sanderson et al., 2002b). The most updated IUCN red list
assessment lists the species as threatened and reports a glo-
bal population 50 000–60 000 animals, (Quigley et al.,
2017), although a more recent estimate is substantially larger
at 138 000–208 000 individuals (Jędrzejewski et al., 2018).
Jaguars have experienced substantial range reduction and are
currently confined to only half of their former range (Jędrze-
jewski et al., 2018). The main reasons for this decline have
been largely attributed to habitat loss, prey depletion and
human persecution (Quigley et al., 2017). Protected areas
have been highlighted as important for the long-term sus-
tainability of the species (Sollmann, Torres, & Silveira,
2008), which has its primary stronghold in high productivity
areas in the Amazon basin, which also hosts low human
population densities (Jędrzejewski et al., 2018). Subse-
quently, Brazil hosts a major part of the global jaguar popu-
lation.

In arid regions of Brazil, jaguar populations are frag-
mented and occur at low densities (Jędrzejewski et al.,
2018). They have also received substantially less attention
compared to populations in the Amazon and Pantanal
(Astete, Sollmann & Silveira, 2008). The Cerrado biome of
central Brazil consists of semi-humid tropical savannah. It is
Brazil’s second largest biome, covering a total area of
approximately two million km² (Carvalho, De Marco & Fer-
reira, 2009). Although the Cerrado biome has been listed as
a world biodiversity conservation hotspot (Myers et al.,
2000), it has undergone drastic land use change with 80 %
now considered as degraded habitat (Cavalcanti & Joly,
2002.). This land degradation has mainly been caused by an
ongoing expansion of the agricultural industry (Klink &
Machado, 2005). Only 2% of the Cerrado biome is currently
protected. The Emas National Park is a small national park
of 1320 km², and is important for the conservation of native
Cerrado fauna and flora. However, the park is largely iso-
lated from other protected areas, and is predominately sur-
rounded by agricultural land. This has been raised as a cause
of concern for the long-term sustainability of the small but
resident jaguar population within and around the park (Soll-
mann et al., 2011).

In this study, we use the jaguar population in and around
Emas National Park as a case study to evaluate the demo-
graphic sustainability of a large carnivore population within
a small and potentially isolated protected area. Our study
adds to previous research based on a survey conducted two
years prior to the data presented here (Sollmann et al.,
2011). While this previous study provided a point estimate
of jaguar density within the park, we here provide a range
of plausible densities, and use the corresponding population
sizes from these densities in combination with a Population
Viability Analysis (PVA) to assess the extinction risk of the
jaguar population in and around Emas National Park. We
specifically set out to address the following questions: (1)
What is the sustainable population size of jaguar populations
that do not experience net immigration, and how do these
compare to plausible population sizes in Emas National
Park? (2) Using estimated densities from Emas National
Park, what size areas are required to host sustainable popu-
lations of jaguars without net immigration, and how do these
sizes compare to the size of Emas National Park? (3) How
many immigrants are required to suppress extinction risks in
populations of the size of the one estimated in Emas
National Park? (4) What are the relative effects of population
size, net number of immigrants and immigrant sex ratio on
extinction risk for the population in and around Emas
National Park? We used a camera trapping survey and spa-
tially explicit capture-recapture models to estimate densities
and population sizes in and around Emas National Park, and
applied the derived estimates of population sizes to a
stochastic population model to evaluate the demographic sus-
tainability with and without net immigration from other
jaguar populations.

Materials and methods

Study area

Emas National Park lies on the border between the states of
Goias and Mato Grosso do Sul in south-western Brazil
(18°19’S, 52°45’W; Fig. 1). In 2001, the park was listed by
UNESCO as a world natural heritage site due to its impor-
tant array of flora and fauna which characterise the Cerrado
biome (Amorim & Batalha, 2008). The park covers an area
of 1320 km² and is comprised of open grassland plains
(97%), marsh areas and gallery forest strips (2%) and
patches of shrub fields (1%) (Sollmann et al., 2011). Water
within the park is supplied from two rivers, the Jacuba and
Formosa, both of which originate from inside the park. The park experiences a distinct wet (October–March) and dry (April–September) season. During the wet season, rainfall averages at 1500 mm with very little rain for the rest of the year, and daytime temperatures may exceed 40°C in the dry season. The park is surrounded by intensive crop agriculture plantations, leaving only small fragments of native Cerrado habitat throughout the region. The interior of the park is home to at least 13 endangered mammal species and considered one of the best sites for observing Cerrado fauna (Redford, 1983). Jaguars coexist with other large predators such as pumas *Puma concolor*. Important prey species found within the park are giant anteater *Myrmecophaga tridactyla*, white lipped peccary *Tayassu pecari*, tapir *Tapirus terrestris* and pampas deer *Ozotoceros bezoarticus* (Foster et al., 2013; Sollmann et al., 2013). The interior of the park remains largely undeveloped, and tourism in the area is relatively low.

**Camera trapping survey**

The camera trapping survey was carried out in the dry season of 2010 as part of an ongoing long-term monitoring of jaguars in the region, sharing much of the design with a survey conducted in 2008 (Sollmann et al., 2011). A total of 103 camera trap stations were deployed on a 3.5 × 3.5 km grid (Fig. 1). This spacing corresponds to the diameter of the smallest recorded jaguar home range size (10 km², Rabinowitz & Jr, 1986). Hence, we regard this layout to enable jaguars with home ranges of this size or larger to be captured by at least one station, thus meeting the assumptions of closed capture-recapture models (Maffei et al., 2011). Most cameras were deployed by roads or trails, since these are often used by large felids (Karanth & Nichols, 1998). A station consisted of two motion triggered 35-mm film cameras (LeafRiver C1-BU, Vibrashine Inc., Taylorsville, MS 3968, USA), placed on opposite sides of the road or trail and approximately 30–60 cm off the ground (Silver et al., 2004). The cameras were only active from an hour from sunset to an hour after sunrise, which should not bias any sampling since jaguars in the park are prominently nocturnal (Silveira, 2004). Cameras were deployed from 22 March to 7 April 2010, and remained in use until 2–9 June for a maximum of 80 consecutive days for a single station (mean 78 days, min 65 days). They were checked at 10–14 day intervals to change film, check batteries and ensure the clearance of vegetation in front of the camera that could trigger them. Individual jaguars were identified through their unique coat pattern and capture histories and locations of detections were recorded.

**Estimation of density and population size**

We used a maximum likelihood implementation of spatially explicit capture-recapture (SECR) models to estimate density and population size from the camera records (Efford, 2004; Efford & Fewster, 2013). SECR models improve the accuracy of density estimates compared to non-spatial mark-recapture methods since they do not require ambiguous decisions regarding potential edge effects (Otis et al., 1978, but see discussion below regarding buffer widths). We used the algorithms implemented in the package SECR version 1.3.6 (Efford, 2018) for the R statistical environment (http://www.r-project.org, version 3.4.4 for Linux). These models are based on three parameters, a derived density parameter and two parameters defining the detection function, that is, the function defining the probability of an animal being detected at a given station based on its distance from the animal’s home range centre. For half-normal and exponential detection functions these parameters describe the detection probability at distance of zero (termed g₀ by Efford, 2018) and the other (σ) is a spatial scale parameter reflecting animal movement (Borchers & Efford, 2008).

Although the earlier study from the same area used an a-priori defined model structure including sex-specific encounter rates and movement (Sollmann et al., 2011), we used a penalized likelihood-based approach to select an optimal model from a range of candidate models of varying complexity. Our model set included parametrizations of

![Figure 1](image-url) Location of Emas national park in south west Brazil, as well as the locations of camera trap stations inside the park, their camera capture records and the buffer zones used for the spatially explicit density and population size estimates. Buffer zones were defined by buffer widths ranging from 1 to 50 km outside of the camera grid. A buffer width of 10 km approximately corresponds to the average diameter of jaguar home ranges recorded in the literature.
sex-specific estimates of both the \( g_0 \) and the \( \sigma \) parameter as well as a time trend covariate for the \( g_0 \) detection rate parameter. Since we had both known and unknown sex among our detected animals, we used hybrid mixture models for all parameter combinations that included sex-specific estimates (Pledger, 2000). These parameter combinations generated a set of 16 candidate models ranging in complexity from 3 to 8 parameters. We used Akaike’s Information Criterion corrected for small sample sizes (AICc: Akaike, 1974) and a threshold of 2 \( \Delta \)AICc units to identify models of equivalent empirical support (Burnham & Anderson, 2002). Model selection was done using the recommended buffer width of 4 times initial \( \sigma \), which corresponded to a buffer width of 40 km.

Likelihood implementations of SECR models estimate the location of unknown centres of home ranges by summarizing the likelihood over all possible locations within a specified area, termed the area of integration, weighted by the detection probability at each location (Borchers & Efford, 2008). The area of integration could theoretically be unbounded, but for practical reasons it is often limited to the area inside a buffer which extends from the outermost coordinates of the trap locations. SECR models are generally regarded as robust to over specifying the buffer width, as long as it is wide enough to ensure that animals at its edge have zero probability of being detected. However, large carnivores are often persecuted outside protected areas. Therefore, these areas effectively represent lower quality or directly uninhabitable habitats (e.g. Woodroffe & Ginsberg, 1998; Somers et al., 2012; Swanepeol et al., 2015), which often result in largely truncated patterns of animal movements. Because SECR models estimate uniform densities within the area of integration by default, buffers extending far outside of protected areas are likely to underestimate densities in cases when animal movements are truncated to occur mainly within protected area borders (Sollmann et al., 2011). The model framework allows for non-uniform distributions to be modelled. However, in the case of buffers extending outside of protected areas, such a solution is not possible if surveys are confined to within protected area borders. In such cases, the buffer area extending the survey will be completely confined with the two different habitat classes (i.e. inside and outside the protected area), which prevents any estimation of differences in densities between them. In the absence of data from outside the reserve, which prevented us from estimating potential differences in densities inside and outside of Emas; we chose to apply a range of plausible buffer widths to provide a heuristic evaluation of the effects of including areas outside the reserve in our calculations. We included buffer widths from 1 km (approximately corresponding to the borders of Emas National Park) to 50 km (Fig. 1), which reflects the diameter of the largest home range size recorded for the Cerrado biome (Morato et al., 2016). For the shortest buffer widths of 1 and 2.5 km, we extended the buffer around stations more than 1 and 2.5 km from the borders so that we did not exclude any areas within Emas National Park from the area of integration.

Although spatially explicit capture-recapture models were developed to estimate population density, they can also be used to estimate population size (Efford & Fewster, 2013). We assumed that all detected animals belonged to the population of concern, and hence used our models to estimate the proportion of undetected animals. This is analogous to the realized estimated population size (Johnson, Laake, & Ver Hoef, 2010), and was calculated by multiplying the estimated density by the size of the area of integration.

### Population viability model

We used a matrix-based age and sex structured stochastic population model as the basis for our population viability analysis. The model was created in the R language. The model contained 4 age classes: juveniles (0–1 years), sub adults (1–2 years), adults (3–10 years) and old animals (>10 years). It traced each sex separately for adult and old animals. Each year of simulation, age specific survival and fecundity were drawn from binary distributions, and litter size from Poisson distributions. The model did not include a carrying capacity or any density dependence. We justify this simplification primarily because PVA models evaluating extinction risks typically operate at values grossly under biological carrying capacity, unless the carrying capacity is close to or below sustainable population size (Mills, 2012). In the case of large carnivores, which in modern landscapes are primarily restricted by persecution and not by resource limitation, we regard this to be rarely the case. In addition, we also lack data to parameterize density dependent demographics, as well as data to estimate carrying capacity for the Emas region.

We ran two sets of simulations. First, we ran a set of closed populations (i.e. without any form of migration) ranging in initial population size from 10 to 700 animals. Second, we ran a series of simulations including net immigration. In these simulations, we drew number of immigrants every year from Poisson distributions with means ranging from zero to 10 animals. For each level of average number of immigrants, we sequentially altered the sex ratio from 50% to 95% males. We let all immigrants enter the population as 3 year old animals (Miller, 2013). This second set of simulations were run over initial population sizes ranging from 10 to 60, based on estimated population sizes from Emas National Park. We ran each set of parameter combinations 1000 times. The models used discrete time steps of one year. For each simulation ran, we captured the projected population size after 50 years of simulation, and binary coded it as extinct if it contained less than one animal of each sex. We regarded 50 years as an appropriate trade-off between a time span that is long enough to capture demographic processes but still sufficiently short to be relevant for management purposes (Dalerum et al., 2008). Details of the specific parameter values and their sources are given in supporting information, Table S1. We opted to use literature values since we did not have specific parameter values for the population in and around Emas National Park.
To provide a heuristic evaluation of the relative effects of initial population size, net immigration and immigration sex ratio, we calculated the standardized beta values for each of these variables from a generalized linear model (GLM) using a binomial error function and a logit link. Such an approach is in line with treating simulation studies as an experimental system, which has been suggested as a fruitful approach to benefit from simulated data (Peck, 2004). The GLM used the binary model output (extinct or not extinct) as the response, and initial population size, net immigration, immigration sex ratio as well as the two- and three-way interaction effects as predictors. We standardized all predictors by dividing them by their standard deviations so that the strength of their effects could be compared directly. However, we have not presented any p-values associated with these standardized coefficients, since any alpha error would be arbitrarily defined by the number of simulation runs the coefficients were based on.

As with the SECR models, the PVA and subsequent analyses were performed using the R statistical environment version 3.4.4 for Linux. Pseudo code for the population model is available in supporting information, Appendix S1.

**Results**

**Density and population size**

We detected 10 individual jaguars during our survey, five of which were males, three females and two of unknown sex (Table 1). The two of unknown sex were only detected once. All other jaguars were detected at least twice, with a maximum number of 14 detections for any individual animal. The detections were distributed across the Emas National Park, although the majority of detections were in its southern half (Fig. 1). Of the jaguars detected more than once, all except one male were detected at more than one station, with one male detected at seven stations and one male and two females detected at six stations each. The average distances between stations ranged from 0 to 21.53 km, with a maximum distance of 35.33 km. Two of the females and two males were also detected in a survey two years earlier (Table 1).

The most parsimonious density model used an exponential detection function and did not include any covariates of sex or time trends (Table 2). This model was 5.37 AICc units lower than the model with the second lowest AICc score, which was the model using a time trend for the detection parameter g0. More advanced models including covariates for a time trend and sex-specific detection and movement parameters all showed lower performance (Table 2).

A buffer width of 10 km, corresponding to approximately the diameter of average recorded jaguar home range sizes, generated an average density of 0.34 jaguars per 100 km$^2$ (95% CI = 0.18–0.69 jaguars per 100 km$^2$). However, density estimates became unbiased only at a buffer width of 30 km, with a corresponding density of 0.17 jaguars per 100 km$^2$ (95% CI = 0.08–0.34 jaguars per 100 km$^2$). At smaller buffer widths, densities increased sharply (Fig. 2a), reaching an average density of 0.75 jaguars per 100 km$^2$ (95% CI = 0.40–1.39 jaguars per 100 km$^2$) with a buffer width of 1 km, corresponding approximately to the entire detected population being confined within the Emas National Park borders (Fig. 1). A previously used buffer width of 40 km generated a density of 0.16 jaguars per 100 km$^2$ (95% CI = 0.07–0.35 jaguars per 100 km$^2$).

Estimated realized population size with a 10 km buffer width was 10.33 animals (95% CI = 10.02–16.26). Population sizes increased with larger buffer widths, reaching an average of 25.34 jaguars (95% CI = 14.99–57.21) at a buffer width of 50 km (Fig. 2b). The proportion of the estimated population that were residing within Emas National Park borders declined with increasing buffer width, being 0.43 (95% CI = 0.28–0.45) at a buffer width of 10 km and 0.08 (95% CI = 0.04–0.14) at a buffer width of 50 km (Fig. 2c).

**Population viability**

Closed populations exhibited substantial extinction risks even at considerable population sizes. A population size of 300 animals was required to suppress extinction risk to below 10% over 50 years (Fig. 3a). Population sizes corresponding to the population size estimate using a 10 km buffer width (10–16 animals) had over 90% extinction risk, and even the

| Jaguar ID | Sex | Number of detections | Number of stations | Average distance between stations (km) | Range distance between stations (km) | Detected also in 2008 |
|-----------|-----|----------------------|--------------------|----------------------------------------|--------------------------------------|-----------------------|
| Jaguar 6  | F   | 7                    | 6                  | 11.17                                  | 0–21.21                              | Y                     |
| Jaguar 9  | F   | 8                    | 6                  | 13.31                                  | 2.93–29.58                           | Y                     |
| Jaguar 19 | F   | 2                    | 2                  | 7.44                                   | 7.44                                 | N                     |
| Jaguar 10 | M   | 14                   | 6                  | 9.41                                   | 0–31.31                              | N                     |
| Jaguar 11 | M   | 4                    | 3                  | 11.61                                  | 0–20.87                              | Y                     |
| Jaguar 16 | M   | 7                    | 7                  | 21.53                                  | 3.43–35.33                           | Y                     |
| Jaguar 20 | M   | 2                    | 1                  | 0                                      | 0                                    | N                     |
| Jaguar 21 | M   | 4                    | 3                  | 3.66                                   | 0–7.54                               | N                     |
| Jaguar 22 | U   | 1                    | 1                  |                                        |                                      | N                     |
| Jaguar 23 | U   | 1                    | 1                  |                                        |                                      | N                     |
upper 95% CI of the population size using a 50 km buffer width (i.e. approximately 60 jaguars) had 70% extinction risk (Fig. 3a). Sustainable population sizes required considerable areas based on our estimated densities, with populations with extinction risks below 10% requiring an area of 8000 km², based on the average density using a 10 km buffer; and requiring an area of 14900 km² based on estimated densities using a 50 km buffer width (Fig. 3b).

Using initial population sizes of 10–60 animals, even a modest number of net immigrants suppressed extinction risk

Parameter names follow the nomenclature of Efford (2018):

g0 = detection probability at zero distance of camera station to a specific home range centre.

r = animal movement parameter used to spatially scale the detection function.

Pmix = parameter estimating sex ratio in hybrid mixture models used to model sex specific parameter estimates in the presence of detected animals with unknown sex.

Table 2 AICc scores, Δ AICc scores, model structures and detection function for a set of 20 candidate models evaluated for optimal fit to the Emas jaguar data. A threshold of 2 Δ AICc units was used to define a model with better empirical support.

| Model structure 1 | Detection function | Number of parameters | AICc   | Δ AICc |
|-------------------|--------------------|---------------------|--------|--------|
| g0 = 1; σ = 1     | Exponential        | 3                   | 748.20 | 0.00   |
| g0 = Time; σ = 1  | Exponential        | 4                   | 753.57 | 5.37   |
| g0 = 1; σ = 1     | Half-normal        | 3                   | 757.44 | 9.24   |
| g0 = Time; σ = 1  | Half-normal        | 4                   | 762.81 | 14.61  |
| g0 = Sex; σ = 1; Pmix = Sex | Exponential | 5 | 769.19 | 20.99 |
| g0 = 1; σ = Sex; Pmix = Sex | Exponential | 5 | 773.24 | 25.03 |
| g0 = Sex; σ = 1; Pmix = Sex | Half-normal | 5 | 780.73 | 32.53 |
| g0 = 1; σ = Sex; Pmix = Sex | Half-normal | 5 | 782.70 | 34.50 |
| g0 = Sex; σ = Sex; Pmix = Sex | Exponential | 5 | 783.94 | 35.74 |
| g0 = Time; σ = Sex; Pmix = Sex | Exponential | 6 | 787.61 | 39.41 |
| g0 = Sex; σ = Sex; Pmix = Sex | Half-normal | 5 | 793.84 | 43.91 |
| g0 = Time; σ = Sex; Pmix = Sex | Half-normal | 6 | 797.07 | 48.86 |
| g0 = Time × Sex; σ = 1; Pmix = Sex | Exponential | 7 | 812.66 | 64.46 |
| g0 = Time × Sex; σ = 1; Pmix = Sex | Half-normal | 7 | 824.24 | 76.04 |
| g0 = Time × Sex; σ = Sex; Pmix = Sex | Exponential | 8 | 902.41 | 154.21 |
| g0 = Time × Sex; σ = Sex; Pmix = Sex | Half-normal | 8 | 914.24 | 166.04 |

| Figure 2 | Densities (a) and realized population sizes (b) of jaguars in and around Emas national park, estimated from camera trap data and spatially explicit mark re-capture models with buffer widths ranging from 1 to 50 km outside the camera grid, as well as the estimated proportion of the population that would reside inside the park borders of population size estimates from models run over the same range of buffer widths (c). A buffer width of 10 km approximately corresponds to the average diameter of recorded jaguar home ranges, whereas a buffer width of 50 km corresponds to the diameter of the upper limit of the 95 CI for home range sizes recorded from the Cerrado biome. Since the buffer zones all extend outside the Emas national park borders, the densities and population sizes are estimated under the assumption of equal jaguar densities inside and outside the park borders. |
towards zero, with 4 (50% male immigrants, Fig. 4a), 5 (75% male immigrants, Fig. 4b) and 6 (95% male immigrants, Fig. 4c) immigrants required. Overall, number of immigrants had the strongest effect of jaguar extinction risk ($\beta = -2.57$), followed by immigrant sex ratio ($\beta = 0.33$) and initial population size ($\beta = -0.17$). However, immigrant sex ratio had an intermediate effect on number of immigrants on extinction risk ($\beta = 0.33$). This interaction between sex ratio and number of immigrants was not influenced by initial population size ($\beta = 0.01$), nor did initial population size directly influence the effect of sex ratio ($\beta = 0.01$) nor the effect of number of immigrants on extinction risk ($\beta = 0.03$).
in the Atlantic Forest, Cullen, 2006; 4.4 in the Amazon, when using the same buffer width as Sollmann et al. parts of the jaguar range (Eizirik et al., 2001; De la Torre et al., 2018). Emas National Park is, with its 1320 km², substantially smaller than the average size of 6674 km² reported for protected jaguar areas in Brazil (Sollmann et al., 2008), but not substantially smaller than the average reserve size in the Cerrado biome (1936 km²). Indeed, it is considerably larger than the average size of protected jaguar areas in the Caatinga (734 km²), the Pantanal (679 km²) and the Atlantic forest (431 km²). Our results also suggest that viable jaguar populations without net immigration require areas of a very large size, greater than 10 000 km², and we note that protected areas of such sizes are only common in the Amazon. This finding highlights that it may be logistically and economically challenging to create protected areas large enough to sustain viable jaguar populations in large parts of the jaguar range within Brazil. This suggestion is corroborated by jaguar home range sizes of up to 150 km² in the Cerrado biome (Silveira, 2004), and agrees with Crawshaw et al. (2004) who similarly noted the challenges of preserving jaguar populations inside protected areas. Moreover only 4% of globally important jaguar habitats are effectively protected (Sanderson et al., 2002a). A similar situation has been reported for leopards (Panthera pardus) in South Africa, where only 25% of suitable leopard habitat was found to be formally protected (Swanepole et al., 2013). Since area protection does not appear to be a very viable option for large carnivore management, at least not in some environments, we re-iterate previous suggestions that conflict resolution in human dominated landscapes may provide one of the most efficient means to manage large carnivores for long-term sustainability (e.g. Chapron et al., 2014).

Our findings emphasise the importance of connectivity for jaguar population viability, since only a few immigrants were required to substantially reduce extinction risk, even in small populations. Our simulations also suggested that improving net immigration may be more important than increasing population sizes in small isolated populations. Furthermore, we achieved these results using simulations that only evaluated the demographic effects of dispersal. Several genetic processes, such as inbreeding and genetic drift, can have detrimental impacts on the viability of small and genetically isolated populations (Dixon et al., 2007; Haag et al., 2010; McManus et al., 2015). Therefore, the effects of dispersal on population viability are likely to have been greater if we had included genetic processes in our simulations as well. The

Discussion

Although protected areas may be important for large carnivore populations by buffering them from anthropogenic impacts (Santini et al., 2016), our results suggest that the jaguar population in and around Emas National Park may suffer substantial extinction risk. Our camera trapping data suggested a population size of 10–60 animals, although we appreciate that these values are based on models with low precision of the estimated densities. In spite of this, we regard our interpretation as robust since even the higher value in this range, a situation in which a substantial part of the population would reside outside the park, is substantially lower than what our simulations suggest as sustainable without any net immigration. We therefore suggest that promoting an increase in jaguar immigration from neighbouring populations would greatly benefit jaguar conservation in and around Emas National Park. Although this region is in an area of relatively low densities (Jędziewski et al., 2018), there is strong potential for successful implementation of jaguar dispersal corridors into the Emas population (Roques et al., 2018). Our density estimate (e.g. a maximum of 0.75 jaguars per 100 km² in our study) is comparable to an earlier estimate in the Atlantic forest (0.93–1.74 individuals per 100 km², Paviolo et al., 2008), but substantially lower than estimated densities both elsewhere in the Cerrado biome (2.0 per 100 km², Silveira, 2004) and in other parts of the species’ range (2.67 in the Caatinga, Silveira et al., 2010; 2.22 in the Atlantic Forest, Cullen, 2006; 4.4 in the Amazon, Tobler et al., 2013; 10.3 in the Pantanal, Soisalo & Cavalcanti, 2006). This finding agrees with a general assessment of jaguar densities across South America (Jędziewski et al., 2018). In addition, our results may suggest a decline in jaguar density between 2008 (0.29 jaguars per 100 km², Sollmann et al., 2011) and 2010 (0.16 jaguars per 100 km², when using the same buffer width as Sollmann et al., 2011), which further highlights the necessity of this area to remain in demographic contact with regions of higher jaguar densities.

We found that closed reserves of the size of Emas National Park do not appear to be large enough to maintain long-term viable jaguar populations without any net immigration. This conclusion agrees with similar findings in other parts of the jaguar range (Eizirik et al., 2001; De la Torre et al., 2018). Emas National Park is, with its 1320 km², substantially smaller than the average size of 6674 km² reported for protected jaguar areas in Brazil (Sollmann et al., 2008), but not substantially smaller than the average reserve size in the Cerrado biome (1936 km²). Indeed, it is considerably larger than the average size of protected jaguar areas in the Caatinga (734 km²), the Pantanal (679 km²) and the Atlantic forest (431 km²). Our results also suggest that viable jaguar populations without net immigration require areas of a very large size, greater than 10 000 km², and we note that protected areas of such sizes are only common in the Amazon. This finding highlights that it may be logistically and economically challenging to create protected areas large enough to sustain viable jaguar populations in large parts of the jaguar range within Brazil. This suggestion is corroborated by jaguar home range sizes of up to 150 km² in the Cerrado biome (Silveira, 2004), and agrees with Crawshaw et al. (2004) who similarly noted the challenges of preserving jaguar populations inside protected areas. Moreover only 4% of globally important jaguar habitats are effectively protected (Sanderson et al., 2002a). A similar situation has been reported for leopards (Panthera pardus) in South Africa, where only 25% of suitable leopard habitat was found to be formally protected (Swanepole et al., 2013). Since area protection does not appear to be a very viable option for large carnivore management, at least not in some environments, we re-iterate previous suggestions that conflict resolution in human dominated landscapes may provide one of the most efficient means to manage large carnivores for long-term sustainability (e.g. Chapron et al., 2014).

Our findings emphasise the importance of connectivity for jaguar population viability, since only a few immigrants were required to substantially reduce extinction risk, even in small populations. Our simulations also suggested that improving net immigration may be more important than increasing population sizes in small isolated populations. Furthermore, we achieved these results using simulations that only evaluated the demographic effects of dispersal. Several genetic processes, such as inbreeding and genetic drift, can have detrimental impacts on the viability of small and genetically isolated populations (Dixon et al., 2007; Haag et al., 2010; McManus et al., 2015). Therefore, the effects of dispersal on population viability are likely to have been greater if we had included genetic processes in our simulations as well. The

Figure 4 Extinction risk after 50 years of simulation of jaguar populations ranging in initial population sizes from 10 to 60 animals that were subject to a net immigration of 0–10 animals with a sex ratio of 50% (a), 75% (b) and 95% (c) males. Extinction risk was calculated using an age-structured stochastic PVA model parametrized using data from jaguar literature and 10–60 animals represents the lower and upper bounds of the realistic range of population sizes in and around Emas National park, Brazil.
importance of identifying and maintaining dispersal corridors has similarly been noted for many other large carnivore species (Dixon et al., 2006; Shepherd, & Whittington, 2006; Wegg, Yadav, & Lamichhane, 2018), as well as by other studies on jaguars (Roques et al., 2016). Most long-range dispersal is generally through non-protected land (Somers et al., 2012), which may have lower survival than protected areas (Swane poel et al., 2015). The importance of maintaining dispersal corridors therefore provides further arguments for the necessity of focusing large carnivore conservation and management on conflict resolution and sustainable co-existence between carnivores and humans in anthropogenic landscapes.

Our case study shows that, while SECR models are useful and widely used tools for estimating densities from mark capture data, their use may be limited by incomplete sample designs associated with unknown variation in densities across protected area borders (Foster & Harmsen, 2012). Although SECR models are generally robust to over-specifying the buffer width, this is under the assumption that densities are equal, or at least similar, across the whole area of integration unless differences are specified as habitat covariates (Efford & Fewster, 2013). Unless sampling is also done outside protected area borders, such a parameterization is not possible. Extending the buffer width too far outside the protected area may therefore produce under-estimated densities inside protected area borders. Our results highlight that our sampling design suffers these exact problems. As a heuristic solution to this issue, we ran our SECR models over a range of reasonable buffer widths to evaluate the potential effect of including areas outside of the reserve border in the absence of data from this area. Since the buffer widths were highly influential on our density and subsequent population size estimates, we recommend that studies of species inside protected areas take this potential problem into account, and extend the trapping area also outside the protected area of concern wherever possible.

Our study combined information from a camera trapping effort, which generated plausible population sizes, and PVA simulations, along with extinction risks for those population sizes. We conclude that the jaguar population in Emas National Park, a small protected area in the Cerrado biome of Brazil, is likely demographically unsustainable without net immigration from neighbouring populations. More broadly, large areas required to host viable jaguar populations combined with strong effects of inter-population dispersal for population viability highlight the importance of conflict management outside protected areas for jaguar conservation. We suggest that these results are applicable to many other large carnivore species, and argue that finding sustainable solutions for co-existence between large carnivores and humans outside protected areas should be a prioritized activity for large carnivore conservation worldwide.

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**Supporting information**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** Parameters used for the PVA models, including their sources.

**Appendix S1.** Pseudo code for an age and sex structured matrix based population viability model using the R language.