LJMU Research Online

Finnegan, SP, Galvez Bravo, L, Silveira, L, Torres, NM, Jacomo, AT, Alves, GB and Dalerum, F

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

http://researchonline.ljmu.ac.uk/id/eprint/12910/

Article

Citation (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

Finnegan, SP, Galvez Bravo, L, Silveira, L, Torres, NM, Jacomo, AT, Alves, GB and Dalerum, F (2020) Reserve size, dispersal and population viability of wide ranging carnivores: the case of jaguars in Emas National Park, Brazil. Animal Conservation. ISSN 1367-9430

Animal Conservation

Animal Conservation. Print ISSN 1367-9430

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

S. P. Finnegan[1,2,3], L. Galvez-Bravo[2], L. Silveira[3], N. M. Tôrres[3,4], A. T. A Jácomo[3], G. B. Alves[3,4] & F. Dalerum[5,6,7]

1 Department of Environmental and Forest Biology, College of Environmental Science and Forestry, State University of New York, New York, NY, USA
2 School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, UK
3 Jaguar Conservation Fund/Instituto Onça-Pintada, Mineiros, Goias, Brazil
4 Federal University of Uberlândia, Uberlândia, Brazil
5 Mixed Unit of Biodiversity (UMIB), University of Oviedo, Oviedo, Spain
6 Department of Zoology and Entomology, Mammal Research Institute, University of Pretoria, Pretoria, South Africa
7 Department of Zoology, Stockholm University, Stockholm, Sweden

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

Correspondence
Shannon Patricia Finnegan, Department of Environmental and Forest Biology, College of Environmental Science and Forestry, State University of New York, 1 Forestry Drive, Syracuse, NY, 13210, USA.
E-mail: shannonfinnegan8@yahoo.com

Editor: Julie Young
Associate Editor: Randeep Singh

Received 27 March 2019; accepted 07 May 2020

doi:10.1111/acv.12608

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 (Ensenrink & 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 (Woodroffe & 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 protected 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 protected 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 conservation biology, which has seen a shift from a utilitarian view of environmental resources to its current focus on sustainable incorporation of human societies into their ecological 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*., 2002*b*). The most updated IUCN red list assessment lists the species as threatened and reports a global 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 (Jędrzejewski *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 sustainability 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). Subsequently, Brazil hosts a major part of the global jaguar population.

In arid regions of Brazil, jaguar populations are fragmented 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 km^2 (Carvalho, De Marco & Ferreira, 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 km^2, and is important for the conservation of native Cerrado fauna and flora. However, the park is largely isolated from other protected areas, and is predominately surrounded 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 (Sollmann *et al*., 2011).

In this study, we use the jaguar population in and around Emas National Park as a case study to evaluate the demographic 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 populations 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 spatially 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 sustainability 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 important array of flora and fauna which characterise the Cerrado biome (Amorim & Batalha, 2008). The park covers an area of 1320 km^2 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 km^2, 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

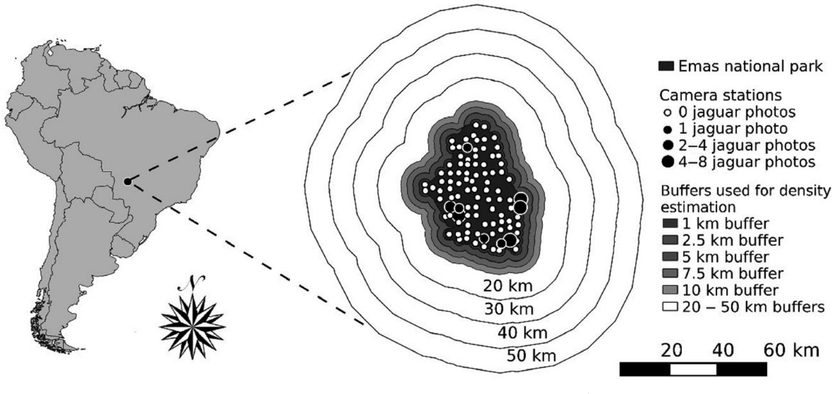

Figure 1 Location of Emas national park in south west Brazil, as well as the locations of camera trap stations inside the park, their camera capture records and the buffer zones used for the spatially explicit density and population size estimates. Buffer zones were defined by buffer widths ranging from 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 g0 and the σ parameter as well as a time trend covariate for the g0 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 ΔAICc units to identify models of equivalent empirical support (Burnham & Anderson, 2002). Model selection was done using the recommended buffer width of 4 times initial σ, 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; Swanepoel *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 confounded 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

Table 1 Detected jaguars in Emas National Park, the number of times they were detected, the number of stations they were detected at and the distances between them, and if the animals were also detected in a survey 2008.

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

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	783.94	35.74
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

[1] Parameter names follow the nomenclature of Efford (2018):

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

σ = 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.

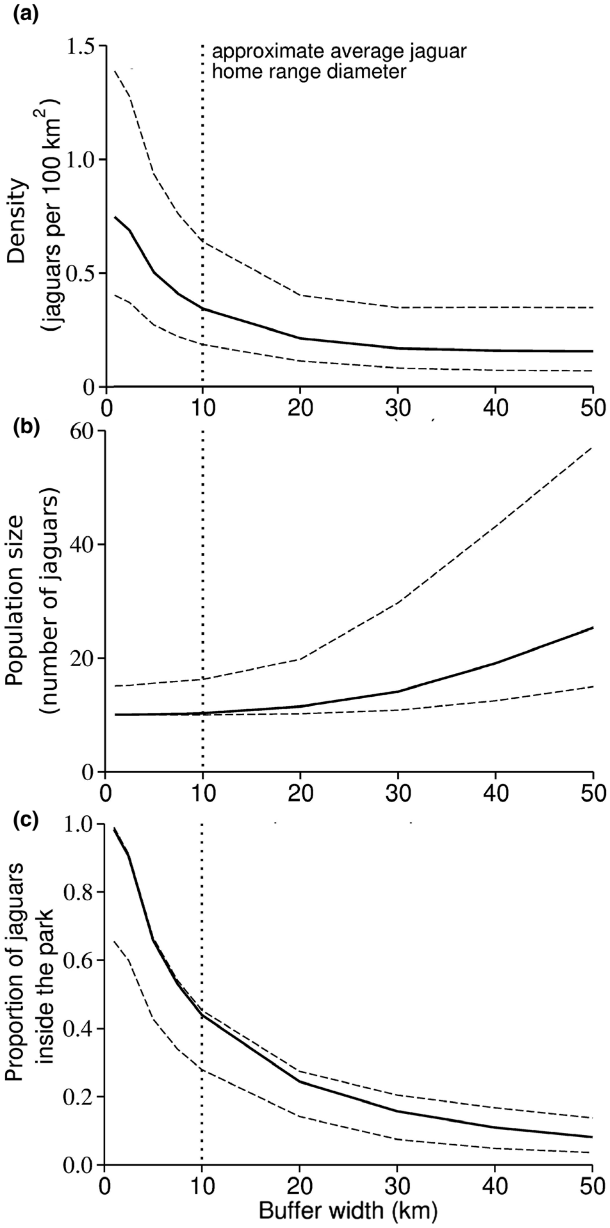

Figure 2 Densities (a) and realized population sizes (b) of jaguars in and around Emas national park, estimated from camera trap data and spatially explicit mark re-capture models with buffer widths ranging from 1 to 50 km outside the camera grid, as well as the estimated proportion of the population 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.

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 km^2, based on the average density using a 10 km buffer; and requiring an area of 14900 km^2 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

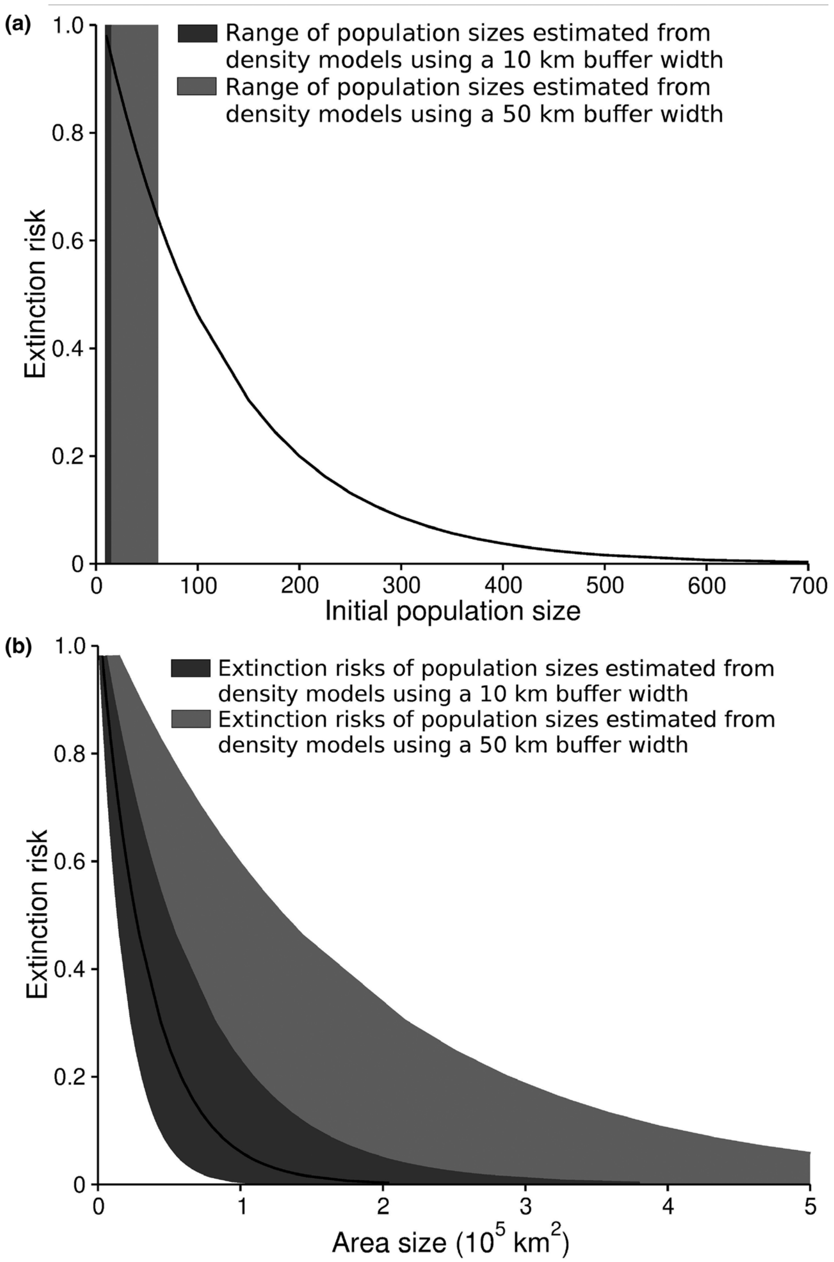

Figure 3 Extinction risk after 50 years of simulation of closed jaguar populations with initial population sizes from 10 to 700 individuals (a), and extinction risks of populations residing in areas with population sizes corresponding to densities estimated from Emas National Park (b). Shaded areas represent population sizes and densities in and around Emas National Park based on lower and upper 95% confidence limits of densities estimated from spatially explicit mark-recapture models using a buffer width of 10 km, which is approximately the diameter of average recorded jaguar home range sizes, and of models using a buffer width of 50 km, which is approximately the diameter of the largest recorded jaguar home range sizes in the Cerrado biome.

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 ($\beta = 0.53$) 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 ($\beta = 0.03$).

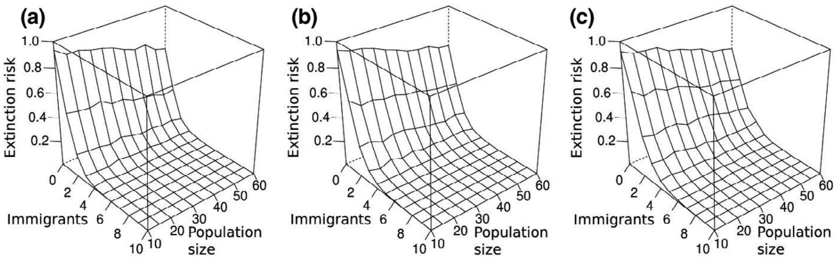

Figure 4 Extinction risk after 50 years of simulation of jaguar populations ranging in initial population sizes from 10 to 60 animals that were subject to a net immigration of 0–10 animals with a sex ratio of 50% (a), 75% (b) and 95% (c) males. Extinction risk was calculated using an age-structured stochastic 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.

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 (Jędrzejewski *et al*., 2018), there is strong potential for successful implementation of jaguar dispersal corridors into the Emas population (Roques *et al*., 2016). Our density estimate (e.g. a maximum of 0.75 jaguars per 100 km^2 in our study) is comparable to an earlier estimate in the Atlantic forest (0.93–1.74 individuals per 100 km^2, Paviolo *et al*., 2008), but substantially lower than estimated densities both elsewhere in the Cerrado biome (2.0 per 100 km^2, 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 (Jędrzejewski *et al*., 2018). In addition, our results may suggest a decline in jaguar density between 2008 (0.29 jaguars per 100 km^2, Sollmann *et al*., 2011) and 2010 (0.16 jaguars per 100 km^2, 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 km^2, substantially smaller than the average size of 6674 km^2 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 km^2). Indeed, it is considerably larger than the average size of protected jaguar areas in the Caatinga (734 km^2), the Pantanal (679 km^2) and the Atlantic forest (431 km^2). Our results also suggest that viable jaguar populations without net immigration require areas of a very large size, greater than 10 000 km^2, 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 km^2 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*., 2002*a*). 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 (Swanepoel *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 importance of identifying and maintaining dispersal corridors has similarly been noted for many other large carnivore species (Dixon *et al*., 2006; Shepherd, & Whittington, 2006; Wegge, 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 (Swanepoel *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 recapture 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.

Acknowledgements

Funding was provided by Memphis Zoo and a Ramón y Cajal fellowship from the Spanish Ministry of Economy and Competitiveness (awarded to FD, RYC-2013-14662). LGB benefited from a Faculty of Science ECR Fellowship from Liverpool John Moores University. The authors thank all members of the Jaguar Conservation Fund who contributed to data collection for this study. The manuscript benefited greatly from the comments of Dr. Mariela Gantchoff and Dr. Jacob Hill. The authors thank the three anonymous reviewers who provided valuable input to the manuscript.

References

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Trans. Autom. Control* **19**, 716–723.

Amorim, P.K. & Batalha, M.A. (2008). Soil chemical factors and grassland species density in Emas National Park (central Brazil). *Braz. J. Biol.* **68**, 279–285.

Astete, S., Sollmann, R. & Silveira, L. (2008). Comparative ecology of jaguars in Brazil. *Cat News* **4**, 9–14.

Athreya, V., Odden, M., Linnell, J.D., Krishnaswamy, J. & Karanth, U. (2013). Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. *PLoS One* **8**, e57872.

Belton, L., Cameron, E.Z. & Dalerum, F. (2018). Social networks of spotted hyaenas in areas of contrasting human activity and infrastructure. *Anim. Behav.* **135**, 13–23.

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biol. Let.* **3**, 620–623.

Borchers, D.L. & Efford, M.G. (2008). Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics* **64**, 377–385.

Brashares, J.S., Arcese, P. & Sam, M.K. (2001). Human demography and reserve size predict wildlife extinction in West Africa. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 2473–2478.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer.

Carvalho, F.M., De Marco, P. & Ferreira, L.G. (2009). The Cerrado into-pieces: Habitat fragmentation as a function of landscape use in the savannas of central Brazil. *Biol. Cons.* **142**, 1392–1403.

Cavalcanti, R.B. & Joly, C.A. (2002). Biodiversity and conservation priorities in the Cerrado region. In *The Cerrados of Brazil. Ecology and Natural History of a Neotropical Savanna*: 351–367. Oliveira, P.S. & Marquis, R.J. (Eds). New York: Columbia University Press.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López-Bao, J.V. et al (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* **346**, 1517–1519.

Crawshaw Jr, P.G., Mahler, J.K., Indrusiak, C.I.B.E.L.E., Cavalcanti, S.M., Leite-Pitman, M.R.P. & Silvius, K.M. (2004). Ecology and conservation of the jaguar (Panthera onca) in Iguaçu National Park, Brazil. In *People in Nature: Wildlife Conservation in South and Central*

America: 286–296. Silvius, K.M., Bodmer, R.E. & Fragoso, J.M.V. (Eds). New York: Columbia University Press.

Cullen Jr, L.(2006). Jaguars as landscape detectives for the conservation of Atlantic Forests in Brazil. PhD thesis. University of Kent, Kent.

Dalerum, F. (2014). What is the role of conservation biology for solving the environmental crisis? *Ambio* **43**, 839–846.

Dalerum, F., Shults, B. & Kunkel, K. (2008). Estimating sustainable harvest in wolverine populations using logistic regression. *J. Wildl. Manage.* **72**, 1125–1132.

Dalerum, F., Cameron, E.Z., Kunkel, K.E. & Somers, M.J. (2009). Continental patterns of carnivore guild depletions: implications for prioritizing global carnivore conservation. *Biol. Let.* **5**, 35–38.

Davies-Mostert, H.T., Mills, M.G.L. & Macdonald, D.W. (2015). The demography and dynamics of an expanding, managed African wild dog metapopulation. *Af. J. Wildl. Res.* **45**, 258–273.

De La Torre, J.A., González-Maya, J.F., Zarza, H., Ceballos, G. & Medellín, R.A. (2018). The jaguar's spots are darker than they appear: assessing the global conservation status of the jaguar *Panthera onca*. *Oryx* **52**, 300–315.

Dickman, A. (2010). Complexities of conflict: The importance of considering social factors for effectively resolving human–wildlife conflict. *Anim. Conserv.* **13**, 458–466.

Dixon, J.D., Oli, M.K., Wooten, M.C., Eason, T.H., Mc Cown, J.W. & Paetkau, D. (2006). Effectiveness of a regional corridor in connecting two Florida black bear populations. *Conserv. Biol.* **20**, 155–162.

Dixon, J.D., Oli, M.K., Wooten, M.C., Eason, T.H., McCown, J.W. & Cunningham, M.W. (2007). Genetic consequences of habitat fragmentation and loss: the case of the Florida black bear (*Ursus americanus floridanus*). *Conserv. Genet.* **8**, 455–464.

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

Efford, M.G. (2018). SECR: spatially explicit capture-recapture models. R package version 3.1.6. https://CRAN.R-project.org/package=secr (accessed January 15, 2019)

Efford, M.G. & Fewster, R.M. (2013). Estimating population size by spatially explicit capture–recapture. *Oikos* **122**, 918–928.

Eizirik, E., Kim, J.H., Menotti-Raymond, M., Crawshaw, P.G. Jr, O'Brien, S.J. & Johnson, W.E. (2001). Phylogeography, population history and conservation genetics of jaguars (Panthera onca, Mammalia, Felidae). *Mol. Ecol.* **10**, 65–79.

Eriksson, T. & Dalerum, F. (2018). Identifying potential areas for an expanding wolf population in Sweden. *Biol. Cons.* **220**, 170–181.

Esenrink, M. & Vogel, G. (2006). The carnivore comeback. *Science* **314**, 746–749.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J. & Marquis, R.J. (2011). Trophic downgrading of planet Earth. *Science* **333**, 301–306.

Foster, R.J. & Harmsen, B.J. (2012). A critique of density estimation from camera-trap data. *J. Wildl. Manage.* **76**, 224–236.

Foster, V.C., Sarmento, P., Sollmann, R., Tôrres, N., Jácomo, A.T.A., Negrões, N., Fonseca, C. & Silveira, L. (2013). Jaguar and puma activity patterns and predator-prey interactions in four Brazilian biomes. *Biotropica* **45**, 373–379.

Gaston, K.J., Jackson, S.F., Cantú-Salazar, L. & Cruz-Piñón, G. (2008). The ecological performance of protected areas. *Annu. Rev. Ecol. Evol. Syst.* **39**, 93–113.

Haag, T., Santos, A.S., Sana, D.A., Morato, R.G., Cullen Jr, L., Crawshaw Jr, P.G. & Eizirik, E. (2010). The effect of habitat fragmentation on the genetic structure of a top predator: loss of diversity and high differentiation among remnant populations of Atlantic Forest jaguars (*Panthera onca*). *Mol. Ecol.* **19**, 4906–4921.

Hovardas, T. (2018) *Large carnivore conservation and management: human dimensions*. New York: Routeledge.

Jędrzejewski, W., Robinson, H.S., Abarca, M., Zeller, K.A., Velasquez, G., Paemelaere, E.A.D., Goldberg, J.F., Payan, E., Hoogesteijn, R., Boede, E.O., Schmidt, K., Lampo, M., Viloria, A.L., Carre, R., Robinson, N., Lukacs, P.M., Nowak, J.J., Salom-Perez, R., Castañeda, F., Boron, V. & Quigley, H. (2018). Estimating large carnivore populations at global scale based on spatial predictions of density and distribution – Application to the jaguar (*Panthera onca*). *PLoS One* **13**, e0194719.

Johnson, D.S., Laake, J.L. & Ver Hoef, J.M. (2010). A model-based approach for making ecological inference from distance sampling data. *Biometrics* **66**, 310–318.

Karanth, K.U. & Nichols, J.D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* **79**, 2852–2862.

Klink, C.A. & Machado, R.B. (2005). Conservation of the Brazilian Cerrado. *Conserv. Biol.* **19**, 707–713.

Linnell, J.D.C., Swenson, J.E. & Andersen, R. (2000). Conservation of biodiversity in Scandinavian boreal forest: large carnivores as flagships, umbrellas, indicators, or keystones? *Biodivers. Conserv.* **9**, 857–868.

Maffei, L., Noss, A.J., Silver, S.C. & Kelly, M.J. (2011). Abundance/density case study: Jaguars in the Americas. In *Camera traps in Animal Ecology*: 119–144. O'Connell, A.F., Nichols, J.D. & Karanth, K.U. (Eds). Tokyo: Springer.

McManus, J.S., Dalton, D.L., Kotzé, A., Smuts, B., Dickman, A., Marshal, J.P. & Keith, M. (2015). Gene flow and population structure of a solitary top carnivore in a human-dominated landscape. *Ecol. Evol.* **5**, 335–344.

Miller, P. (2013). *Population Viability Analysis for the Jaguar (Panthera onca) in the Northwestern Range*. Final report. Tucson: US Fish and Wildlife Service.

Mills, L.S. (2012). *Conservation of Wildlife Populations: Demography, Genetics, and Management*. Chichester: John Wiley & Sons.

Morato, R.G., Stabach, J.A., Fleming, C.H., Calabrese, J.M., De Paula, R.C., Ferraz, K.M. & Paviolo, A. (2016). Space use and movement of a neotropical top predator: the endangered jaguar. *PLoS One* **11**, e0168176.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858.

Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978). Statistical inference from capture data on closed animal populations. *Wildl. Monograph.* **62**, 3–135.

Paviolo, A., De Angelo, C.D., Di Blanco, Y.E. & Di Bitetti, M.S. (2008). Jaguar *Panthera onca* population decline in the upper Paraná Atlantic Forest of Argentina and Brazil. *Oryx* **42**, 554–561.

Peck, S.L. (2004). Simulation as experiment: a philosophical reassessment for biological modeling. *Trends Ecol. Evol.* **19**, 530–534.

Penteriani, V., del Mar Delgado, M., Pinchera, F., Naves, J., Fernández-Gil, A., Kojola, I., Härkönen, S., Norberg, H., Frank, J., Fedriani, J.M., Sahlén, V., Støen, O.G., Swenson, J.E., Wabakken, P., Pellegrini, P., Herrero, S. & López-Bao, J.V. (2016). Human behaviour can trigger large carnivore attacks in developed countries. *Sci. Rep.* **6**, 20552.

Pledger, S. (2000). Unified maximum likelihood estimates for closed capture–recapture models using mixtures. *Biometrics* **56**, 434–442.

Quigley, H., Foster, R., Petracca, L., Payan, E., Salom, R. & Harmsen, B. (2017). *Panthera onca*. The IUCN Red List of Threatened Species. Gland: IUCN.

Rabinowitz, A.R. & Jr, N.B. (1986). Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. *J. Zool.* **210**, 149–159.

Redford, K.H. (1983). Lista preliminar de mamíferos do Emas National Park. *Brasil Florestal* **55**, 29–33.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P. & Schmitz, O.J. (2014). Status and ecological effects of the world's largest carnivores. *Science* **343**, 1241484.

Roques, S., Sollman, R., Jácomo, A., Tôrres, N., Silveira, L., Chávez, C., Keller, C., do Prado, D.M., Torres, P.C., dos Santos, C.J., da Luz, X.B.G., Magnusson, W.E., Godoy, J.A., Ceballos, G. & Palomares, F. (2016). Effects of habitat deterioration on the population genetics and conservation of the jaguar. *Conserv. Genet.* **17**, 125–139.

Sanderson, E.W., Chetkiewicz, C.L.B., Medellín, R.A., Rabinowitz, A., Redford, K.H., Robinson, J.G. & Taber, A.B. (2002*a*). Un análisis geográfico del estado de conservación y distribución de los jaguares a través de su área de distribución. *El jaguar en el nuevo milenio, RA Medellín, C. Equihua, CLB Chetkiewicz, PG Crawshaw Jr., A. Rabinowitz, KH Redford, JG Robinson, EW Sanderson y AB Taber (comps.). Fondo de Cultura Económica, Universidad Nacional Autónoma de México, Wildlife Conservation Society, México, DF*, 551-600.

Sanderson, E.W., Redford, K.H., Chetkiewicz, C.L.B., Medellin, R.A., Rabinowitz, A.R., Robinson, J.G. & Taber, A.B. (2002*b*). Planning to save a species: the jaguar as a model. *Conserv. Biol.* **16**, 58–72.

Santini, L., Boitani, L., Maiorano, L. & Rondinini, C. (2016). Effectiveness of protected areas in conserving large carnivores in Europe. In *Protected areas: are they safeguarding biodiversity*: 122–133. Chichester: John Wiley & Sons.

Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., McHugh, K. & Hiraldo, F. (2008). Top predators as conservation tools: ecological rationale, assumptions, and efficacy. *Annu. Rev. Ecol. Evol. Syst.* **39**, 1–19.

Shepherd, B. & Whittington, J. (2006). Response of wolves to corridor restoration and human use management. *Ecol. Soc.* **11**, 1.

Silveira, L. (2004). Ecologia comparada e conservação da onça-pintada (Panthera onca) e onça-parda (Puma concolor), no cerrado e pantanal. PhD Thesis. Universidade de, Brasília, Brasília.

Silveira, L., Jácomo, A.T., Astete, S., Sollmann, R., Tôrres, N.M., Furtado, M.M. & Marinho-Filho, J. (2010). Density of the near threatened jaguar *Panthera onca* in the Caatinga of north-eastern Brazil. *Oryx* **44**, 104–109.

Silver, S.C., Ostro, L.E., Marsh, L.K., Maffei, L., Noss, A.J., Kelly, M.J. & 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, M.K. & Cavalcanti, S.M. (2006). Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. *Biol. Cons.* **129**, 487–496.

Sollmann, R., Torres, N.M. & Silveira, L. (2008). Jaguar conservation in Brazil: the role of protected areas. *Cat News* **4**, 15–20.

Sollmann, R., Furtado, M.M., Gardner, B., Hofer, H., Jácomo, A.T., Tôrres, N.M. & 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. Cons.* **144**, 1017–1024.

Sollmann, R., Betsch, J., Furtado, M.M., Hofer, H., Jácomo, A.T.A., Palomares, F., Roques, S., Tôrres, N.M., Vynne, C. & Silveira, L. (2013). Note on the diet of the jaguar in central Brazil. *Eur. J. Wildl. Res.* **59**, 445–448.

Somers, M.J., Gusset, M. & Dalerum, F. (2012). Modelling the effect of fences on the viability of spatially structured populations of African wild dogs. In *Fencing for Conservation*: 187–196. Somers, M.J. & Hayward, M. (Eds). New York: Springer.

Swanepoel, L., Lindsey, P., Somers, M.J., Van Hoven, W. & Dalerum, F. (2013). Extent and fragmentation of suitable leopard habitat in South Africa. *Anim. Conserv.* **16**, 41–50.

Swanepoel, L., Somers, M.J., Van Hoven, W., Scheiss-Mejier, M., Owen, C., Snyman, A., Martins, Q., Camacho, G., Boshoff, W. & Dalerum, F. (2015). Survival in southern African leopard populations. *Oryx* **49**, 595–603.

Thirgood, S., Woodroffe, R. & Rabinowitz, A. (2005). The impact of human-wildlife conflict on human lives and livelihoods. In *People and Wildlife: Conflict or Coexistence?*: 13–26. Woodroffe, R., Thirgood, S. & Rabinowitz, A. (Eds). Cambridge: Cambridge University Press.

Tobler, M.W., Carrillo-Percastegui, S.E., Hartley, A.Z. & Powell, G.V. (2013). High jaguar densities and large population sizes in the core habitat of the southwestern Amazon. *Biol. Cons.* **159**, 375–381.

Treves, A. & Karanth, K.U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. *Conserv. Biol.* **17**, 1491–1499.

Wegge, P., Yadav, S.K. & Lamichhane, B.R. (2018). Are corridors good for tigers *Panthera tigris* but bad for people? An assessment of the Khata corridor in lowland Nepal. *Oryx* **52**, 35–45.

Woodroffe, R. (2001). Strategies for carnivore conservation: lessons from contemporary extincitons. In *Carnivore Conservation*: 61–92. Gittleman, J.L., Funk, S.M., MacDonald, D.W. & Wayne, R.K. (Eds). Cambridge: Cambridge University Press.

Woodroffe, R. & Ginsberg, J.R. (1998). Edge effects and the extinction of populations inside protected areas. *Science* **280**, 2126–2128.

Zarzo-Arias, A., Penteriani, V., del Mar Delgado, M., Torre, P.P., García-González, R., Mateo-Sánchez, M.C. & Dalerum, F. (2019). Identifying potential areas of expansion for the endangered brown bear (*Ursus arctos*) population in the Cantabrian Mountains (NW Spain). *PLoS One* **14**, e0209972.

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.