Jaguars on the move: modeling movement to mitigate fragmentation from road expansion in the Mayan Forest

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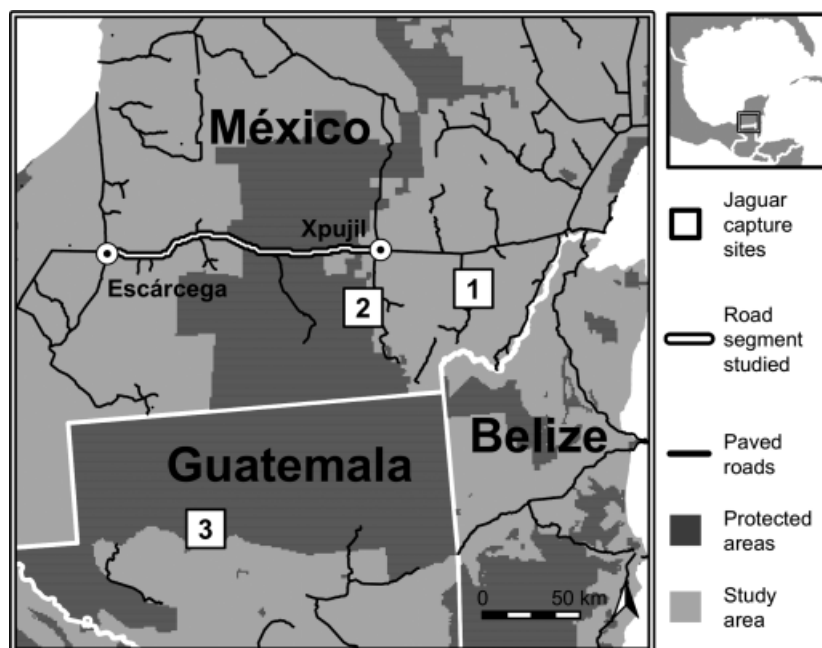
Abstract

Road-induced habitat fragmentation is one of the greatest threats to large carnivores. Wildlife passes have been used to reduce fragmentation by mitigating the effects of roads as barriers to animal movement. However, direct observations of animals crossing roads are extremely rare and thus indirect methods are necessary to locate crossings. Yet, current methods fail to incorporate the animals' movement behavior and thus have little predictive power. Based on the principles of resource selection functions and state-space modeling, we developed a Bayesian movement model applied to radio-telemetry and GPS data to infer the movement behavior of jaguars *Panthera onca* as a response to vegetation, roads and human population density in the Mayan Forests of Mexico and Guatemala. We used the results of the model to simulate jaguars moving along a road that bisects the major reserve system in the area. The aim of the simulations was to identify suitable locations for wildlife passes. We found that jaguars move preferentially to undisturbed forests and that females avoid moving close to roads and to areas with even low levels of human occupation. Males also avoid roads, but to a lesser degree, and appear undisturbed by human population density. Simulations reflected these differences: potential crossing sites for females are limited to a strip of a few kilometers, whereas males are able to cross at many different sites. Still, we identified a 1 km strip along the road where the likelihood of crossing for both sexes is highest, ideal for the construction of a wildlife pass. Our study contributes to the ecology of one of the world's least-studied large carnivores and provides a modeling framework that greatly improves the location of wildlife passes. Moreover, our approach can greatly advance region-wide conservation plans for the location of corridors and conservation units.

Introduction

Habitat fragmentation is a primary threat to wildlife, particularly large carnivores (Wiens, 1996; Crooks, 2002; Fahrig, 2003). Road-induced fragmentation reduces habitat availability while increasing population isolation and edge effects, all of which can potentially compound into dramatic population declines for large carnivores (Bender, Contreras & Fahrig, 1998; Woodroffe & Ginsberg, 1998). Roads promote access to forest fringes for resource exploitation such as illegal logging and hunting (Wilkie *et al.*, 2000) and increase mortality through vehicle collisions (Maehr, 1997) while potentially acting as barriers for animal movement (Forman & Alexander, 1998). The widening of existing roads not only weakens connectivity for large carnivores but also can accelerate human development in the region, increasing habitat fragmentation and antagonistic interac-

tions between carnivores and humans (Sweanor, Logan & Hornocker, 2000). Wildlife passes have been used to mitigate the effects of roads on habitat connectivity (Clevenger & Waltho, 2005; Dodd *et al.*, 2007), but the methods to identify suitable sites are still poorly developed when direct observations of animal crossings are not available or when new roads are constructed.

Although a considerable number of studies have evaluated the effectiveness of existing wildlife passes (Cain *et al.*, 2003; Clevenger & Waltho, 2005; Dodd *et al.*, 2007; Kusak *et al.*, 2009), little has been published on methods to identify appropriate locations for such structures. Commonly, wildlife passes have been located based on expert opinion or on statistical analysis of habitat use and suitability (Quigley & Crawshaw, 1992; Clevenger *et al.*, 2002), both of which are limited to static temporal representations of occurrence as a function of landscape elements. As a consequence, such

Figure 1 Study area and jaguar capture sites (open square dots): (1) Ejido Caoba, Quintana Roo; (2) south-west Calakmul Biosphere Reserve, Campeche; (3) Petén, Guatemala. The thicker white/black line delineates the Escárcega–Xpujil segment to be widened and where jaguar road crossing structures needed to be identified. For clarity, unpaved roads were excluded from the map.

methods are expected to have limited ability to identify features such as corridors and passes that are essentially related to movement (Foster & Humphrey, 1995; Beier & Noss, 1998; Goodwin, 2003). On the other hand, the relationship between movement modeling and management has seldom been explored. In the last few decades, a vast literature on movement models has been produced (see reviews in Nathan *et al.*, 2008 and Schick *et al.*, 2008), but few have touched on the applied side of movement ecology, and none of them have been used to identify suitable locations for wildlife passes. Meanwhile, important advances in the use of resource selection functions (RSF) to locate corridors have been made recently (Chetkiewicz & Boyce, 2009). However, these efforts still do not integrate RSF into a movement framework, and thus require the use of alternative methods such as least cost path analysis to find adequate corridors.

The Calakmul region in the Yucatan Peninsula of Mexico is one of the top priority sites for the conservation of jaguars *Panthera onca* (Sanderson *et al.*, 2002), and a key element of the Mesoamerican Hotspot (Myers *et al.*, 2000). This region has been particularly threatened by the expansion of the road network, which has severely fragmented the habitat of jaguars and many other species (Conde *et al.*, 2007). A widening plan of the Escárcega–Xpujil segment of the Federal Highway 186, which cuts through the Calakmul Biosphere Reserve, threatens to further fragment this invaluable jaguar sanctuary. To find suitable sites for the construction of wildlife passes for jaguars along this road, we developed a Bayesian hierarchical movement model applied to telemetry and GPS tracking data that combines the principles of RSF and state-space modeling. Our model estimates the probability that a jaguar moves from one

landscape cell to another as a function of its gender, vegetation, proximity to roads and human population density, while also predicting missing observations and accounting for different sources of uncertainty. With the result of the model, we simulated jaguars moving along the Escárcega–Xpujil road segment to locate sites with the highest likelihood of jaguar crossings.

Methods

Study area

The Mayan Forest is located in the heart of the largest patch of tropical forest north of the Darién (Fig. 1). The area includes the Guatemalan Petén and the forests in Campeche and Quintana Roo states in Mexico. The region is predominantly subtropical moist forest, with a dry season that extends from February to June and an average annual rainfall of 1350 mm (Holdridge *et al.*, 1971).

Jaguar location data

Between 1998 and 2007, 11 jaguars (seven females and four males) were captured in three different sites within the study area (Fig. 1). The captured jaguars were chemically anesthetized using a projectile dart (Ceballos *et al.*, 2002), examined for general body condition, measured and weighed. Five jaguars were fitted with radio-telemetry collars (Telonics Inc., Mesa, AZ, USA; http://www.telonics.com) and six with GPS collars (Lotek Engineering, Newmarket, ON, Canada; http://www.lotek.com). Latitude and longitude locations were recorded at varying time intervals over 2–12 months periods.

Table 1 Jaguar *Panthera onca* location data description

Id	Sex	Region	Data type	Points Available	Total	Ratio	Time (days)
1	Female	Caob	GPS	45	134	0.336	33
2	Female	Caob	GPS	265	1738	0.152	434
3	Female	Caob	GPS	193	1129	0.171	282
4	Female	Caob	GPS	9	77	0.117	19
5	Female	Calak	TELE	13	47	0.277	12
6	Female	Calak	TELE	6	13	0.462	3
7	Female	Calak	TELE	4	21	0.19	5
8	Male	Calak	TELE	15	48	0.313	12
9	Male	Calak	TELE/GPS	250	1549	0.161	387
10	Male	Guat	GPS	862	1277	0.675	319
11	Male	Guat	GPS	178	245	0.727	61
Total				1840	6278	0.325	1567

The region column refers to the area where each individual was captured (see Fig. 1): Caob, forestry Ejido Caoba; Calak, east edge of the Calakmul Biosphere Reserve; Guat, Peten, Guatemala. The data type column refers to the type of tracking device used: TELE, radio-telemetry collar; GPS, GPS collar. The ratio column refers to the ratio of available to total modeled points for each jaguar. The time column shows the total number of days (rounded) each jaguar was modeled.

Temporal and spatial resolution

We established the temporal resolution for this analysis to 6 h (+ /− 1 h) between movement points, (i.e. four points per day). This resolution allowed us to depict the natural daily changes in activity of jaguars (Seymour, 1989) while minimizing computing burden. Thus, for each jaguar we assembled *movement paths* as time series of location records spaced in 6-h intervals. Because the reading schedule for most tracking devices differed from this 6-h interval, the number of available records for our analysis was lower than the actual total number of readings. Thus, each jaguar path had a combination of available and missing records. Overall, we had 1840 readings with time and location information and 4438 missing records, totaling 6278 points to be analyzed (Table 1).

We converted all spatial data within the study area (Fig. 1) to raster format with a resolution of 1 km^2 grid cells. We assigned each jaguar location to the corresponding cell on the study area grid, and created a vector of cells per jaguar j, $\mathbf{c}_j$, divided into elements with known locations, but, that due to reading error could fall in a contiguous cell, and elements with unknown locations that needed to be estimated fully.

Environmental and socio-economic data

We compiled a geospatial database of environmental and socio-economic variables, which included normalized difference vegetation index grids (NDVI; Derring & Haas, 1980) calculated from four MODIS Surface Reflectance Daily L2G Global images (MOD09GA) taken in March 2000, 2003, 2005 and 2010 (USGS Land Process Distributed Active Archive Center; https://lpdaac.usgs.gov/lpdaac/products/). We also included in the database distance to roads and human population density grids calculated from vector data obtained from the Selva Maya Zoque and Olmeca

database (García & Secaira, 2006). For a full description of the spatial data processing, see Appendix S1.
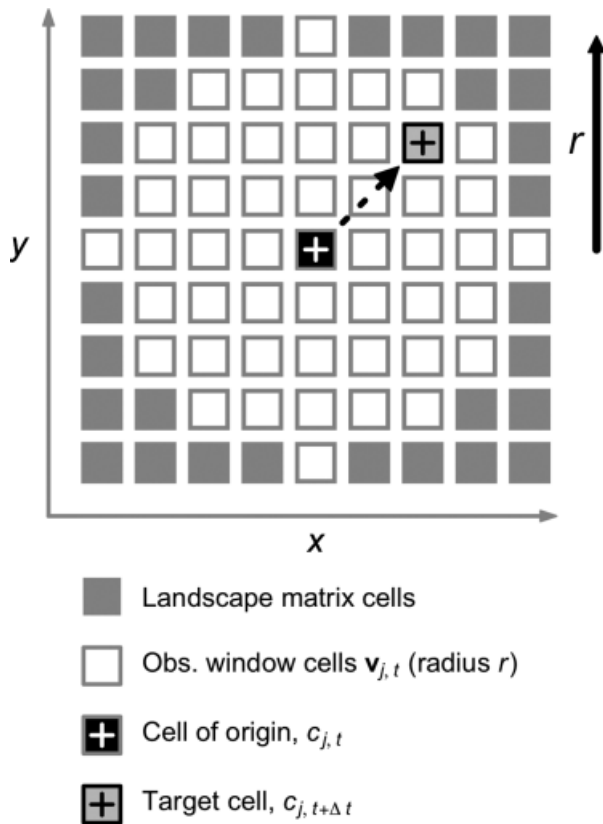
Movement model

We developed a model that estimates the probability that a jaguar moves from one cell to another as a function of environmental variables, based on the principles of RSF (Manly, McDonald & Thomas, 1993; Boyce *et al.*, 2002; Nielson *et al.*, 2009). Our model evaluates the multinomial probability that an individual j at time t moves from a cell of origin, $c_{j,t}$, with coordinates $[x_{j,t}, y_{j,t}]$ to a target cell, $c_{j,t+\Delta t}$, at time $t + \Delta t$ ($\Delta t = 6$ h). The model uses an observation window as spatial reference, represented by the vector of window cells $\mathbf{v}_{j,t}$, centered on $c_{j,t}$ to which the jaguar can move (Fig. 2). This observation window is delimited by a radius r that determines which cells in the vicinity of the cell of origin are contained in $\mathbf{v}_{j,t}$. We set the radius to $r = 10$ km based on the maximum Euclidian distance between recorded jaguar points in a 6-h interval. Thus, the Markov nature of the movement process is captured by the fact that the probability of moving to the target cell is conditioned on the cell of origin, based on the observation window $\mathbf{v}_{j,t}$. This yields a multinomial probability of movement which we calculate as

$$p(c_{j,t+\Delta t}|c_{j,t}, \mathbf{v}_{j,t}, \mathbf{z}_{j,t}, \mathbf{b}) = \frac{\exp(\mathbf{z}_{j,t+\Delta t}\mathbf{b})}{\sum_{i:c_i \in \mathbf{v}_{j,t}} \exp(\mathbf{z}_{i,t}\mathbf{b})} \quad (1)$$

Equation (1) is a multinomial link function where each cell c_i contained in $\mathbf{v}_{j,t}$ has associated with it a vector of explanatory variables, $\mathbf{z}_i$, linked to the probability of movement through a columnar vector of parameters $\mathbf{b}$ to be estimated.

We evaluated the following explanatory variables and interactions (i.e. elements of the $\mathbf{z}$ vectors):
• *NDVI*: proxy for primary productivity

Figure 2 Observation window $\mathbf{v}_{j,t}$ used as a spatial reference for the probability that a jaguar moves from a cell of origin, $c_{j,t}$, to a target cell $c_{j,t+\Delta t}$ between times t and $t+\Delta t$. For display purposes, the observation window depicted here is smaller than the window used for the analysis.

- DR_f: distance to roads × females
- DR_m: distance to roads × males
- PD_f: human population density × females
- PD_m: human population density × males

To account for changes in land use between years, we linked each movement point and its observation window to the NDVI with the closest date (from the 2000, 2003 and 2005 images).

Several sources of uncertainty arise due to measurement error and missing records, which make the cells associated to each jaguar location a latent (unknown) state. Thus, the association between the jaguar's location and a cell in the landscape depends not only on the movement *process* defined in equation (1) but also requires a *data model* that accounts for tracking device error. This procedure is analogous to the state-space formulation commonly used with time series of population growth (Clark & Bjørnstad, 2004). Owing to the large number of unknowns (i.e. all parameters and locations) and sources of uncertainty (e.g. location reading errors, missing records, parameter uncertainty), inference for this model is best drawn from a Bayesian

framework (Clark, 2007). The conditional posterior for movement to a cell $c_{j,t}$ is constructed as

$$p(c_{j,t}|\cdots) \propto \overbrace{p(c_{j,t}|c_{j,t-\Delta t}, \mathbf{v}_{j,t-\Delta t}, \mathbf{b}, \mathbf{Z}_{j,t-\Delta t})p(c_{j,t+\Delta t}|c_{j,t}, \mathbf{v}_{j,t}, \mathbf{b}, \mathbf{Z}_{j,t})}^{\text{Process model}}$$
$$\times \overbrace{p(d_{j,t}|0, \tau^2)}^{\text{Data model}}$$

$$(2)$$

where $\mathbf{Z}_{j,t}$ is the matrix of covariates associated to each cell in $\mathbf{v}_{j,t}$, $d_{j,t}$ is the distance in meters between the centroid of cell $c_{j,t}$ and the jaguar location as taken by the tracking device at time t and τ^2 is the variance of the tracking device's error. The process model in equation (2) takes into account the first-order Markov nature of the movement process by considering the conditional relationship between $c_{j,t}$ and the cell at the previous step, $c_{j,t-\Delta t}$. However, because the cell at the following step (i.e. $c_{j,t+\Delta t}$) is also conditioned on $c_{j,t}$, inference on the probability of $c_{j,t}$ also requires the inclusion of the cell in the following step. The last expression in equation (2) corresponds to the data model, which accounts for the tracking device's error. For cells with missing observations, the data model is not included and the location of the cell needs to be estimated. We assumed that the data model follows a truncated normal distribution, $d_{j,t} \sim N_0(0, \tau^2)$, truncated at 0 and with mean (mode) 0 and standard deviation $\tau = 70\,\text{m}$ for GPS points (Rempel, Rodgers & Abraham, 1995) and $\tau = 300\,\text{m}$ for telemetry points (Ceballos *et al.*, 2002).

The full Bayesian model for the posterior distribution of all unknowns is

$$p(\mathbf{b}, \mathbf{C}|\mathbf{d}, \mathbf{V}, \mathbf{Z})$$
$$\propto \prod_{j=1}^{N} \prod_{t=1}^{T_j} p(c_{j,t}|c_{j,t-\Delta t}, \mathbf{v}_{j,t-\Delta t}, \mathbf{b}, \mathbf{Z}_{j,t-\Delta t})p(c_{j,t+\Delta t}|c_{j,t}, \mathbf{v}_{j,t}, \mathbf{b}, \mathbf{Z}_{j,t})$$
$$\times \prod_{j=1}^{N} \prod_{t \in \mathbf{t}_j^1} p(d_{j,t}|0, \tau^2)$$
$$\times p(\mathbf{b}|\mathbf{b}_0, \sigma^2\mathbf{I})$$

$$(3)$$

where $\mathbf{C}$ is the vector of cells occupied by all jaguars at all modeled times, $\mathbf{d}$ is the vector of distances between the actual tracking device locations and the cells' centroids (for known observations), N is the total number of jaguars followed ($N = 11$), $\mathbf{t}_j^1$ is the vector of times for known locations for jaguar j and T_j is the time at the last observation for jaguar j. The last expression on the right-hand side of equation (3) is the prior distribution for $\mathbf{b}$, which follows a multivariate normal distribution with mean vector $\mathbf{b}_0$ and variance covariance matrix $\sigma^2\mathbf{I}$. We used non-informative priors for the parameters with all elements in $\mathbf{b}_0$ equal to 0 and $\sigma^2 = 100$.

We implemented a Markov Chain Monte Carlo (MCMC) algorithm to obtain posterior distributions for the parameters and latent jaguar locations (Gelfand & Smith, 1990). All conditional posteriors were sampled using a Metropolis algorithm (Clark, 2007). We ran 10 parallel

MCMC sequences of 10 000 iterations each with overdispersed starting parameters. To assess convergence, we computed the potential scale reduction for all parameter sequences after discarding the initial 5000 steps (i.e. burnin) as $\widehat{R} = \sqrt{\widehat{v}^{+}/W}$, where W is a measure of the within-sequence variance and $\widehat{v}^{+}$ is a weighted average of the between-sequence variance (B) and W (Gelman *et al.*, 2004). Convergence is attained when $\widehat{R}$ is close to 1. Further diagnostics of model performance that included simulation and cross-validation studies can be found in Appendix S2.

Movement simulations and wildlife passes

We used the results from the movement model to simulate individual jaguars moving along the Escárcega–Xpujil road segment in Campeche, México (Fig. 1). We randomly selected 10 000 starting points around the road using as a baseline a published jaguar habitat use model (Conde *et al.*, 2010). From each one of these points, one female and one male jaguar were 'released' and their movement was simulated. Each simulated individual was followed for 100 days, moving at time intervals of $\Delta t = 6$ h. At every time t, a jaguar j moved from a cell of origin $c_{j,t}$ to a target cell $c_{j,t+\Delta t}$ within an observation window of radius $r = 10$ km (see 'Movement model'). At each step, the target cell was randomly selected by computing the multinomial probability of moving from the cell of origin to any cell within the observation window. Uncertainty was further added by randomly selecting a set of estimated parameters from the converged MCMC sequences for each jaguar simulated. We used the NDVI calculated from the 2010 MODIS image to base our simulations on current conditions. From the resulting movement paths, we identified the points on the road segment (every kilometer) where each simulated jaguar crossed. We calculated a road-crossing index (RCI) for each sex as the average number of times all 10 000 jaguars used each point. All points with RCI values above the 90% upper percentile were selected to find a final point (or set of points) as a potential site for the construction of a wildlife pass.

We performed all statistical analyses and spatial data processing in the free software R 2.10 (R Development Core Team, 2009).

Results

Movement model

The resulting posterior distributions for the movement model parameters (all sequences converging satisfactorily: $\widehat{R} < 1.07$; Table 2) showed that the probability of movement into a target cell for all jaguars increased with higher NDVI values (Fig. 3), associated with denser forests. In general, our estimates confirmed that jaguars avoided moving in the proximity of roads. However, this effect was stronger in females, for which the change in probability as a function of distance to roads was steeper than for males (Fig. 3). The largest differences between sexes were associated with human population density; females strongly avoided areas with even small densities, while all males had a negligible tendency to move close to areas with higher densities (Table 2 and Fig. 3). These results were consistent even after excluding jaguars with the largest number of points (see cross-validation analysis in Appendix S2).
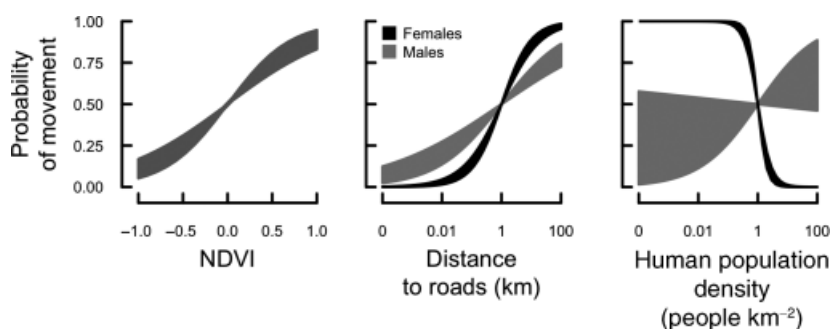
Prediction of road-crossing sites

Our predictions on the movement of jaguars along the Escárcega–Xpujil road segment show that males crossed the road all along its width with higher frequencies than females (male RCI = 0.0209–0.0585; female RCI = 0.0001–0.0137;

Table 2 Median, 95% lower (2.5%) and upper (97.5%) credible intervals and potential scale reduction ($\widehat{R}$) for the estimated parameters of the Bayesian movement model for jaguars *Panthera onca* in the Mayan Forests of Mexico and Guatemala

Environmental variable	Jaguar identity	Median	2.5%	97.5%	$\widehat{R}$
NDVI	All jaguars	2.227	1.599	2.882	1.034
Distance to roads	Females	0.776	0.662	0.904	1.047
	Males	0.305	0.213	0.399	1.065
Human population density	Females	−2.386	−2.923	−1.901	1.058
	Males	0.219	−0.033	0.445	1.037

All values were rounded to the three first digits.
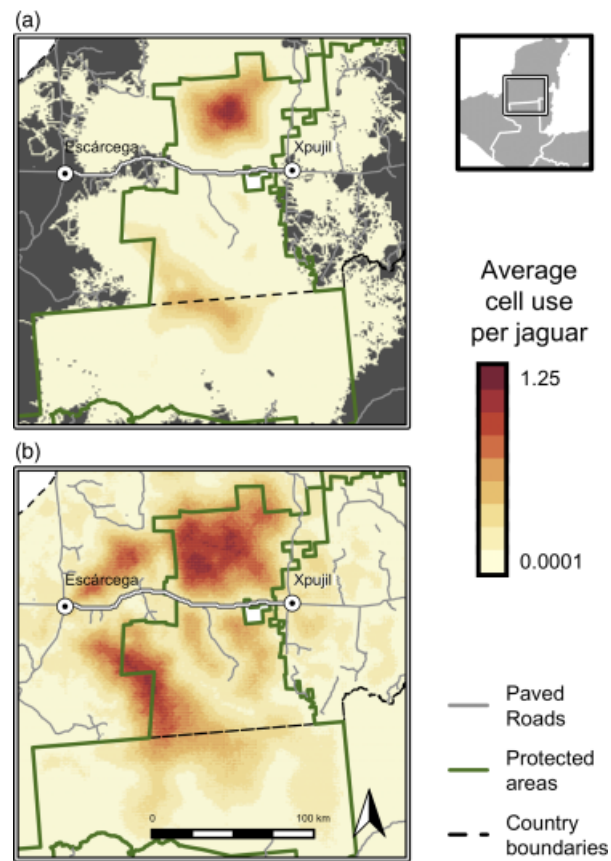NDVI, normalized difference vegetation index.

Figure 3 Probability of jaguar movement to a target cell as a function of its normalized difference vegetation index values (i.e. vegetation), its distance to roads and its human population density. The width of the polygons corresponds to the 95% credible intervals.
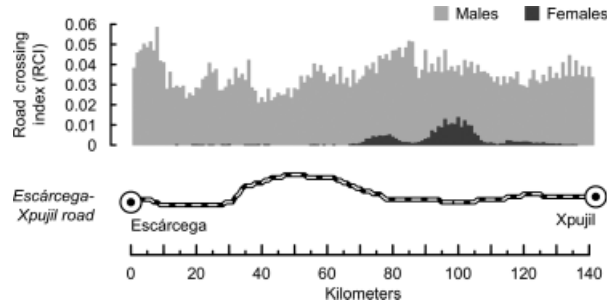
Fig. 4). Also, high RCI values for females where clustered along the east portion of the road segment, while male high RCIs were (uniformly) scattered across the whole length of the road segment (Fig. 5). After finding which points had RCI values above the 90 percentile for both sexes, we were able to locate a crossing point where both sexes had high RCI values and where a jaguar pass could be built (Fig. 6).

Discussion

Analysis of jaguar movement patterns allowed the identification of crossing sites on a road cutting through one of the most important biological sanctuaries in the Mayan forests of Mexico and Guatemala. We show that jaguars are attracted to densely forested areas, as shown by their tendency to move to cells with high NDVI values. Moreover, the probability of moving from one site to the next is low if the target cell is closer to roads or has higher human population density than the origin. However, this response differs markedly between the sexes; females have a stronger aversion than males to proximity to roads while males seem

Figure 5 Road-crossing index (RCI) for simulated males and females at every kilometer along the Escárcega–Xpujil road segment. The RCI represents the average number of times each kilometer was crossed by 10 000 individuals of each sex.

Figure 6 Proposed crossing site (jaguar crossing) for the construction of a jaguar wildlife pass along the Escárcega–Xpujil road segment. The only recorded jaguar road kill matches the selected location (S. Calmé, pers. comm.). For clarity, unpaved roads were excluded from the map.

unaffected by areas with medium population density. These results are robust despite the large proportion of missing records and measurement error (see Simulation study in Appendix S2). As a result of these gender differences, females have a considerably more restricted number of locations at which they are likely to cross the Escárcega–Xpujil road segment (Fig. 5). These potential crossing sites were located between the two largest patches of protected forest in the region, where human population density was lowest along the road segment. We identified a 1 km section of the road where the likelihood of crossing was highest for both sexes (Fig. 6), ideal for a wildlife pass.

Our results are consistent with previous projects on the habitat use of jaguars and other large carnivores with similar behavior (Maehr, 1997; Kerley et al., 2002; Conde et al., 2010). For example, Conde et al. (2010) found that jaguars in the Mayan Forests occur with higher probability in well-preserved forest patches than on secondary growth or agricultural lands. They also found that the probability of occurrence for female jaguars declined with proximity to roads. In fact, it can be expected that their susceptibility to roads should change based on road density (Whittington, Clair & Mercer, 2005) and traffic load (Eloff & van Niekerk,

Figure 4 Simulated movement paths of 10 000 female (a) and 10 000 male (b) jaguars around the Escárcega–Xpujil road (bold white line). The yellow-to-red gradient represent the average number of times each cell was used by a jaguar out of 10 000 simulated individuals per sex. For clarity, unpaved roads were excluded from the map.

2008). Also, human population density has been associated with major carnivore declines (Woodroffe, 2000). Concurrent with this, our findings show that females avoid moving into areas with even low densities. This pattern could respond to direct persecution of jaguars by local landowners (Woodroffe, 2000). Also, illegal hunting for bush meat is pervasive in rural areas of Mexico and Guatemala (Reyna-Hurtado & Tanner, 2005), which could exacerbate competition for resources between local settlers and jaguars, depleting their prey basis in areas close to towns and roads (Karanth *et al.*, 2004). Because parental care is limited to females, it is expected that their movement patterns will be restricted to areas where resources are sufficient to successfully raise their cubs (Gehrt & Fritzell, 1998), while minimizing risk from human activities (Bunnefeld *et al.*, 2006).

Movement models and connectivity

The aim of implementing wildlife passes and corridors is to facilitate the movement of individuals between habitat patches that otherwise would be disconnected (Beier & Noss, 1998). This simple and obvious relationship between movement and management emphasizes that methods that do not explicitly analyze individual movement patterns will be of limited use to identify suitable locations for such structures (Foster & Humphrey, 1995; Goodwin, 2003). Despite this fact, Goodwin (2003) showed that very few empirical studies have treated landscape connectivity as a result of the interaction of movement with landscape elements, while this approach was more pervasive in simulation studies. With this in mind, the aim of our study was to bridge the gap between inference of movement behavior and forward (predictive) modeling of movement patterns for animals, using jaguars as a case study, to inform specific management strategies.

Ideally, wildlife passes should be located based on GPS or telemetry data of animals moving around roads, which would provide direct evidence of the exact locations animals are using as crossings. Such was the case of the construction of wildlife passes for Florida panthers during the conversion of State Road 84 to Interstate 75 in Florida (Land & Lotz, 1996). However, in the absence of animal location data in the vicinity of roads or when the construction of a new road is imminent, indirect methods are required to find appropriate locations. In this sense, our model helps to overcome important data and modeling limitations. For instance, radio-telemetry data have large measurement errors, and thus are commonly discarded when higher precision GPS data are also available. Our model uses a state-space framework to integrate both into the inference process increasing the number of individuals analyzed. This model also provides a statistical framework that accounts for a large proportion of missing observations, a common issue in wildlife tracking studies (Appendix S2; for an alternative approach, see Nielson *et al.*, 2009).

One potential limitation of this particular study is the lack of validation data such as road kills or direct observations of animals crossing the road, a common caveat for the location of wildlife passes (Clevenger *et al.*, 2002). Nonetheless, the only available jaguar road kill record matched the selected crossing site from our model (S. Calmé, pers. comm.).

Conservation and management implications

The implementation of studies with radio-telemetry or GPS tracking devices is costly. However, these costs are negligible if we consider the magnitude of investment required to build wildlife passes, which can become a major financial burden for developing countries such as Mexico. The benefits of a relatively small initial investment in reliable field data and robust science can greatly improve conservation for a wide range of species. In this sense, this project was conceived as a strategy to insure that the decision on where to build wildlife passes was based on the most robust combination of data and statistical modeling. Furthermore, in the context of major international efforts to protect jaguars and their habitat as a focal species in the Americas, such as the Panthera Corridor Initiative (Rabinowitz & Zeller, 2010), the analytical tools we provide here will contribute to improve the location of corridors and conservation units region-wide.

Acknowledgements

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Environmental and socioeconomic data processing.
Appendix S2. Diagnostics.

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