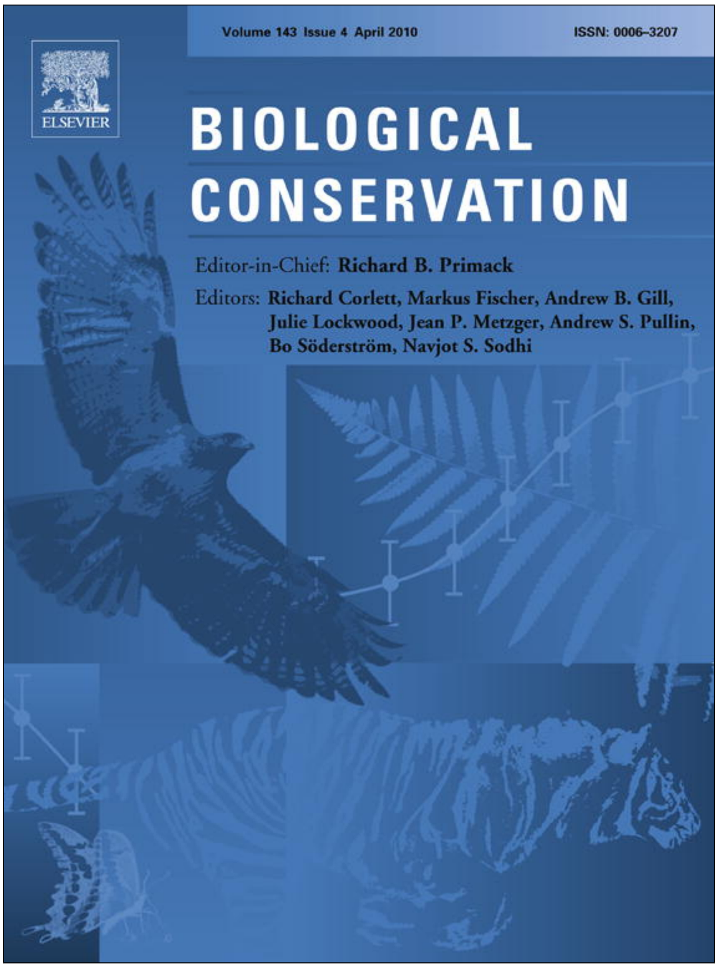
Volume 143 Issue 4 April 2010
ISSN: 0006-3207
ELSEVIER
BIOLOGICAL
CONSERVATION
Editor-in-Chief: Richard B. Primack
Editors: Richard Corlett, Markus Fischer, Andrew B. Gill,
Julie Lockwood, Jean P. Metzger, Andrew S. Pullin,
Bo Söderström, Navjot S. Sodhi

Biological Conservation 143 (2010) 939–945

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*

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A R T I C L E   I N F O

Article history:
Received 22 September 2009
Received in revised form 30 December 2009
Accepted 2 January 2010
Available online 4 February 2010

Keywords:
Jaguar
Wildlife corridors
Carnivores
Connectivity
Range-wide conservation
Dispersal

A B S T R A C T

Large, wide-ranging carnivores face greater threats and more persistent declines than most other mammal species. An important conservation tool for these carnivores has been range-wide priority-setting exercises that have helped identify critical threats and key populations. However, such exercises often fail to identify functional movement corridors or account for genetic connectivity. We present a new model for jaguar (*Panthera onca*) conservation that uses a geographic information system (GIS) and expert input to create a dispersal cost surface and identify least-cost corridors connecting the 90 known populations across the jaguar's range. Results indicate 78% of historic jaguar range, an area of approximately 14.9 million km^2, still holds potential for jaguar movement and dispersal. We identified 182 potential corridors between populations, ranging from 3 to 1607 km in length; 44 of these corridors are characterized as being of immediate concern due to their limited width, and thus their high potential for being severed. Resultant maps, displaying priority populations and corridors, are used to direct field-based research and conservation efforts. Field assessment and refinement of the corridors is ongoing. This is the first attempt to create and implement such a holistic model of range-wide conservation for a large carnivore species.

1. Introduction

Over the past century, species extinction has accelerated an estimated 1000 times more rapidly than expected background rates (Pimm et al., 1995; Millennium Ecosystem Assessment, 2005). The acknowledged causes of such extinction rates include the extensive loss of wild habitats and the deterioration of genetic diversity within increasingly small, isolated populations. Larger, wide-ranging carnivore species have historically shown periods of extensive range collapse and high extinction rates (Purvis et al., 2001) and are, at present, in persistent and continuing decline (Ginsberg, 2001).

Range-wide priority-setting exercises for large carnivores have been important tools for shifting the traditional conservation paradigm from a focus on discrete populations or geographic regions to a consideration of how aggregate populations or metapopulations contribute to the biology, conservation, and extinction potential of a species as a whole (Wikramanayake et al., 1998, 2004; Sanderson et al., 2002, 2006; Thorbjarnarson et al., 2005). Such exercises also necessitate conservation thinking beyond protected areas, in regions of heaviest carnivore mortality (Woodroffe and Ginsberg, 1998). Unfortunately, most range-wide priority-setting exercises have fallen short on addressing corridors and connectivity. Corridors can provide one of the most basic requirements for species persistence–genetic exchange. Reduction or loss of genetic exchange leads to smaller effective population sizes (Frankham, 1996), increased levels of genetic drift and inbreeding (Soulé and Mills, 1998; Young and Clarke, 2000; Stockwell et al., 2003), and potential deleterious effects on sperm production, mating ability, female fecundity, and juvenile survival (Frankham et al., 2002). Such effects eventually compromise adaptive potential (Saccheri et al., 1998; Lehmann and Perrin, 2006), reduce fitness, and contribute to extinction risk for a population and, ultimately, for the species (Frankham, 2005). Finally, corridors may increase the chances of persistence in small populations by providing opportunities for ameliorating the negative effects of demographic and environmental stochasticity (Brown and Kodric-Brown, 1977; Hilty et al., 2006).

We present an approach that moves beyond the traditional range-wide species conservation models by identifying, assessing, and implementing potential travel corridors between core populations of the jaguar (*Panthera onca*). The jaguar, a near-threatened species (IUCN, 2009) and the largest cat in the New World, historically occupied a continuous range from the southern United States to central Argentina (Swank and Teer, 1989). By the end of the 20th century, hunting for the fur trade, persecution for livestock depredation, and habitat loss caused an estimated 54% reduction in the

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0006-3207/$ - see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2010.01.002

historic range of the jaguar, with high levels of habitat fragmentation (Sanderson et al., 2002). Yet studies of genetic variation among jaguars using mitochondrial DNA from fecal samples showed little evidence of significant geographical partitions and barriers to gene flow range-wide (Eizirik et al., 2001; Johnson et al., 2002; Ruiz-Garcia et al., 2006). The genetic data supported earlier morphometric analyses (Larson, 1997) indicating a single taxon, counter to the division of jaguars into any of the eight subspecies accepted at the time (Pocock, 1939).

These studies highlight the fact that the jaguar has maintained relatively high levels of gene flow throughout its range in the recent past. Given this, and the demographic benefits of corridors, we recognized that identifying connectivity between jaguar breeding areas is a vital component in conservation planning for the species. This paper describes our process for indentifying potential jaguar corridors between the 90 known populations of jaguars, or Jaguar Conservation Units (JCUs), identified in earlier range-wide priority-setting exercises (Sanderson et al., 2002; Zeller, 2007).

2. Methods

We chose a least-cost functional connectivity model (Adriaensen et al., 2003; Epps et al., 2007) to analyze jaguar range for corridors. Because functional connectivity requires accounting for both landscape structure and species' responses to the landscape (Pither and Taylor, 1998), we used a grid-based model in which movement costs were assigned to each landscape element in the intervening matrix (Ray et al., 2002). We sought to quantify the potential difficulty, or ease, with which jaguars could move across any given landscape within jaguar range in a permeability matrix (Bélisle, 2005; McRae, 2006). Using such a matrix allows us to expand beyond the simple notion of habitat connectivity, where two patches are connected by a swath of similar habitat type, by quantifying different landscape features that a large carnivore such as a jaguar might use (Singleton et al., 2002). With such a landscape matrix in place, we could then perform a least-cost-corridor analysis between known jaguar populations in order to delineate potential movement corridors across the matrix.

2.1. Geographic information system (GIS) layer compilation

Using ArcGIS v9 software, we chose six GIS-based landscape characteristics considered to most affect jaguar movement and survival: land cover type, percent tree and shrub cover, elevation, distance from roads, distance from settlements, and human population density (Table 1). Land cover type, percent tree and shrub cover, and elevation are closely related to movement behavior in many large mammal species (Carroll et al., 2003; Naves et al., 2003; Dickson et al., 2005), whereas distance from roads, distance from settlements, and human population density are considered to be correlated with human persecution of jaguars, including direct mortality (Naves et al., 2003; Rabinowitz, 2005; Woodroffe et al., 2005). Layers were standardized to the same projection and resampled to a 1 km^2 grid. The roads and settlements vector layers were converted into distance grids using the Spatial Analyst Euclidean Distance function.

2.2. Creation of cost surface or permeability matrix

Least-cost path analyses and individual-based movement models for wide-ranging animals depend on an understanding of how individuals move (Dickson et al., 2005). Since scientific data on jaguar dispersal was not available, we asked 15 jaguar experts throughout jaguar range to assign cost values to the attributes of the individual landscape layers based on how costly a particular attribute would be to jaguar movement. Cost values ranged from 0 (no cost to jaguar movement) to 10 (a high cost for jaguar movement). Attributes could be assigned an N/A if the physical characteristics of that cell would prevent a jaguar from moving through it. Experts also provided a value representing the cumulative cost of all the layers beyond which a jaguar would not likely travel. We averaged the values across the jaguar's range to obtain an overall movement cost for the attributes of each landscape layer (Table 2). Movement costs were then applied to each cell of the six grids and the grids were combined into one layer by adding them in Raster Calculator. To create the final cost surface or permeability matrix, we reclassified the output from the Raster Calculator so that all the pixels whose sums were above 25 (the average cumulative score indicating a barrier to movement) represented a break in the matrix.

2.3. Corridor delineation

To determine optimal routes of travel across the permeability matrix, we used the Cost-Distance function in Spatial Analyst to create movement cost grids from each of the 90 JCUs. This tool accumulates costs as it moves away from a population, taking into account distance and direction. These cost-distance grids were used as inputs for the Corridor function in Spatial Analyst. We used the Corridor function between all proximate pairs of jaguar populations to derive least-cost corridors between these populations. To combine all overlapping corridors and display the best routes for jaguar movement, we used the minimum mosaic method and then extracted the lowest 0.1% of grid cell values. While no empirical

Table 1
Geographic data bases used for creating the jaguar permeability matrix.

Data Base	Dataset name and scale	Year of data	Source
Elevation	Global 30 arc-second elevation data set 1 km resolution	1996	Center for earth resources observation and science (EROS)
Land cover type	Global land cover 2000 1 km resolution	1999–2000	Global land cover 2000
Percent tree and shrub cover	Continuous vegetation fields 500 m resolution	2000	Global land cover facility
Population settlements	Vector map level 0 population settlements 1:1,000,000 scale	1960s–1990s	National imagery and mapping agency (NIMA)
Human population density	Gridded population of the world v3 2.5 min resolution	2000	Center for international earth science information network (CIESIN)
Roads	Vector map level 0 roads 1:1,000,000 scale	1960s–1990s	National imagery and mapping agency (NIMA)

Table 2
Classes of landscape layers and expert-determined cost values for jaguar movement. Possible values ranged from 0 (no cost to jaguar movement) to 10 (a high cost for jaguar movement). A class could also be assigned an N/A if its physical characteristics would create a barrier to jaguar movement.

Landscape Layer	Land Cover Type		Percent Tree and Shrub Cover		Human Population Density (people/km2)		Elevation (meters)		Distance from Roads (kilometers)		Distance from Settlements (kilometers)	
	Class	*Cost Value*	*Class*	*Cost Value*	*Class*	*Cost Value*	*Class*	*Cost Value*	*Class*	*Cost Value*	*Class*	*Cost Value*
	Tree Cover, broadleaved, evergreen	0	0 – 10%	9	0-20	1	0 – 1000	0	0 to 2	7	0 – 2	8
	Tree Cover, broadleaved, deciduous	0	10% - 20%	7	20-40	5	1000 – 2000	2	2 to 4	4	2 – 4	5
	Tree Cover, needle- leaved, evergreen	1	20% - 40%	5	40-80	7	2000 – 3000	7	4 to 8	2	4 – 8	4
	Tree Cover, mixed leaf Type	0	40% - 60%	2	80 - 160	9	3000 – 5000	10	80 to 160	1	8 - 16	1
	Tree Cover, regularly flooded, fresh water	2	60% - 80%	0	160-320	10	>5000	N/A	> 16	0	> 16	0
	Tree Cover, regularly flooded, saline water	2	80% - 100%	0	>320	N/A						
	Mosaic: Tree cover/other natural vegetation	1										
	Shrub Cover, evergreen	2										
	Shrub Cover, deciduous	3										
	Herbaceous Cover	5										
	Sparse herbaceous or sparse shrub cover	6										
	Regularly flooded shrub and/or herbaceous cover	5										
	Cultivated and managed areas	8										
	Mosaic: Cropland/Tree Cover/ Other natural Vegetation	5										
	Mosaic: Cropland/Shrub or grass cover	7										
	Bare areas	8										
	Water Bodies	6										
	Snow and Ice	N/A										
	Artificial surfaces and associated areas	10										

data exist on the width at which corridors fully lose their functionality, corridor width likely becomes more important as the corridor length increases. Beier (1993) suggested cougar corridors to be at least 400 m wide, while Florida panthers disperse through areas 3–7 km wide (Kautz et al., 2006). In this model, we made special demarcation of corridors less than 10 km in width at any point along their length; these were designated *corridors of concern* due their potential to be severed or become genetic bottlenecks.

2.4. Field-based corridor assessment and corridor refinement

While the least-cost corridors focus our efforts on areas with potential connections between jaguar populations, these analyses do not account for jaguar prey availability, inherent errors with GIS data, changes to the landscape since the GIS data were collected, and the error associated with subjective expert opinion of resistance values (Beier et al., 2008). Therefore, we are currently assessing the GIS-based corridors in the field. Using detailed land cover classifications developed from recent satellite imagery for areas between JCUs, we examine the landscape for habitat that may have been erroneously excluded from the least-cost corridor analysis. We then apply a grid-based data collection protocol using standardized interview techniques with local people about jaguars and prey species (Zeller et al., unpublished results) as an indirect index to create presence–absence data for an occupancy analysis (MacKenzie et al., 2002; Stanley and Royle, 2005). Only first-hand sightings of jaguars or jaguar sign by the interviewees are recorded. We check the reliability of responses using photographs of target species. We also include sightings or sign of jaguar collected by the field teams in the presence–absence data. The resultant probability of habitat use of jaguars and prey are used to identify the most functional corridors between JCUs. Where appropriate, corridor boundaries are adjusted based on these field assessment data.

3. Results

The final permeability matrix from this analysis (Fig. 1), represents areas that could potentially be used by a dispersing jaguar. The results indicate that 78% of the jaguar's historic range still allows for potential jaguar movement. The least-cost corridor analysis resulted in corridors connecting all JCUs except two, between the Sierra de las Minas JCU in southern Guatemala and the Pico Bonito/Texiguat JCU in north central Honduras. Fig. 2 portrays the 182 resultant corridors. These corridors represent areas with both the shortest distance and least dispersal cost between jaguar populations. The total area of all 90 JCU's is 1.9 million km^2 (Zeller, 2007), while the total area of the corridors connecting these JCUs is 2,562,378 km^2. For Mexico and Central America, the average corridor length between known jaguar populations is 174.42 km (range: 3–1102 km) compared to South America with an average corridor length of 489.14 km (range: 12–1607 km). Including the Guatemala/Honduras connection, the model indicates five *corridors of concern* in Central America and Mexico and 39 *corridors of concern* in South America (Fig. 2).

Of the 32 JCUs that were ranked as having the highest priority for jaguar conservation (Zeller, 2007), 17 are linked to other JCUs by *corridors of concern.* Clusters of the highest priority JCUs and *corridors of concern* are found in the extreme northern and southern parts of jaguar range as well as in Colombia, a critical link for jaguar connectivity between Central and South America (Fig. 2). These clusters point to areas where efforts would significantly contribute to a range-wide jaguar conservation strategy.

Fig. 1. Jaguar dispersal permeability matrix. The lower the value the more permeable a pixel is to jaguar movement.

4. Discussion

The negative effects of habitat loss and fragmentation, particularly on large-bodied, wide-ranging, solitary carnivores is well documented (Crooks, 2002). Conservation biology theory suggests that corridors between isolated habitat patches may maintain levels of genetic exchange through inter-population dispersal (Hanski and Ovaskainen, 2000; Mech and Hallett, 2001) and may contribute positively to demographic factors and metapopulation dynamics (Gilpin and Hanski, 1991; Hanski, 1998). While corridor cost and functionality can be questioned (Simberloff and Cox, 1987; Simberloff et al., 1992; Horskins et al., 2006), a growing body of literature supports corridors as valuable conservation tools (Beier and Noss, 1998) that can help preserve the viability of a species (Gilpin and Soulé, 1986; Noss, 1987; Lidicker and Koenig, 1996; Mech and Hallett, 2001; Coulon et al., 2004; Wikramanayake et al., 2004; Hilty et al., 2006).

Ours is the first attempt to identify and implement functional corridors throughout the entire range of a large carnivore species. In our model, we used a permeability matrix to identify potential dispersal corridors between known jaguar breeding populations. In conjunction with data from previous analyses (Sanderson et al., 2002; Zeller, 2007), our results help to prioritize not only individual jaguar populations, but corridors between populations for a truly range-wide framework for jaguar conservation and planning.

The jaguar situation is unique. While most landscape analyses detect genetic discontinuities of a species after the fact (McRae

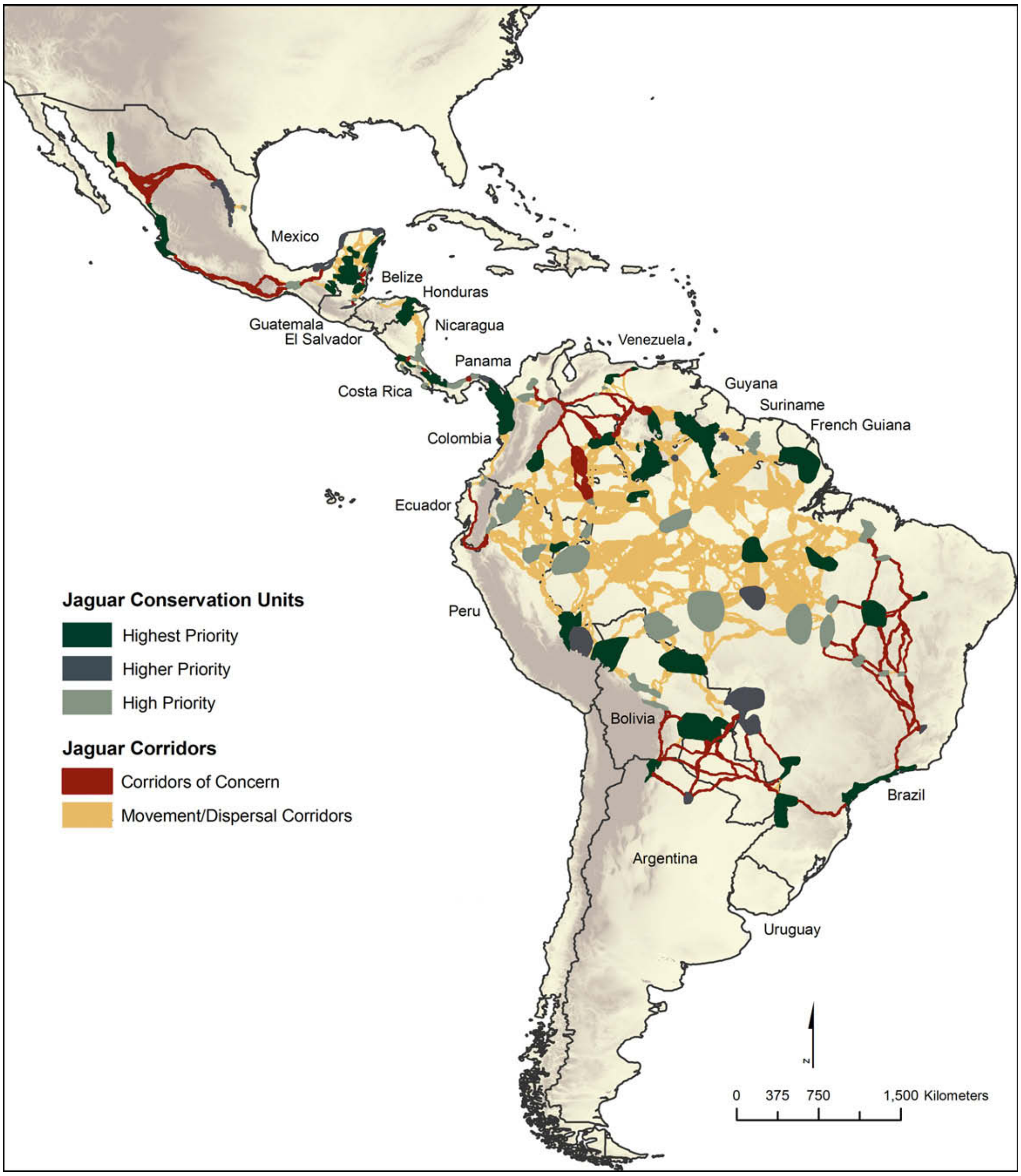

Fig. 2. Jaguar Conservation Units, Least-Cost Jaguar Corridors and Corridors of Concern. Jaguar Conservation Units and their level of prioritization from the latest range-wide priority-setting exercise (Zeller, 2007) are displayed along with the least-cost jaguar corridors and corridors of concern from our jaguar connectivity model.

and Beier, 2007), preliminary genetic data on jaguars indicate potential linkages between jaguar populations that were not previously considered. This allows us to examine how landscape features might be allowing, rather than preventing, jaguar dispersal and movements between seemingly disparate populations.

For the jaguar, the permeability matrix can be defined by the landscape characteristics that appear to still facilitate movement and gene flow between separated populations (Harris and Scheck, 1991). With 78% of the jaguar's historic range still potentially allowing movement through the landscape, we have the opportunity to identify specific routes of travel that can be used by jaguars. While we recognize this may no longer be possible for most other large-bodied, wide-ranging carnivore species, potential dispersal pathways that can enhance effective population sizes, or create metapopulations, should always be considered in any comprehensive species conservation plan.

While scientific data on jaguar dispersal or long range movements are lacking, de Almeida (1990) cites jaguars moving 15 km or more in a single night on hunting patrols in the Brazilian Pantanal. Crawshaw and Quigley (1991) and Crawshaw (1995) documented dispersal distances of 30 and 64 km respectively for male jaguars in different areas of Brazil. One jaguar dispersed for three months, a second for eight months before being killed. Leopold (1959) speculated that a jaguar killed in California in the 1950s had traveled more than 800 km from its point of origin.

Clearly, the occasional jaguar traversing corridors ranging from 3 to 1607 km in length throughout their range is not unlikely. However, as distances between core jaguar populations increase, relatively small patches of habitat that might not normally support even a single resident jaguar take on greater importance. Such stepping stone islands, where a jaguar might rest and/or feed, greatly increase the ability of individuals to disperse (Sondgerath and Schroder, 2001) and thus become important landscape features for possible connectivity (Harris, 1984). The identification and maintenance of these stepping stones will be an integral element in corridor conservation and planning.

The fact that many dispersing carnivores are killed once they travel outside of protected areas is balanced by the fact that very few individuals need to succeed in their trek to other populations. Mills and Allendorf (1996) suggested that populations needed at least one migrant but not above 10 migrants per generation to preserve genetic vigor. Recent data indicate that isolated jaguar populations that have shown divergent genetic patterns are eventually "rescued" by the occasional immigrant that disperses into these populations (E. Eizirik, personal communication). Computer simulations also indicate that subdivided populations typically preserve more alleles and maintain more heterozygotes over the long term than do intact populations with the same total numbers of individuals (Boecklen, 1986) – suggesting that smaller populations connected by occasional migrants may have genetic advantages. To account for demographic and environmental stochasticity and markedly increase the probability of population persistence, it was found that as few as one to four cougars per decade are needed to immigrate into a small population ($\sim$20 animals) (Beier, 1993).

An important goal of our work was to create a valid framework for practical conservation actions on the ground. The least-cost corridor model provides that framework, given a quantifiable set of limits on physical and biological features important to jaguars. The scale of the analysis, the fact that animals don't always act the way we predict, and the limitations of least-cost corridors (see McRae (2006) and Theobald (2006)), means that this model output should be regarded as a first step and not a substitute for actual field surveys. Field assessment and the incorporation of data on the actual use of a corridor by jaguars and their prey is necessary before corridor boundaries are finalized and presented to governments, local communities, and conservation planners. The field data also allow us to integrate the presence of prey species into the identification of the corridors, making these connections important not only for jaguars, but for a suite of species, thereby increasing their contribution to biological conservation throughout jaguar range.

The maps and analyses presented here represent a practical range-wide conservation strategy for the jaguar as well as a platform for regional and site-based actions for the species. We also believe that this model provides important insight for conservation planning initiatives for other species. Implementation of the jaguar corridor, including additional research and conservation in the JCUs, is ongoing and will need continuous monitoring. While the *corridors of concern* are our first priority, other factors such as manpower, politics, and funding, play a role in where, when, and how we implement the jaguar corridor. Field surveys by our teams and other scientists in Mexico, Central America, Colombia and Brazil have already indicated jaguar presence in predicted corridor areas. One recent data point of note includes the photograph of a jaguar in a corridor of concern in central Mexico where jaguars had been thought long extirpated (Monroy-Vilchis et al., 2008).

For a corridor of any significant scale to have a chance at success and sustainability, conservation practitioners must negotiate a maze of land tenure, land use, jurisdiction issues, and legal issues before deciding upon strategies and approaches. Each corridor has its own unique set of circumstances, threats, and opportunities that need to be addressed for implementation to occur. Long-term financial and political commitments are a key component of the process.

Acknowledgements

We would like to thank the following jaguar experts for their input on the dispersal parameters used in this analysis: M. Aranda, S. Cavalcanti, A. Gonzalez-Fernandez, B. Harmsen, M. Kelly, A. Kuroiwa, R. McNab, B. Miller, R. Moreno, A. Noss, J. Polisar, O. Rosas Rosas, S. Silver, and R. Wallace. We are grateful to the Liz Claiborne and Art Ortenberg Foundation, the Wildlife Conservation Society, and the United States Department of State for the funding and support of this work. We wish to thank H. Quigley, L. Hunter, and the journal reviewers for critical review of the manuscript.

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