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Conservation Biology

Contributed Paper

Effectiveness of Panama as an intercontinental land bridge for large mammals

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Abstract: Habitat fragmentation is a primary driver of wildlife loss, and establishment of biological corridors is a common strategy to mitigate this problem. A flagship example is the Mesoamerican Biological Corridor (MBC), which aims to connect protected forest areas between Mexico and Panama to allow dispersal and gene flow of forest organisms. Because forests across Central America have continued to degrade, the functioning of the MBC has been questioned, but reliable estimates of species occurrence were unavailable. Large mammals are suitable indicators of forest functioning, so we assessed their conservation status across the Isthmus of Panama, the narrowest section of the MBC. We used large-scale camera-trap surveys and hierarchical multispecies occupancy models in a Bayesian framework to estimate the occupancy of 9 medium to large mammals and developed an occupancy-weighted connectivity metric to evaluate species-specific functional connectivity. White-lipped peccary (*Tayassu pecari*), jaguar (*Panthera onca*), giant anteater (*Myrmecophaga tridactyla*), white-tailed deer (*Odocoileus virginianus*), and tapir (*Tapirus bairdii*) had low expected occupancy along the MBC in Panama. Puma (*Puma concolor*), red brocket deer (*Mazama temama*), ocelot (*Leopardus pardalis*), and collared peccary (*Pecari tajacu*), which are more adaptable, had higher occupancy, even in areas with low forest cover near infrastructure. However, the majority of species were subject to ≥1 gap that was larger than their known dispersal distances, suggesting poor connectivity along the MBC in Panama. Based on our results, forests in Darien, Donoso–Santa Fe, and La Amistad International Park are critical for survival of large terrestrial mammals in Panama and 2 areas need restoration.

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Efectividad de Panamá como un Puente Terrestre Intercontinental para Mamíferos Mayores

Resumen: La fragmentación del hábitat es un causante primario de la pérdida de biodiversidad, y el establecimiento de corredores biológicos es una estrategia común para mitigar este problema. El Corredor Biológico Mesoamericano *(CBM)* es un ejemplo notable que pretende conectar áreas boscosas protegidas entre México y Panamá para permitir la dispersión y flujo genético de organismos del bosque. El funcionamiento del CBM se ha cuestionado debido a que la degradación de los bosques en Centroamérica continúa, pero no se dispone de estimaciones confiables de la ocurrencia de especies. Los mamíferos grandes son indicadores adecuados del funcionamiento de los bosques tropicales Por lo tanto evaluamos su estado de conservación en el Istmo de Panamá, la sección más angosta del CBM. Utilizamos muestreos con cámaras trampa y modelos de ocupación para múltiples especies bajo un modelo Bayesiano para estimar la ocupación de 9 especies de mamíferos medianos a grandes, y desarrollamos una métrica de conectividad ponderada por la ocupación para evaluar la conectividad funcional para cada especie. El puerco de monte *(Tayassu pecari)*, jaguar *(Panthera onca)*, hormiguero gigante *(Myrmecophaga tridactyla)*, venado cola blanca *(Oidocoileus virginianus)*, y tapir *(Tapirus bairdii)* presentaron una ocupación baja en el CBM en Panamá. El puma *(Puma concolor)*, venado corzo *(Mazama temama)*, ocelote *(Leopardus pardalis)* y el saino *(Pecari tajacu)*, que son más adaptables, presentaron mayor ocupación, aún en áreas con poca cobertura boscosa, cercanas a infraestructura. Sin embargo, la mayoría de las especies estuvo sujeta a $\geq$ 1 vacío que era mayor que sus distancias de dispersión conocidas, lo que sugiere una conectividad pobre a lo largo del CBM en Panamá. Basados en nuestros resultados, los bosques de Darién, Donoso-Santa Fé y el Parque Internacional La Amistad son críticos para la supervivencia de mamíferos terrestres grandes en Panamá mientras que 2 áreas requieren restauración.

Palabras Clave: Bosque neotropical, conectividad del paisaje, Corredor Biológico Mesoamericano, distribución a nivel de comunidad, estadística bayesiana, modelaje de ocupación jerárquica

摘要: 生境破碎化是野生动物数量下降的首要原因, 而应对这一问题的常用策略则是建设生物廊道。一个典型的例子是中美洲生物廊道 *(Mesoamerican Biological Corridor)*, 它的建立旨在连接墨西哥和巴拿马之间的森林保护地, 帮助森林中的生物进行扩散和基因交流。然而, 由于中美洲范围内的森林在持续退化, 中美洲生物廊道的功能已受到质疑, 但目前仍没有该地区物种分布的可靠评估。大型哺乳动物可以作为森林功能的指示种, 因此, 我们评估了中美洲生物廊道最狭窄的地区——巴拿马地峡大型哺乳动物的保护状况。我们利用大规模红外相机调查和贝叶斯框架下的分级多物种占有模型, 估计了九种中大型哺乳动物的分布情况, 并发展出一个生境占有率加权的连接度指标来评估物种特异的功能连接度。结果显示, 白唇西猯 (*Tayassu pecari*) 、美洲豹 (*Panthera onca*) 、大食蚁兽 (*Myrmecophaga tridactyla*) 、白尾鹿 (*Odocoileus virginianus*) 和中美貘 (*Tapirus bairdii*) 在巴拿马的中美洲生物廊道一带估计的生境占有率较低。美洲狮 (*Puma concolor*) 、墨西哥鹿 (*Mazama temama*) 、美洲豹猫 (*Leopardus pardalis*) 和领西猯 (*Pecari tajacu*) 则适应性更强, 生境占有率更高, 即便是在基础设施附近森林覆盖率较低的地区也是如此。然而, 大多数物种都面临着至少一个超出其已知扩散距离的问题, 这表明巴拿马的中美洲生物廊道沿线连接度较低。基于以上结果, 达里恩、多诺索-圣达菲和拉米斯塔德国际公园的森林对于巴拿马及其连接的两个需要恢复的地区所生存的大型哺乳动物则显得至关重要。**【翻译: 胡怡思; 审校: 聂永刚】**

关键词: 贝叶斯统计, 群落水平分布, 分级占有模型, 景观连接度, 中美洲生物廊道, 新热带森林

Introduction

Habitat fragmentation is a primary driver of wildlife loss (Crooks et al. 2017). Degradation of habitat combined with the expansion of human populations impedes species dispersal, reduces gene flow, isolates populations, and can lead to local extinction, especially under climate change (Pardini et al. 2010). Maintaining or restoring functional connectivity of natural areas mitigates effects of habitat degradation (Cushman et al. 2013) and biological corridors are often used to provide connectivity because they facilitate the movement of individuals and gene flow (Chetkiewicz et al. 2006). Corridors are species and process specific (e.g., migration and dispersal). Thus, they do not necessarily consist of breeding habitat, but are rather intended to provide connectivity between habitat patches, the effectiveness of which depends on habitat quality, protection against poaching, and dispersal ability of the species (Beier et al. 2008).

One of the world's largest corridor projects is the Mesoamerican Biological Corridor (MBC). Initiated in the 1990s, the MBC aims to connect protected areas between southeastern Mexico and Panama (Buck Holland 2012). The narrowest part of the MBC is the Isthmus of Panama, where the Great American Biotic Interchange occurred (Marshall 1988). Panama is therefore fundamental for the movement and gene flow of numerous Neotropical forest species (Leigh et al. 2013).

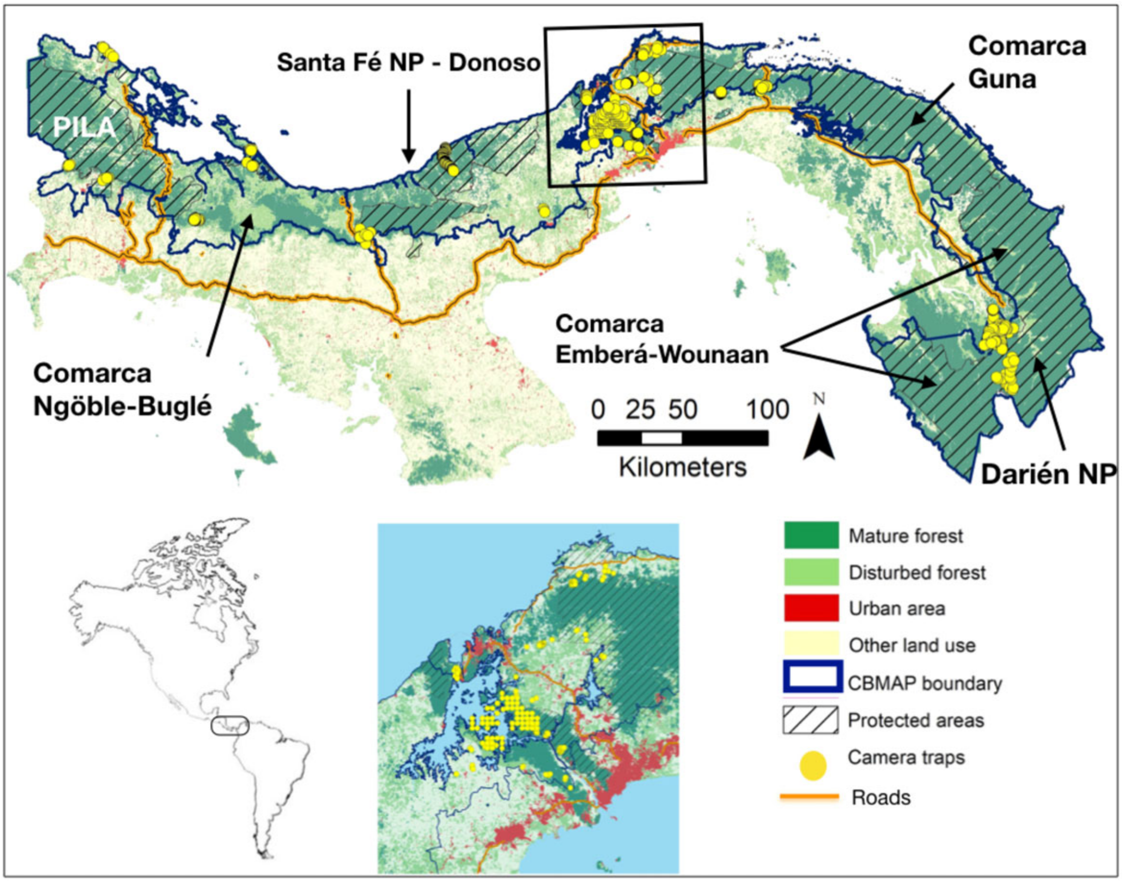

Figure 1. Land cover, Mesoamerican Biological Corridor in Panama (CBMAP), and protected areas in the CBMAP, main roads, and locations of camera traps in Panama (inset, central Panama; PILA, La Amistad International Park).

Although the Isthmus of Panama has functioned as a natural land bridge for wildlife for millions of years (Leigh et al. 2013) and studies from the early 20th century show that most native mammals occurred throughout the entire country (Goldman 1920), today the MBC in Panama appears disrupted. Panama has seen steady economic growth over the past decades related to large infrastructure projects (e.g., expansion of the Panama Canal, enlargement of the principal airport and seaports, and building of new highways and mass transit lines) and large investments in real estate, tourism, energy (e.g., hydroelectric dams), and extractive industries (e.g., gold and copper mines) (Spalding 2017). Although urbanization is greatest near the Panama Canal (Rompré et al. 2008), which cuts through the Isthmus, human encroachment and resource extraction are increasingly affecting the rest of the country, including coastal zones, protected areas, and semiautonomous indigenous lands (comarcas) on Panama's Atlantic slope, precisely where much of the forest remains (Fig. 1) (Spalding 2017). Despite millions of dollars invested in the MBC (Grandia 2007), its effectiveness has not been assessed.

A group of species that are suitable indicators of global human impacts and habitat degradation, and that can hence be used to gauge the effectiveness of the MBC, are large-bodied mammals (Morrison et al. 2007). Large mammals are generally at a higher risk of extinction in disturbed landscapes than other taxa because their large home ranges and low population densities at broad spatial scales mean their populations are more likely to be fragmented (Crooks et al. 2017) and because they are heavily hunted (Benítez-López et al. 2017).

Direct approaches to assess the connectivity and performance of wildlife corridors often require either genetic data (e.g., Wultsch et al. 2016*a*, 2016*b*; Keeley et al. 2017) or empirical data on dispersal paths (e.g., McClure et al. 2016; Zeller et al. 2018). However, acquiring a useful sample size of locations of dispersing individuals and implementing large-scale genetic surveys remain costly and challenging (Wultsch et al. 2016*a*; Zeller et al. 2018). An alternative, indirect approach is to assess species occupancy (i.e., the proportion of area occupied by a species [MacKenzie et al. 2002]). Such data are generally less challenging to acquire for a larger suite of species and on a large scale (Zeller et al. 2012). Occupancy modeling overcomes the problem of elusiveness and low densities of forest mammals by explicitly accounting for imperfect detections (MacKenzie et al. 2002). This in turn allows computation of an occupancy-weighted connectivity (OWC) value, which can be used to estimate species-specific connectivity across landscapes (e.g., Sutherland et al. 2014, 2015). If the MBC functions well for large mammals, habitat patches should be occupied by mammal populations across the entire length of the MBC and gaps between these areas should not exceed the dispersal capacity of these species. This is a conservative assumption because the functioning of a corridor also depends on permeability of the gaps and effective protection of habitat patches (e.g., from poaching) (Zeller et al. 2012; Keeley et al. 2018).

We sought to assess connectivity across the Panamanian portion of the MBC for medium to large terrestrial mammals. Most previous connectivity studies focused on a single species as a surrogate (often a large carnivore), but 1 species may not reflect the needs of the larger community (Beier et al. 2009; Cushman & Landguth 2012), so we took a multispecies approach (Rich et al. 2016). We deployed camera traps across the Isthmus of Panama to estimate occupancy and predict species-specific connectivity.

Methods

Study Area and Focal Species

Panama lies in the moist Neotropics, and of the 43% of land that remains forested, 44% is protected (FAO 2010). Outside protected areas, the country is a mosaic of old-growth and secondary forest patches surrounded by agriculture, pastures, and human settlements (Condit et al. 2001). The MBC overlaps the Atlantic side of the isthmus, where most of the forest remains (Fig. 1).

We studied 9 medium to large (i.e., >12 kg) mammal species: ungulates, Baird's tapir (*Tapirus bairdii*), white-lipped peccary *(Tayassu pecari)*, collared peccary (*Pecari tajacu)*, white-tailed deer (*Odocoileus virginianus*), Central American red brocket deer (*Mazama temama*), carnivores, jaguar (*Panthera onca*), puma (*Puma concolor*), ocelot (*Leopardus pardalis*), and insectivore, giant anteater (*Myrmecophaga tridactyla*). All are mostly forest specialists, but they differ in sensitivity to habitat disturbance. Jaguars, white-lipped peccaries, and giant anteaters are rare and listed as endangered in Panama, whereas tapirs are listed as critically endangered (MiAmbiente 2016). They are primarily threatened by habitat loss and hunting for meat or in retaliation for depredation of domestic animals (Meyer et al. 2013, 2019; Moreno et al. 2015). Ocelot, puma, and red brocket deer are moderately sensitive to anthropogenic disturbance (Jordan et al. 2016; Zeller et al. 2018), and white-tailed deer and collared peccary should be more tolerant to disturbance (Reyna-Hurtado & Tanner 2007).

Camera-Trapping Surveys

Detection and nondetection data on large mammals were obtained from arrays of camera traps established along the CBMAP from the border with Colombia in the east to the border of Costa Rica in the west (Fig. 1). We surveyed 28 forested sites. Sixteen were protected (national park, multiple use protected area, nature monument, biological reserve, and wilderness area [Supporting Information]) and 12 were unprotected forest fragments between protected sites in agriculture matrix. The sites differed in disturbance level and protection status.

Our data set included 418 camera stations (henceforth points) deployed mostly in 2012–2017 (1 site surveyed in 2006). We treated each camera point surveyed during a particular year as a distinct point and obtained 727 unique detection histories. We included year as a random effect to ensure this did not affect results.

For each camera point, we built species-specific detection histories by using a maximum of 90 days of camera-trap data divided into 15 days of sampling (yielding 6 sampling occasions). The repeated sampling protocol allowed for a species that was present but not detected to be differentiated from absence at each camera point (MacKenzie et al. 2002).

Environmental and Sampling Variables

The sampling design differed between surveys depending on the objectives of the initial study (e.g., estimation of jaguar density or survey of entire mammal community [Supporting Information]). Therefore, models of detection probability were fitted with 3 sampling covariates: number of camera units at each station (1 or 2, unit), location of cameras (on trail or grid, trail), and sampling effort (number of days camera deployed, effort).

We modeled the effect of anthropogenic and landscape variables (5 environmental covariates) on the probability of occupancy: distance to nearest road (road), density of human settlements (villages) (i.e., number of villages per unit area), elevation (elev), percent tree cover (FCOV) in 2015 (Hansen et al. 2013), and negative distance within protected areas as a measure of remoteness. We chose these based on our expertise and the literature (Supporting Information). We generated raster layers of 30-m resolution in ArcMap (version 10.1, ESRI, Redlands, California). We determined the strongest scale of response for village and FCOV (Supporting Information). We centered and scaled the covariates (Schielzeth 2010) and checked for multicollinearity (defined as $\text{rho} > |0.6|$) (Supporting Information).

Occupancy Models

We used the hierarchical modeling framework described by Dorazio and Royle (2005) and code provided by Zipkin and Royle (2009) to estimate occupancy of the focal mammals across the CBMAP. This model estimates species-specific model parameters as random effects of a community-level distribution, which permits more precise parameter estimates for rare species than traditional species-level analyses (Zipkin et al. 2009; Kéry & Royle 2016). This model was particularly advantageous for species with sparse data across all years, especially tapir, white-lipped peccary, giant anteater, and jaguar.

We tested the global model to estimate the probability of occupancy while detection probability remained constant (i.e., set to the most parameterized state) by fitting all 5 point-specific habitat covariates as follows:

$$\begin{aligned}\text{logit}\left(\Psi_{ij}\right) &= \alpha_i + \alpha_{i1}\text{elev} + \alpha_{i2}\text{ village} + \alpha_{i3}\text{DWPA}\\ &\quad + \alpha_{i4}\text{FCOV} + \alpha_{i5}\text{ road},\end{aligned} \tag{1}$$

where Ψ_{ij} is the probability of occupancy of species i at camera point j and α_i is the coefficient of variables 1 to 5 specific to each species i.

Subsequently, we ran the global model by allowing the detection to vary with 1 sampling covariate at a time:

$$\text{logit}\left(p_{ijk}\right) = \beta_i + \beta_{i1}\text{ sampling covariate}, \tag{2}$$

where p_{ijk} is probability of detection of species i at camera point j during sampling k.

We reran the best supported model twice by adding year as random effect on occupancy and then on detection (Table 1).

We discriminated between our models with the Watanabe–Akaike information criterion (WAIC) (Hooten & Hobbs 2015), a fully Bayesian approximation of out-of-sample predictive accuracy. Interpretation is similar to that of AIC (Watanabe 2010). After identifying the best occupancy model, we back transformed the parameters' coefficients of the model to draw species-specific occupancy maps with the raster calculator tool in ArcMap.

From Occupancy to Connectivity

To derive species-specific connectivity from occupancy, we computed the weighted connectivity metric which is the binary analogue of density-weighted connectivity (Sutherland et al. 2015; Morin et al. 2017) and represents the cumulative probability of a specific area (or pixel) being connected to other areas. This approach is partly derived from metapopulation theory (i.e., the concept of computing connectivity as the sum of weighted dispersal contributions [e.g., Sutherland et al. 2014; Chandler et al. 2015]). For each species, we centered a dispersal kernel on each pixel, weighted it by the estimated occupancy, and computed cumulative use of pixels by all pixels on the landscape (Sutherland et al. 2015). Thus, for any species, the connectivity of any pixel x is given by the occupancy-weighted contributions of all y neighboring pixels:

$$S_x = \sum_{y=1} \hat{\psi}_y \times e^{-d_{xy}/\alpha}, \tag{3}$$

where S_x is the connectivity metric for pixel x, $\hat{\psi}_y$ is the estimated occupancy of the species in pixel y, d_{xy} is the distance between pixel x and y, and α is the species-specific average dispersal distance of species.

We used information from the literature to determine the average dispersal distance of each species to the extent possible in areas with an environment similar to Panama forests (Table 2). This resulted in species-specific surfaces of OWC, which formally integrates existing knowledge of species dispersal capacity and spatially explicit estimates of occurrence to provide a measure of relative functional connectivity across Panama.

Results

Cameras recorded 5315 independent detections of the 9 focal species in 43,294 camera-trap nights. Giant anteater was the least detected species (62 independent captures at 38 sites, naïve occupancy: 0.05). Collared peccary was the most detected species (556 independent captures at 370 sites, naïve occupancy: 0.51). Village density explained occupancy best at a scale of 10 km around each camera, and forest cover explained occupancy best with a threshold of 75% within 150 m of each camera point (Supporting Information). We used these scales in our global model. The scale-reduction factor and trace plots indicated convergence for all models (Supporting Information).

Based on the WAIC values, adding sampling effort explained a significant amount of variation in detection probability and slightly increased the performance of the global model (WAIC global d1 = 35.39 vs. WAIC global = 36.58) (Table 1). There was no support to include year because the resulting models were >7 Δ units from the best supported model. This further supports our decision to pool data across years.

Covariates affecting occupancy probabilities differed by species in sign and intensity (Table 3). Except for puma, occupancy tended to increase as distance inside the protected areas increased, especially for white-lipped peccary and white-tailed deer. Except for jaguar and puma, species responded positively to forest cover. Ocelot, collared peccary, and white-tailed deer tended to occur away from roads, whereas for the other species, occupancy increased as distance to road decreased, although this relationship was not significant. There was no significant negative influence of density of village on

Table 1. Mammal occupancy and detection models tested in a Bayesian hierarchical framework.[a]

Name	*Model*	*WAIC*	*Δ WAIC*
Global[b]	$\text{logit}\ (\Psi_{ij}) = \alpha_i + \alpha_{i1}\text{elev} + \alpha_{i2}\text{village} + \alpha_{i3}\text{DWPA} + \alpha_{i4}\text{FCOV} + \alpha_{i5}\ \text{road}$	36.58	0.00
Global Y[b]	$\text{logit}\ (\Psi_{ij}) = \alpha_i + [\ldots] + \alpha_{\text{i}6}\text{year}$	44.04	7.46
Global d1[c]	$\text{logit}\ (\Theta_{ijk}) = \beta_i + \beta_{i1}\text{effort}$	35.39	0.00
Global d2[c]	$\text{logit}\ (\Theta_{ij\text{k}}) = \beta_i + \beta_{i2}\text{trail}$	37.64	2.25
Global d3[c]	$\text{logit}\ (\Theta_{ijk}) = \beta_i + \beta_{i3}\text{unit}$	42.36	6.97
Global d1Y[c]	$\text{logit}\ (\Theta_{ijk}) = \beta_i + \beta_{i1}\text{effort} + \beta_{i4}\text{year}$	46.79	11.40

[a] *Relative performance based on the Watanabe-Akaike Information criterion score (WAIC).*
Abbreviations: DWPA, distance within protected area; FCOV, forest cover with a threshold of 75% and within 150 m; elev, elevation; village, density of villages within 10 km; effort, number of camera nights; unit, number of cameras per station.
[b] *Detection constant (i.e., only occupancy is modeled).*
[c] *Detection allowed to vary with 1 sampling covariate.*

Table 2. Dispersal distance reported for 9 focal species.[a]

	Distance (km)	*n*	*Average*	*Method*	*Movement mode*	*Site*	*Source*
Jaguar	70–91	2	80	telemetry	dispersal	Brazil	R. Morato, personal communication
Puma	60–80	2	70	telemetry	dispersal	Brazil	R. Morato, personal communication
	28–131	11	55	telemetry	dispersal	California, USA	Zeller et al. 2018; K. Zeller, personal communication
	45	1	45	telemetry	translocation	Darien, Panama	N.M. & R.M. data
			56				
Ocelot	6	1	6	camera trap		central Panama	R.M & J. Willis. data
White-lipped peccary	10–25	2	17	telemetry		Pantanal, Brazil	A. Keuroghlian, personal communication
Collared peccary	11	1	11	telemetry	translocation	Chaco, Argentina	Hurtado Martinez 2017
	3–6	2		genetics		Texas, USA	Cooper et al. 2010
Red brocket deer[b]	DD						data deficient
White-tailed deer	1.4–1.7	5	1.5	telemetry	max DDT	Campeche, Mexico	Contreras-Moreno 2018
	22	na	6.4	telemetry	dispersal	northern Florida, USA	Kilgo et al. 1996
Tapir	8	1	8	telemetry	capture-release	Calakmul, Mexico	Reyna-Hurtado et al. 2016
Giant anteater	5–51	11	13	telemetry	translocation	Ibera, Argentina	Di Blanco et al. 2010

[a] *When possible, we reported the dispersal distance from sites comparable to the moist tropical forests of Panama (i.e., Mesoamerica and the Amazon).*
[b] *We found no data for Mazama temama or for other Mazama spp., so we used the dispersal distance of white-tailed deer.*
Abbreviations: n, number of individuals; DD, data deficient; DDT, daily distance travel.

species. In general, elevation had little effect on the occupancy, as suggested by the small coefficients.

Because the parameter coefficients varied across species, so did the occupancy maps (Fig. 2). Large forest tracts in the far east (Darién) and west (La Amistad International Park [IP]) connected to forest in bordering countries had higher relative occupancy than the other areas for all species. The Donoso–Santa Fé forest block also constitutes a zone where all the species occur albeit with a lower occupancy. The OWC maps (Fig. 3 & Supporting Information), which depict the connectivity level for each species, corroborated that Darién was a stronghold for the majority of the species, except puma, even when there was a large reduction in connectivity. Conversely, there were 2 areas where connectivity would likely be lost first, which would affect dispersal of all species but puma: between Donoso and the Panama Canal (Central Panama) and in the comarca Ngöble-Buglé.

Discussion

Because parts of Panama have degraded over time, its effectiveness as a corridor for wildlife has been questioned. However, reliable estimates of species occurrence and connectivity at the country level were unavailable, despite the need to prioritize areas of high conservation value and for restoration.

Our approach allowed us to evaluate how the MBC performed for the occurrence of large mammals. The OWC, which formally integrates existing knowledge of species dispersal capacity and spatially explicit estimates

Table 3. Species-specific coefficients and 95% credible intervals (CRI) for each parameter (occupancy and detection) and covariates based on the global model (global d1).[a]

Parameter[b]	$\bar{x}$	95% CRI		$\bar{x}$	95% CRI		$\bar{x}$	95% CRI		$\bar{x}$	95% CRI		$\bar{x}$	95% CI	
	jaguar			puma			ocelot			white-tailed deer			red brocket deer		
Occupancy															
α (constant)	−1.64	−2.14	−1.05	−0.50	−0.85	−0.09	0.02	−0.23	0.31	−2.04	−2.37	−1.74	−0.76	−1.02	−0.47
elev	−0.10	−0.43	0.20	−0.02	−0.27	0.24	0.06	−0.14	0.30	0.12	−0.10	0.33	0.15	−0.04	0.35
village	−0.07	−0.40	0.25	0.08	−0.17	0.35	0.19	−0.03	0.42	−0.21	−0.52	0.07	0.10	−0.12	0.34
DWPA	−0.22	−0.59	0.13	0.16	−0.13	0.48	−0.22	−0.46	0.01	−0.56	−0.91	−0.25	−0.28	−0.54	−0.03
FCOV	−0.22	−0.65	0.11	−0.17	−0.49	0.08	0.01	−0.25	0.23	0.58	0.09	1.34	0.23	−0.03	0.52
road	−0.01	−0.37	0.32	−0.15	−0.45	0.12	0.30	0.06	0.57	0.40	0.16	0.67	−0.04	−0.29	0.19
detection															
β (constant)	−1.20	−1.76	−0.70	−0.94	−1.25	−0.65	−0.28	−0.49	−0.06	0.20	−0.18	0.57	−0.33	−0.63	−0.04
effort	−0.06	−0.36	0.23	−0.13	−0.34	0.07	−0.04	−0.21	0.13	0.17	−0.13	0.48	0.15	−0.10	0.40
	collared peccary			white-lipped peccary			Baird’s tapir			giant anteater					
α (constant)	0.09	−0.13	0.31	−2.59	−3.22	−1.87	−1.34	−1.91	−0.59	−1.37	−2.12	−0.47	-	-	-
elev	−0.03	−0.21	0.15	−0.14	−0.55	0.20	0.04	−0.25	0.36	−0.13	−0.52	0.21	-	-	-
village	−0.08	−0.28	0.13	0.00	−0.37	0.36	0.12	−0.21	0.45	−0.19	−0.66	0.21	-	-	-
DWPA	−0.37	−0.60	−0.15	−0.49	−1.01	−0.06	−0.26	−0.65	0.11	−0.12	−0.53	0.33	-	-	-
FCOV	0.13	−0.09	0.33	0.39	−0.10	1.12	0.33	−0.10	0.85	0.11	−0.36	0.65	-	-	-
road	0.27	0.05	0.51	0.07	−0.34	0.45	−0.08	−0.48	0.27	−0.10	−0.58	0.34	-	-	-
detection															
β (constant)	0.03	−0.16	0.23	−0.93	−1.85	−0.11	−1.45	−2.09	−0.88	−2.50	−3.20	−1.86	-	-	-
effort	0.15	−0.01	0.31	0.27	−0.18	0.83	0.07	−0.22	0.38	0.12	−0.18	0.41	-	-	-

[a] *Detection probability varies with sampling effort. Median and SD are in Supporting Information.*

[b] *Abbreviations: DWPA, distance within protected area; FCOV, forest cover with a threshold of 75% and within 150 m; elev, elevation; village, density of villages within 10 km; effort, number of camera nights.*

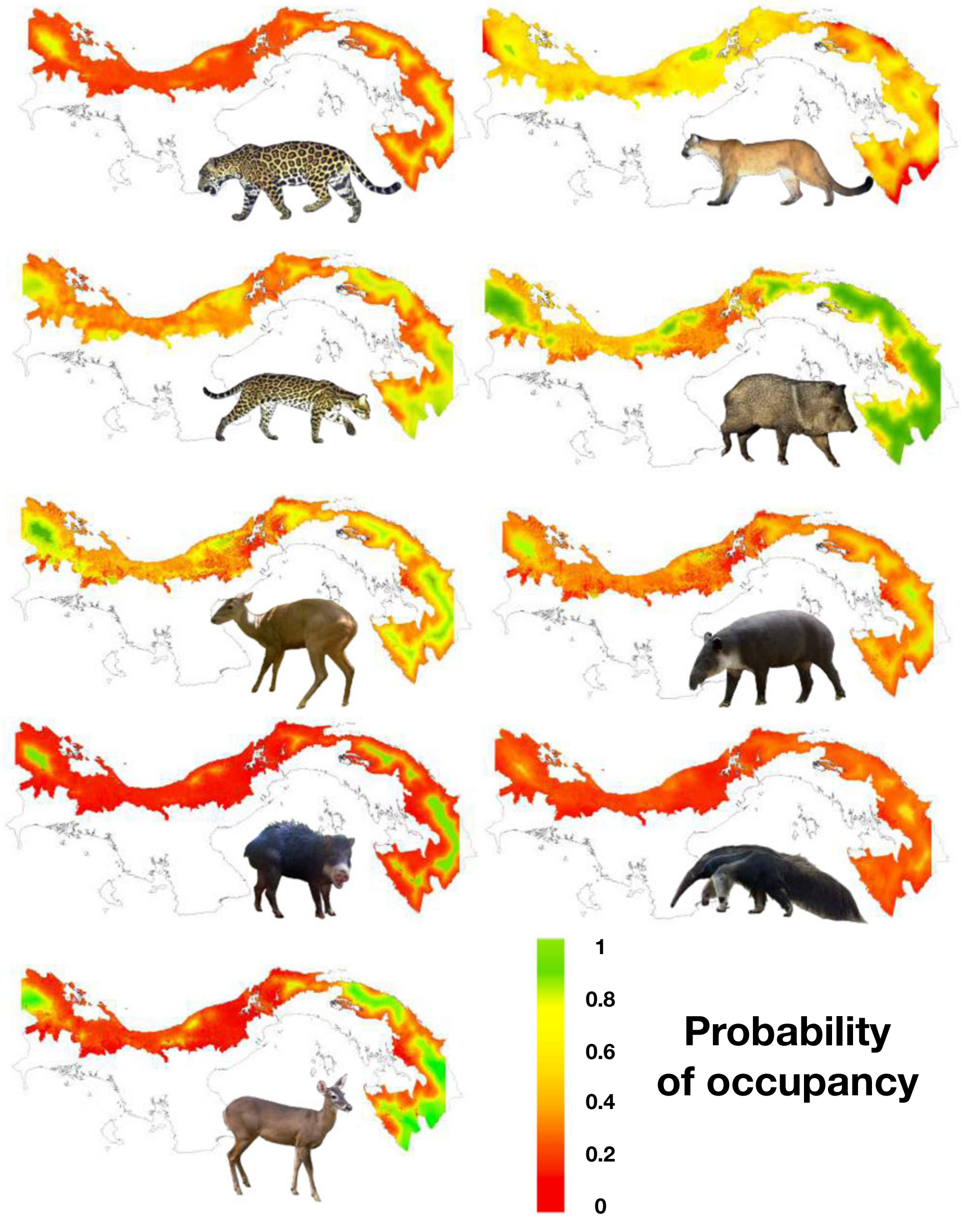

Figure 2. Occupancy probability of 9 large terrestrial mammals along the Mesoamerican Biological Corridor in Panama (red, lowest occupancy; green, highest occupancy) based on a model incorporating 5 variables (forest cover within 150 m; distance within protected area; elevation; density of villages within 10 km; distance to nearest road; detection varies with sampling effort). Species from left to right and top to bottom are jaguar, puma, ocelot, collared peccary, red-brocket deer, Baird's tapir, white-lipped peccary, giant anteater, and white-tailed deer.

of occurrence, describes in a biologically and realistic way the level of functional connectivity across Panama. Because camera-trap surveys and occupancy models are becoming increasingly widespread and available, OWC constitutes an advantageous alternative over other methods (i.e., genetics and movement models).

We found that there was little connectivity for white-lipped peccary and white-tailed deer and that, although 4 of the species (collared peccary, red brocket deer, puma, and ocelot) occurred in most of the sites, a small decrease in connectivity of 20% would disrupt their continuous distributions across Panama. White-lipped peccary, giant anteater, white-tailed deer, jaguar, and tapir had lower probability of occurring in all the sites and were therefore even more at risk of connectivity loss, as evidenced by >1 connectivity gap. This indicates the MBC may not function for the majority of species, especially considering we did not account for potential effects of hunting, which would make connectivity even more challenging.

Although there was no significant negative relationship between mammal occupancy and anthropogenic features, such as roads and villages, the majority of the species responded positively to forest cover, highlighting its importance in maintaining stable animal populations. Moreover, occupancy of all species but puma increased as remoteness increased (distance within protected area), meaning protected areas that are sufficiently large to include poorly accessible zones remain essential for the survival of mammals. Due to the difficulty in measuring the hunting pressure in all the sites (Benítez-López et al.

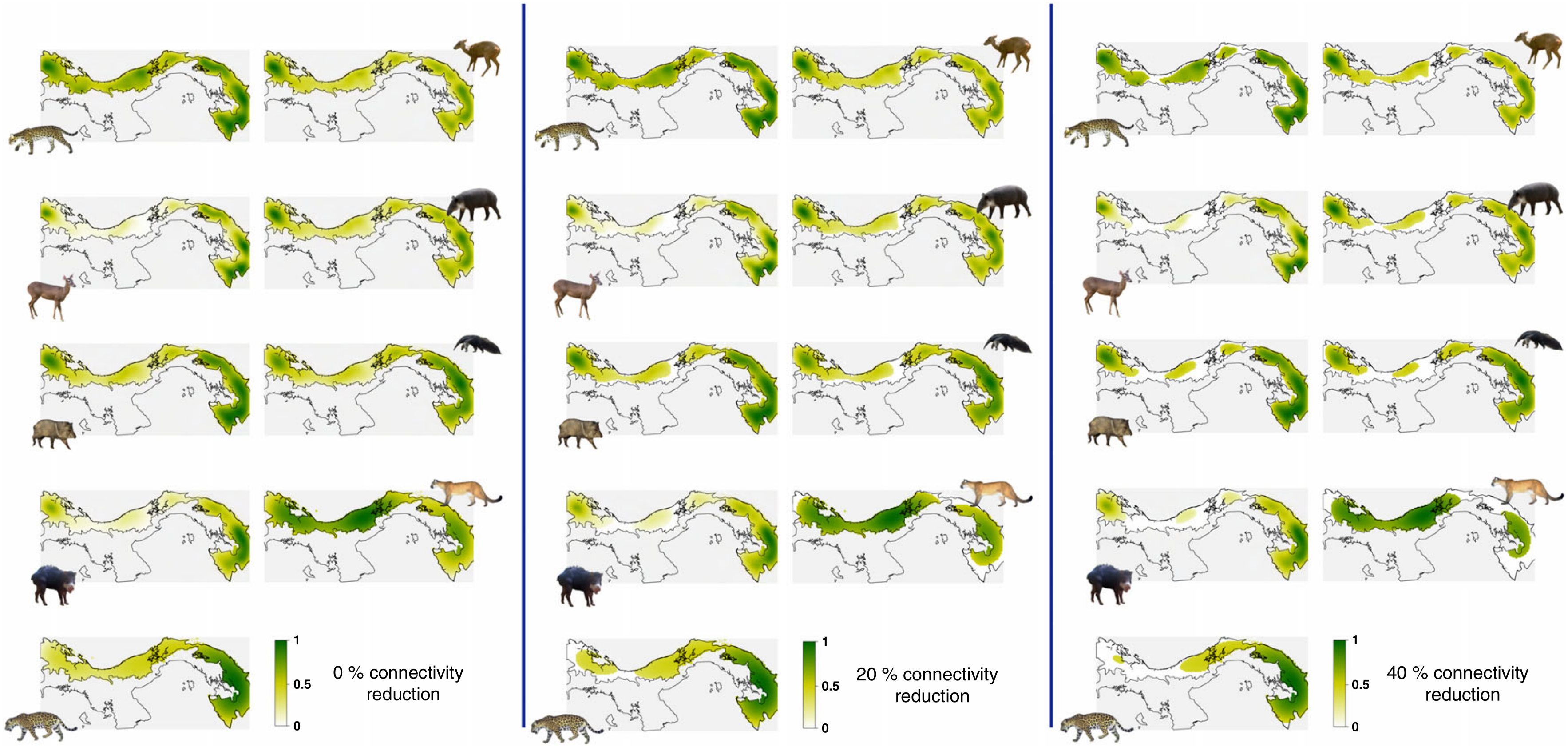

Figure 3. Amount of connectivity for 9 large mammals across the Mesoamerican Biological Corridor portion of Panama (dark green, highest connectivity; white, lowest connectivity). Species from left to right and top to bottom are ocelot, red brocket deer, white-tailed deer, Baird's tapir, collared peccary, giant anteater, white-lipped peccary, puma, and jaguar. The 3 sets of occupancy-weighted connectivity surfaces from right to left represent 100%, 80%, and 60% connectivity. For the latter 2, 20% and 40%, respectively, lower connectivity pixels are not shown. Maps showing occupancy-weighted connectivity surfaces with intervals of 10% connectivity decrease are in Supporting Information.

2017), we did not incorporate this variable in our model, but we speculate it may be a substantial cause of low occurrence or local extirpation of white-lipped peccaries and tapirs in several sites. Poaching affects all guilds in Panama, from ungulates hunted for meat (Moreno & Meyer 2014) to carnivores killed to supply an emergent illegal market in jaguar parts (Reuter et al. 2018) and in retaliation for depredation on cattle and other domestic animals (Moreno et al. 2015). That puma and jaguar are not restricted to areas of high forest cover may exacerbate frequent conflict with ranchers (Moreno et al. 2015).

From our species-specific maps we identified 2 core areas that still harbored most of the large mammals and that were located at the 2 extremes of the Isthmus of Panama. In the east, the large continuous track of forest formed by the comarcas Guna and Emberá-Wounaan together with the Darién National Park (NP) represented the largest amount of contiguous habitat estimated to have high relative occupancy rates for all large mammal species, except puma, and the highest connectivity. Forest resources of the comarcas are exploited in a relatively sustainable way by indigenous peoples who live on and govern the land (Vergara-Asenjo & Potvin 2014). Moreover, Darién NP has so far been safeguarded from excessive human-induced disruption because of its remoteness—the Darién gap is the only place where the Pan-American Highway is interrupted—and because it is near a region where armed conflicts have been occurring for decades, thus affording its forest informal protection. Nevertheless, emerging threats (e.g., roads, fires, and timber extraction) increasingly affect its condition. Darién NP is particularly important at the regional level because it is a high-priority Jaguar Conservation Unit (Sanderson et al. 2002), the second largest stronghold for WLP throughout Mesoamerica (Reyna-Hurtado et al. 2018), and the third largest stronghold for Baird's tapir (Schank et al. 2017). In the west, the transboundary La Amistad IP between Panama and Costa Rica also constitutes an important core area for large mammals. The rugged mountainous terrain and the scarcity of roads to access remote parts have probably prevented it from being overexploited and depleted of large fauna. Our results confirm these areas are of high conservation value and underscore the need to protect them from infrastructure development and human encroachment. Because La Amistad IP and Darién NP are separated by about 500 km of a mosaic of agriculture fields, human settlements, and small forest fragments, the few larger blocks of forest that remain (i.e., Santa Fé NP and Donoso) represent substantial conservation units for large mammals. Even though the occupancy is lower in these areas, they can serve as stepping stones for them to disperse between populations.

We identified 2 principal bottlenecks for connectivity of our focal mammals, even for relatively common and less sensitive species such as collared peccary and ocelot. The first weak link is in Central Panama, which encompasses the Panama Canal watershed. Although forest areas have been preserved to supply water to the Canal, our results indicate a low connectivity level. The canal should be passable to medium-large mammals given its relative narrow width (sometimes <200 m) and little current. Various species cross, including jaguar and puma (Willis 2009); tapir (Meyer et al. 2013); ocelot (R.M. personal observation); red-brocket deer (game warden, personal communication); and other mammals (Northern tamandua [*Tamandua mexicana*], three-toed sloth [*Bradypus variegatus*], Central American agouti [*Dasyprocta punctata*], white-nosed coati [*Nasua narica*], and howler monkey [*Alouatta palliata*] [Esser et al. 2010; M. Santamaria, personal communication; N.M & R.M., personal observation). However, urbanization and infrastructure—especially several highways—constitute a barrier for species movement and combined with high poaching levels have likely led to local extinction of several large mammal species in this area (Meyer et al. 2015).

The other area with low probability of connectivity is the comarca Ngöble-Buglé between La Amistad IP and Donoso. There, development projects, high human population growth, and slash-and-burn agriculture have led to substantial degradation and deforestation (ANAM 2003), even inside protected areas. Consequently, the majority of large mammal species have a low probability of occurrence in that region, which currently has large areas with no suitable habitat.

Our connectivity surfaces represent the best-case scenario given that we did not incorporate risks associated with crossing the landscape, especially the poaching pressure that is both area and species specific. Furthermore, in contrast to other methods in which empirical movement data are used to infer connectivity, the OWC does not incorporate the effect of barriers on movement. Another possible limitation of our occupancy model lies in the uneven sampling effort across Panama. For example, Central Panama was surveyed more intensely than the comarcas Guna and Ngöble-Buglé, resulting in a few gaps between camera trap arrays. Petracca et al. (2018) found a mean probability of habitat use (similar to occupancy) of about 0.4 in the comarca Ngäbe-Buglé and 0.5 in the area spanning Donoso to Central Panama, which is slightly higher than our estimate ($\sim$0.3 in both areas). Unlike our study, they parameterized their models with data from interviews conducted in 25-km^2 units. Generally, with the exception of the white-tailed deer that has been rarely observed in the remote areas of Darien and La Amistad IP, our occupancy maps were consistent with the expected distribution of species based on expert opinion and detection–nondetection data from other studies (i.e., tapir, Meyer et al. [2013] and Schank et al. [2017]; white-lipped peccary, Reyna-Hurtado et al. [2018] and Moreno and Meyer [2014]); therefore, we do not consider this a problem.

Broadly, our findings indicated that Panama has become less permeable for several medium to large mammals. This suggests that a thousand-year-old biogeographical connection is jeopardized due to habitat degradation. Given Panama's increasing economic development and associated replacement of forests by urban and agricultural areas (FAO 2010; Hansen et al. 2013), a reconciliation of economic development with forest and wildlife conservation is uncertain. There are several ongoing projects of particular concern: the construction of a road along the Atlantic coast from the Panama Canal to the west, along which forests are being transformed into private estates and large hotel complexes; an electric interconnection line between Panama and Colombia that will include the construction of roads passing through the forests of Guna Yala and Darién (Spalding 2017). In this context, the scenario of a substantial loss of connectivity in the near future is likely. The disruption of connectivity between tropical forests in Central America, and hence the possible separation of mammal populations (Eizirik et al. 2001; Norton & Ashley et al. 2004; Wultsch et al. 2016*a*), is an indicator of the overall functioning of the MBC for wildlife.

Although landscape genetics would constitute an interesting validation method to assess the effectiveness of the MBC because it reflects both successful movements and reproduction of a species (Robertson et al. 2018), it is as of yet unknown whether the poor connectivity has already affected gene flow between mammal populations in Panama. Genetic information on our focal species is limited in Central America (but see Wultsch et al. [2016*a*, 2016*b*]). One of the only 2 studies using data from Panama shows that genetic diversity of Baird's tapir is low and that the Costa Rican and Panamanian populations were connected by some gene flow prior to disruption of continuous habitat between the countries (Norton & Ashley 2004). The second study indicates reduced levels of gene flow for jaguar across barriers such as the Darién (Eizirik et al. 2001). A drawback when using this approach is that genetically derived connectivity estimates reflect past landscape permeability due to the time it takes to detect barriers (several generations) (Cushman et al. 2013), and hence would not necessarily detect gene flow in a rapidly evolving landscape such as Panama.

Restoring the connectivity between populations of large mammals in Panama is a challenging task, but we see several options for decision makers and land-use planners. The first is the prevention of deforestation in areas critical for connectivity, especially Guna Yala–Darién forest block, La Amistad IP, Donoso, and Santa Fé NP. The second is reducing poaching pressure, which requires stricter law enforcement and effective antipoaching patrols in protected areas. Activities that would provide a source of income to indigenous and forest-dwelling people (e.g., ecotourism and biodiversity monitoring) is another strategy to allow local people to benefit from natural resources, yet this needs to be done in a way that minimizes negative externalities (Winkler 2011). Human-felid conflict can be reduced by working closely with ranchers, providing them with technical and practical guidance, and compensating loss of livestock to predators (Moreno et al. 2015). Finally, tapir and white-lipped peccary should be added to the species conservation agenda of the government of Panama because they tend to be neglected despite their critical status and the indicator role they play in disturbed ecosystems (Reyna-Hurtado et al. 2018).

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Supporting Information

Additional methods (Appendix S1), specifications of camera-trapping surveys (Appendix S2), rationale of habitat covariates used in occupancy models (Appendix S3), home range of focal species (Appendix S4), WAIC scores to determine the strongest scale of response for forest cover and village density (Appendix S5), output of best-supported multispecies occupancy model (Appendix S6) and its trace-plots (Appendix S7), and occupancy-weighted connectivity surfaces for 9 focal species (Appendix S8) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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