



Assessing occupancy and habitat connectivity for Baird's tapir to establish conservation priorities in the Sierra Madre de Chiapas, Mexico



J. Antonio de la Torre^{a,b,*}, Marina Rivero^{b,c}, Gamaliel Camacho^b, Luis Arturo Álvarez-Márquez^d

^a Instituto de Ecología, UNAM, Laboratorio de Ecología y Conservación de Vertebrados Terrestres, Ap. Postal 70-275, C. P. 04510 Ciudad Universitaria, Mexico

^b Bioconciencia A.C., Ciudad de México, Mexico

^c El Colegio de la Frontera Sur, Departamento de Conservación de la Biodiversidad, Lerma, Campeche, Mexico

^d Área de Protección de los Recursos Naturales La Fraileskana, CONANP, Mexico

ARTICLE INFO

Keywords:

Camera traps
Chiapas
Circuit theory
Corridors
Occupancy model
Tapir

ABSTRACT

Baird's tapir (*Tapirus bairdii*) is the largest native mammal that inhabits the Neotropics, and it is enlisted as Endangered by the IUCN Red List. The historic distribution of this species included the area from southern Mexico to northern Colombia. However, its distribution and populations have been reduced drastically during the past 30 years. The main threats for Baird's tapir are the direct persecution for subsistence hunting, habitat destruction, and habitat fragmentation. In this study, we used camera traps and occupancy models to identify the landscape characteristics that were associated with the occurrence of tapirs in the Sierra Madre de Chiapas, which is one of the most important populations of the species in Mexico, with the aim to identify areas with habitat suitability for the species. We used our best occupancy model to generate a resistance matrix to develop a model of habitat connectivity using Circuit Theory. According to the best occupancy model, the most suitable areas for this species were the forested areas located at the highest elevations of the mountain ranges that provided rugged terrain. We identified three critical corridors to allow for the connectivity of tapir populations in the Sierra Madre de Chiapas, and one of these corridors provides connectivity between this population and the population in the Ocoate Biosphere Reserve. With this approach, we propose a conservation strategy for the species that incorporates a more realistic and detailed scheme of Baird's tapir occurrence in the Sierra Madre de Chiapas region. Priority actions to conserve tapirs in the Sierra Madre de Chiapas over the long term include ensuring the complete protection of prime habitat for the species, improved connectivity by protecting forest cover, implementation mitigation measures in areas where paved roads interrupt connectivity of populations, and eradicating poaching of the species in the region completely.

1. Introduction

Most large bodied mammalian species are threatened with extinction due to anthropogenic impacts (Ripple, Chapron et al., 2016; Ripple et al., 2017). Large mammals are particularly vulnerable to habitat destruction and other anthropogenic perturbations due to intrinsic factors such as their low reproductive rates, low densities, and extensive area requirements (Cardillo et al., 2005; Kinnaird, Sanderson, Brien, Wibisono, & Woolmer, 2010; Ripple et al., 2015; Ripple et al., 2017; Schipper et al., 2008). Additionally, the vulnerability of these species to extirpation over the long term is exacerbated because of their high value in subsistence or commercial hunting and medicinal products (Ripple, Chapron et al., 2016). For instance, large herbivores

commonly face dramatic population declines and range contraction, and approximately 60% of these species are threatened with extinction (Ripple et al., 2015). The loss of these species can have cascading effects on other species in the ecosystem where they occur, and this loss can also affect the important economic and social services they provide to humans (Ripple et al., 2015; Ripple, Abernethy et al., 2016). To conserve large mammals over the long term requires an increase in research that addresses solutions for their conservation, especially for lesser known species (Ripple, Abernethy et al., 2016; Ripple et al., 2017).

Baird's tapir (*Tapirus bairdii* – Gill, 1865) is the largest native mammal that inhabits the Neotropics, and it is listed as Endangered by the IUCN Red List (García et al., 2016). The historic distribution of this

* Corresponding author at: Instituto de Ecología, UNAM, Laboratorio de Ecología y Conservación de Vertebrados Terrestres, Ap. Postal 70-275, C. P. 04510 Ciudad Universitaria, Mexico.

E-mail addresses: adelatorre@ieecologia.unam.mx (J.A. de la Torre), crymarihe@hotmail.com (M. Rivero), gama10kh@hotmail.com (G. Camacho), alzmarquez@hotmail.com (L.A. Álvarez-Márquez).

<https://doi.org/10.1016/j.jnc.2017.10.004>

Received 1 September 2017; Received in revised form 12 October 2017; Accepted 24 October 2017
1617-1381/© 2017 Elsevier GmbH. All rights reserved.

species ranged from southern Mexico to northern Colombia (García et al., 2016; Schank et al., 2015). However, its distribution has been reduced drastically to 50% of its original range in the past 30 years (García et al., 2016). The current distribution of this species is limited to large remnants of tropical rainforest, cloud forest, and swamp forest at elevations from sea level to 3600 m above the sea level (m.a.s.l.) (García et al., 2016; Gonzalez-Maya et al., 2009; Naranjo, 2009; Naranjo, Amador-Alcalá, & Reyna-Hurtado, 2015). The main threats to this species are the direct persecution for subsistence hunting, habitat destruction, and habitat fragmentation (Cove et al., 2013; García et al., 2016; Naranjo, 2009; Naranjo et al., 2015). Furthermore, information on the ecology and behavior of the species is limited. Most of the research focused on Baird's tapir has aimed to understand its abundance, habitat use, and feeding ecology (Bolaños-Citalán & Naranjo, 2001; Carbajal-Borges, Godínez-Gómez, & Mendoza, 2014; Carrillo-Reyna & Reyna-Hurtado, 2015; Gonzalez-Maya et al., 2009; Naranjo, 2009; Naranjo et al., 2015; Naranjo & Bodmer, 2002; O'Farrill, Calmé, Sengupta, & Gonzalez, 2012; O'Farrill, Galetti, & Campos-Arceiz, 2013; Pérez-Cortez, Enríquez, Sima-Panti, Reyna-Hurtado, & Naranjo, 2012; Reyna-Hurtado & Tanner, 2005; Tobler, 2002). However, it is essential that we improve our knowledge of the distribution and abundance of this species so that we can design sound conservation programs (Cove et al., 2013; Naranjo, 2009).

One of the most important populations of Baird's tapir occurs in the Sierra Madre de Chiapas (SMC) region, Mexico (García et al., 2016; Naranjo, 2009; Naranjo et al., 2015). The main threats to this species in the SMC are habitat loss and fragmentation, poaching, fires, and road construction (Naranjo, 2009). For this reason, understanding the factors that promote tapir occupancy is essential to develop proper conservation plans to ensure its persistence in this increasingly human-dominated landscape (Cove et al., 2013). Previous studies have shown that tapirs are less abundant in areas with higher human density (Gonzalez-Maya et al., 2009; Tobler, 2002). Although, Baird's tapir occupies a great variety of vegetation types throughout its range, such as tropical rainforest, mangroves, wet grasslands, arid scrub, and pine-oak forest, tapirs prefer primary and secondary vegetation types, and they avoid areas that are modified by human activity (Cove et al., 2013; Naranjo, 2009).

In this study, we determine the factors that promote occupancy of Baird's tapir in the SMC, with the aim of recognizing areas of suitable habitat for the species in the region and the critical areas that are needed to maintain connectivity of populations within this landscape. We propose a conservation strategy for the species that incorporates a more realistic and detailed scheme of tapir occurrence in the SMC region. This study is the first to propose a spatially explicit strategy to conserve a population of Baird's tapirs over the long term. Because tapirs prefer areas with natural cover as their primary habitat, and they avoid areas with high human density (Ferreguetti, Tomas, & Bergallo, 2017; Gonzalez-Maya et al., 2009; Mendoza et al., 2013; Tobler, 2002), we predicted that tapir occupancy would be higher in areas with high forest cover and in areas that were far from human activity. Because Baird's tapirs are relegated to areas of high elevation and isolated habitats in areas of high persecution and habitat destruction (Gonzalez-Maya et al., 2009; Tobler, 2002), we predicted that tapir occupancy in the SMC region would be higher in areas with higher elevation and rugged terrain.

2. Methods

2.1. Study area

The SMC is located in the state of Chiapas, and it is one of the richest regions for biodiversity in Mexico. The study was carried out in the Natural Resources Protection Area La Frailesca (NRPAF). This area is located in the complex of the SMC, between two Biosphere Reserves, El Triunfo and La Sepultura. The NRPAF was established in 1979, and it is

the largest protected area (1775 km²) of the SMC complex (SEMARNAT, 2007). The terrain is rugged and steep with elevations that range from 280 to 2100 m.a.s.l. The climate is tropical to subtropical with a rainy season from May to October. The mean temperature ranges between 22° to 26 °C, with a mean annual rainfall between 1200 to 2000 mm in the mid and low altitudes, and 4000 mm in the highest altitudes (CEIEG, 2010). This region contains tropical rain forests, mountain cloud forests, pine and oak forests, and tropical deciduous forests (Vazquez-Bautista, 2002; Pérez-Farrera et al., 2006). In this area at least 13 large-medium sized mammal species coexist, which include four ungulate species (*T. bairdii*, *Mazama temama*, *Odocoileus virginianus*, and *Pecari tajacu*) and felids such as jaguars (*Panthera onca*) and puma (*Puma concolor*) (Vazquez-Bautista, 2002).

The land tenure in the NRPAF is under control of small landowners and the ejidos, which are peasant communities that are owners of large expanses of land in this area and who have access to sections of land for farming; they also maintain other areas of land mainly for forest conservation (CEIEG, 2010). Subsistence hunting and habitat loss are the main threats for wildlife in the SMC, especially for large mammals.

2.2. Community training

To have effective conservation actions that have positive impacts on wildlife species and ecosystems, it is essential to have the engagement and participation of local communities, especially those that are related to wildlife monitoring and surveillance activities. For this, we implemented two training workshops focused on the camera trapping technique where 35 people participated from six different local communities. In these workshops, participants were trained in basic concepts of biological monitoring, use of GPS, observation and collection of mammal tracks and sign, and the basic concept of camera trap deployment and data analysis. The main aim of these workshops was to form a trained group of local people with skills to implement the biological monitoring program for large mammals in the NRPAF. In addition to these monitoring activities, this group conducted surveillance on the most important trails to reduce illegal activities such as poaching.

2.3. Camera trap surveys

To document tapir occupancy, we deployed a set of 55 camera trap stations with the help of a trained group of local people in an approximately area of 400 km² (Fig. 1). We conducted camera trap surveys from August 2015 to December 2016. Distance between the camera trap stations ranged from 385 to 3373 m, and the mean distance between them was 1073 m (\pm 753 m SD). Since the radius of Baird's tapirs home range in Yucatan Peninsula is around of 3.5 km (estimated home range 39.8 km² – Reyna-Hurtado, Sanvicente-López, Pérez-Flores, Carrillo-Reyna, & Calmé, 2016), we assumed that those tapirs that had their home range center no further than 3.5 km from the camera trap stations could be detected by the camera traps. Sampling effort for each camera trap station varied; stations were active from one month (34 days) to 15 months (452 days). The final sampling effort was 9274 trap days. Camera trap stations were placed at sites where tapir signs (tracks and scat) were observed previously, such as trails in the forest, ponds, and river drainages, or in similar sites to these sites. Because camera trap stations were deployed to maximize tapir detections, we assumed that all camera traps had a similar bias to detect the species.

2.4. Landscape covariates

We compiled a geospatial dataset using a suite of environmental and anthropogenic covariates for our study area (Table 1). For all these explanatory covariates, we first generated raster layers of 30 m of resolution (Table 1). Given that multi-scale models often yield better

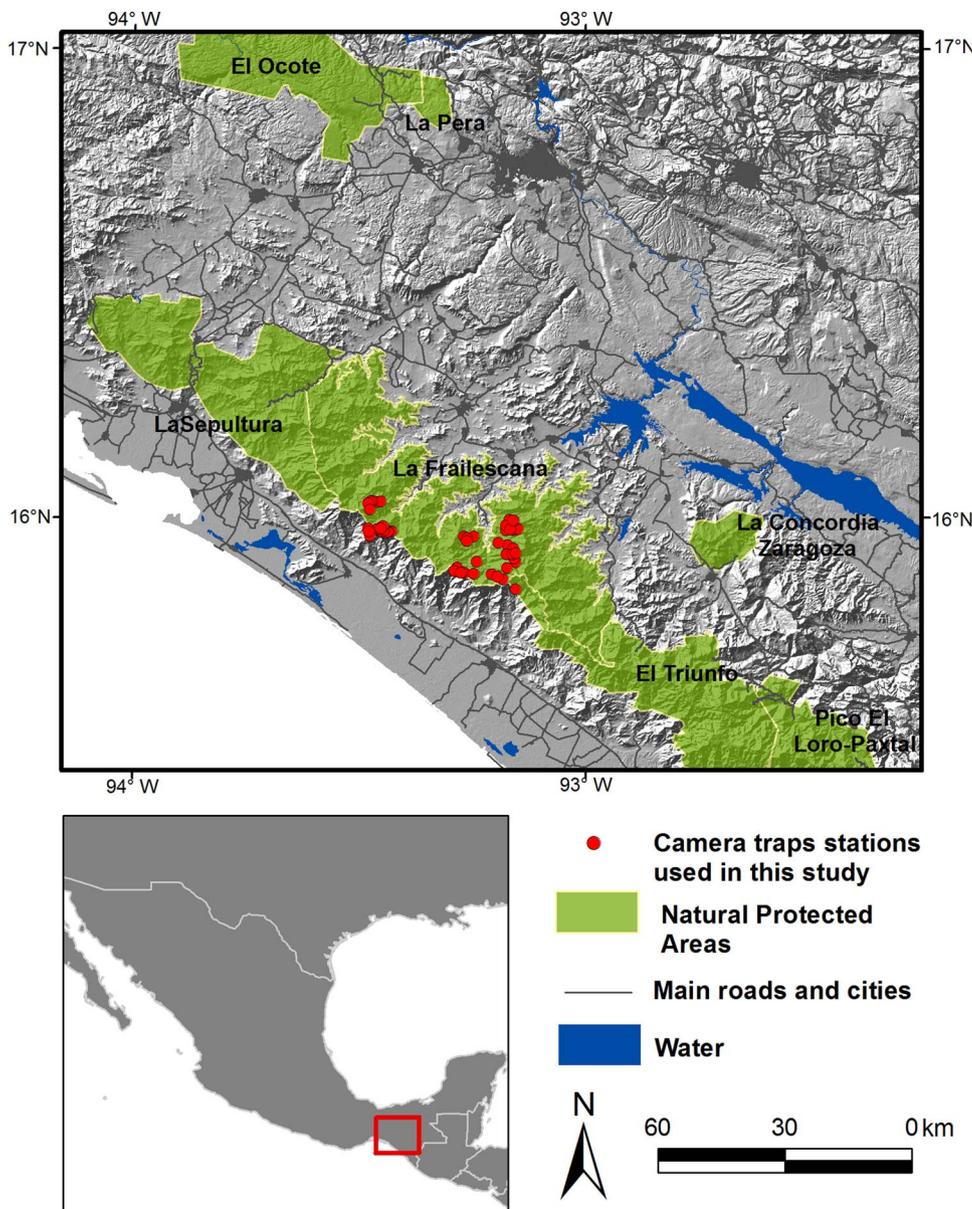


Fig. 1. Location of our study area in the Sierra Madre de Chiapas. The red points represent the localization of the camera trap stations used in this study. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

predictions than single scale models (Grand, Buonaccorsi, Cushman, Griffin, & Neel, 2004; Mateo-Sánchez et al., 2015; Zeller et al., 2016), we evaluated all variables at four spatial scales using circular moving windows with radii of 90 m, 240 m, 510 m, and 1020 m. For this, we used the Focal Statistic tool of ArcGIS 10.2 (ESRI, 2013). This allowed us to obtain an output raster where the value for each output cell was a mean function of the values of all the input cells that were in a specified neighborhood around that location. For creating the raster layers at 90, 240, 510, and 1020 m radii, the original 30 m pixel values were used with the focal mean of 3, 8, 17, and 34 pixels per window, respectively, around each sample location.

2.5. Occupancy models

Tapir detection histories were developed based on photographic records, where 1 represented when the species was detected in a specific day in a specific camera trap station, and 0 represented no detection. Because collapsing sampling periods increased the temporal independence among occasions and increased overall detection probability (Dillon & Kelly, 2007; Tan et al., 2017), we used 15 days as a sampling period. This period length was reasonable, because tapirs

appeared to cycle through their home range every 10–12 days (Jordan, 2015). We extracted the values of the landscape covariates for each camera trap location, and all explanatory covariates were rescaled by subtracting the mean from each variable value and then dividing them by the standard deviation. We tested the covariates for multicollinearity using Pearson’s correlation matrix (STATS package, R 3.1.1). We did not include covariates in the same candidate model that were correlated at > 0.5.

We estimated detection probabilities (p) by sampling on 35 occasions, and we used a single season model. Because Baird’s tapirs show a slow reproductive cycle (approximately a 400-day gestation period), we assumed that the local population was closed throughout the entire sampling period (Jordan, 2015). We used closed occupancy models, and we assumed that occupancy status (Ψ) of the tapirs in our study area was constant (Mackenzie et al., 2002, 2006). In our occupancy analysis, we assessed the covariates that might affect occupancy (Ψ) and detectability (p) to identify tapir habitat preferences and any sources of bias when detecting the species through the camera trapping technique. For models that included variation in occupancy, our first step was to evaluate the most informative scale (90, 240, 510, 1020 m) for each covariate using single-species, single-season occupancy

Table 1
Landscape covariates used to evaluate and predict the occupancy of Baird's tapirs in the Sierra Madre de Chiapas landscape.

Type	Variable name	Abbreviation	Description	Units	Justification
Forest cover	Forest Cover	FCov	Percentage of forest coverage around the pixel	%	Baird's tapirs are restricted mostly to areas of primary forest (Naranjo, 2009; Pérez-Cortez et al., 2012; Tobler, 2002). To appraise habitat quality, we used a High Resolution Global Forest map (Hansen et al., 2013). Given that the High Resolution Global Forest layer allowed the user to set a threshold percentage of tree cover that was to be considered as forest, we additionally used threshold values of 75% and 90% of tree cover to generate raster layers as a proxy of primary forest for our study area.
	Primary forest (> 75% of forest cover)	PFor75	Amount of primary forest (> 75%) around each pixel	count	
	Primary forest (> 90% of forest cover)	PFor90	Amount of primary forest (> 90%) around each pixel	count	
Terrain	Topographic Position Index	TPI	Classification of landscape according the slope position within a different radius. This index incorporated richness and evenness into a single measure.	–	Tapirs are affected by different terrain conditions. For instance, occupancy of tapirs was higher in areas of high topographic complexity, especially if flat areas of suitable habitat had been cleared (Gonzalez-Maya et al., 2009). However, tapirs are frequently associated with lowland areas (Naranjo, 2009; Tobler, 2002). Topographic Position Index was used to characterize the slope's position in the terrain and landform. This index incorporated richness and evenness into a single measure. Using a 30 m digital elevation model, we obtained elevation ranges. Shannon Index was used to evaluate differences in heterogeneity for ruggedness. In general, higher values reflected more diversity and a better balance among unique landform values (Riley, DeGloria, Elliot, 1999).
	Elevation	ELE	Elevation	m.a.s.l.	
	Shannon Topographic Index	SHAN	Differences of ranges of elevation values within a different radius.	–	
Human	Distance to towns	DistT	The minimum distance to the nearest town	km	Human activity and persecution affect habitat use by tapirs negatively due to disturbance and persecution (Cruz et al., 2014; Ferreguetti et al., 2017; Naranjo, 2009). Information of towns and roads was obtained from INEGI (Instituto Nacional de Estadística e Informatica). To evaluate the distances used by tapirs from the boundaries that separated the forest from open modified areas, we used raster layer with the minimum distance to the nearest deforested patches < 0.5 km ² given that the average size of the cleared areas that had been transformed to create grassland for livestock and crops is 0.5 km ² in our study area (equivalent to 50 ha).
	Density of towns	DENT	Density of towns around each pixel using a radio of 3.5 km, which is equivalent to the radius of the home range of Baird's tapirs (Reyna-Hurtado et al., 2016)	count	
	Distance to paved roads	DistR	The minimum distance to the nearest paved roads	km	
	Distance to deforestation edge	DistD	The nearest distance to the deforested patch > 0.5 km ²	km	

models. For models that considered variation in detectability, we used the landscape covariates at the 90 m scale. Additionally, we used the covariates season of the year (SEASON) and the number of active days of the camera trap stations (EFFORT) in the models that included variation in detectability.

We constructed a set of 201 candidate models based on different approaches: a) assuming occupancy and detectability were constant across all sites (null model); b) assuming variation in detectability was a function of covariates; for this we modeled detection probability by allowing the occupancy parameters to remain constant (*p*); c) assuming variation in occupancy (Ψ) was a function of covariates; for this we constructed models with all possible combinations of uncorrelated site covariates, and we considered covariates that had the strongest influence on occupancy were those that attained summed model weights (importance) > 50%; d) assuming that there were variations in both detectability (*p*) and occupancy (Ψ) as a function of covariates; for this we used only the detection covariates that contributed significantly and the occupancy covariates with highest importance values.

Occupancy modeling was performed using Unmarked package for R 3.1.1 (R script A.1), and using the logit link, and using 2000 bootstraps to assess the adjustment fit (*P*) (Fiske et al., 2017; R Core Team, 2016). For the best models, we considered independent variables with confidence intervals that did not include 0 to be informative predictors. Then, we used the Akaike Information Criterion corrected for small sample sizes (AICc) to identify the best occupancy models based on model parsimony (Burnham & Anderson, 2002). We considered models comparable if $\Delta AICc$ was < 2.0, and we compared the AICc weights (*w_i*) to determine the most appropriate models that described the occupancy of the tapirs in our study area.

2.6. Patches occupied by tapirs in the Sierra Madre de Chiapas

We applied our best occupancy model to ArcGIS10.2 using the Raster Calculator Tool (ESRI, 2013) to calculate the probability of tapir occupancy for each cell (30 m pixel). To identify the suitable area to be occupied by tapirs in the SMC, we identified the optimal threshold at which to discriminate occupied sites from non-occupied sites by calculating the Receiver Operating Characteristic (ROC) of our best occupancy model (Pearce & Ferrier, 2000). To implement the ROC analysis, we used a database of 80 records of Baird's tapir which included records from biological data-bases (National System of Information on Biodiversity-CONABIO-Mexico), and also records collected through signs (tracks and scat) and camera traps obtained by other researchers and ourselves (Mendoza et al., 2013). We did not include our camera trap records in this database and this database included records that were obtained within the SMC during 2007–2015. We implemented the ROC analysis using the package “pROC” (Robin et al., 2013) from R 3.1.1 (R Core Team, 2016).

We converted the raster data set of occupancy into polygons using the ArcGIS10.2, and we calculated the surface area, perimeter ratios, and the center of each polygon. Given that the estimated home range area of tapirs in the Yucatan Peninsula was approximately 40 km² (the closest site from which this information was obtained) (Reyna-Hurtado et al., 2016), we identified all the polygons greater than this area. We assumed that these polygons were occupied by tapirs in the SMC, and these polygons were then treated as source habitat patches in our analysis of connectivity.

2.7. Mapping connectivity among patches

We integrated our occupancy model with Circuit Theory to assess the connectivity across the species' occurrence in the SMC (Lapoint, Gallery, Wikelski, & Kays, 2013; McClure, Hansen, & Inman, 2016; McRae, Dickson, Keitt, & Shah, 2008). Additionally, we evaluated the connectivity of the SMC to other important tapir populations that were located in the Ocoté Biosphere Reserve (Naranjo, 2009; Naranjo et al.,

2015). Circuit Theory models the dispersal movements that identify high connectivity in areas that have a higher probability of being crossed by random walkers moving from a source to a destination, and several studies have proven that this approach is a more realistic approximation of dispersal movements than other analysis (Lapoint et al., 2013; McClure et al., 2016). We used the inverse of our best occupancy model surface to generate a resistance surface for the Circuit Theory analysis using reciprocal probability values. With this transformation, we assumed that pixels with higher probability values for tapir occupancy afforded lower costs to movement than those pixels with low occupancy values (Beier, Majka, & Spencer, 2008; Zeller, Mcgarigal, & Whiteley, 2012). We used Circuitscape version 4.0 to model the connectivity between the habitat patches using the pairwise scenario in which the analysis iterated all pairs in a focal node (McRae, Shah, & Mohapatra, 2013).

We generated a cumulative current map between each habitat patch (focal nodes) to identify the areas of high connectivity. Each current map was a continuous grid cell value of current flow, where current values were indicative of predicted movement of random walkers (Lapoint et al., 2013; Rudnick et al., 2012). Therefore, we identified potential corridors visually from current maps and extracted the cells with higher current values, which suggested the areas that had a high probability of tapir movements.

3. Results

3.1. Occupancy models

We obtained a total of 154 independent detections of tapirs, and we observed the species in 25 of the 55 sampling sites, which resulted in naïve occupancy of 0.45 and a detectability of 0.40. From the 201 occupancy models that we produced (Table 2), occupancy was best described by two covariates: 1) elevation (ELE-1020), which had a positive relationship because occupancy increased with increases in elevation ($\Psi = 0.05-0.84$; Fig. 2A) and 2) Shannon topographic index (SHA240), which had a positive relationship because occupancy of tapirs increased as the heterogeneity of the topography increased ($\Psi = 0.02-0.99$; Fig. 2B). On the other hand, detectability was affected by three covariates: 1) elevation (ELE-90), which had a positive

relationship to detectability ($p = 0.01-0.10$; Fig. 3A); 2) distance to deforested patches (DE90), which had a positive relation with the detectability since detectability increased with the distance to deforested patches increases ($p = 0.01-0.13$; Fig. 3B); 3) the number of days that each camera trap was active during each sampling period (EFFORT), in which the detectability increased as the sampling effort increased at each camera trap station ($p = 0.05-0.33$; Fig. 3C).

The best occupancy model only had a $\Delta AICc$ value of 1.57 for the second best ranked model ($w_i = 0.15$) (Table 2). The second ranked model included the covariates elevation (ELE-1020), Shannon topographic index (SHA240), and topographic position index (TPI90) but the variable topographic position index was not informative because the 95% CI overlapped 0. For this reason, we used the first ranked model to explain the occupancy of the Baird’s tapir in the Sierra de Chiapas.

3.2. Tapir occupancy in the Sierra Madre de Chiapas

According to our best occupancy model, the probability of tapir occupancy was correlated with the elevation and with the rugged terrain in the SMC (Fig.B.1). This indicated that areas with more suitable habitat for this species were the forested sites that were located in the highest parts of the mountain ranges with rugged terrain. Area under the ROC curve was 0.72 ($\pm 0.53, 0.85$) for true positives and 0.59 ($\pm 0.43, 0.86$) for false positives, which indicated a reasonable discrimination at a probability threshold of occurrence of 0.02 ($\pm 0.01, 0.19$). Occupancy area for tapirs in the SMC encompassed 4232 km² (the upper 0.02 of probability occupancy), and we identified three polygons greater than 40 km² where tapir presence had been recorded recently in the SMC (Table 3, Fig.B.2). However, only 3455 km² of the estimated occupancy area of Baird’s tapir in the SMC were areas that contained primary forest (Table 3).

3.3. Connectivity of tapir habitat in the Sierra Madre de Chiapas

We identified three critical corridors using Circuit Theory analysis to design a connectivity strategy for the tapir population in the SMC (Table 4; Fig. 4). These corridors allowed for connectivity between the three habitat patches that were identified previously, and provided

Table 2

The best 20 occupancy models and the null model for Baird’s tapir in the Sierra Madre de Chiapas, Mexico estimated by camera trapping between August of 2015 and December 2016, grouped in sampling intervals of 15 consecutive days. With (.) as constant and covariates = differences of ranges of elevation values with a radius of 8 pixels (SHA240); elevation at scales of 90 and 1020 m (ELE90, ELE1020), the nearest distance to the deforested patch > 0.5 km (DE90), the days that each camera trap was active during each sampling period (EFFORT), classification of landscape according to the slope position at a radius of 8 pixels (TPI90), amount of primary forest around each pixel (PFor75, PFor90), percentage of forest coverage at scales of 90 and 1020 (C90, C1020), and season of the year (SEASON). Ψ = occupancy, p = detectability, and the adjustment fit (P) = 0.21.

Rank	Moldel	AICc	$\Delta AICc$	w_i	Number of parameters
1	$\Psi(\text{SHA240} + \text{ELE1020}); p(\text{DE90} + \text{ELE90} + \text{EFFORT})$	506.00	0.00	0.33	7
2	$\Psi(\text{SHA240} + \text{ELE1020} + \text{TPI90}); p(\text{DE90} + \text{ELE90} + \text{EFFORT})$	507.50	1.57	0.15	8
3	$\Psi(\text{SHA240} + \text{ELE1020} + \text{PFor75}); p(\text{DE90} + \text{ELE90} + \text{EFFORT})$	508.50	2.48	0.10	8
4	$\Psi(\text{SHA240} + \text{ELE1020} + \text{C1020}); p(\text{DE90} + \text{ELE90} + \text{EFFORT})$	508.60	2.61	0.09	8
5	$\Psi(\text{SHA240}); p(\text{DE90} + \text{ELE90} + \text{EFFORT})$	509.00	2.99	0.08	6
6	$\Psi(\text{SHA240} + \text{C1020}); p(\text{DE90} + \text{ELE90} + \text{EFFORT})$	509.40	3.47	0.06	7
7	$\Psi(\text{SHA240} + \text{TPI90}); p(\text{DE90} + \text{ELE90} + \text{EFFORT})$	509.50	3.55	0.06	7
8	$\Psi(\text{SHA240} + \text{PFor}); p(\text{DE90} + \text{ELE90} + \text{EFFORT})$	510.70	4.75	0.03	7
9	$\Psi(\text{C1020} + \text{ELE1020} + \text{TPI90} + \text{SHA240} + \text{RIO1020} + \text{PFor90} + \text{PFor75}); p(\text{DE90} + \text{ELE90} + \text{EFFORT})$	513.00	7.03	0.01	12
10	$\Psi(\text{ELE1020}); p(\text{DE90} + \text{ELE90} + \text{EFFORT})$	517.50	11.51	0.001	6
11	$\Psi(\text{ELE1020}); p(\text{DE90} + \text{ELE90} + \text{EFFORT})$	517.90	11.90	0.001	7
12	$\Psi(\text{TPI90} + \text{ELE1020} + \text{PFor75}); p(\text{DE90} + \text{ELE90} + \text{EFFORT})$	518.60	12.61	0.001	8
13	$\Psi(\text{ELE1020} + \text{TPI90}); p(\text{DE90} + \text{ELE90} + \text{EFFORT})$	518.90	12.91	0.001	7
14	$\Psi(\text{ELE1020} + \text{PO1020}); p(\text{DE90} + \text{ELE90} + \text{EFFORT})$	519.00	13.04	< 0.001	7
15	$\Psi(.); p(\text{DE90} + \text{ELE90} + \text{EFFORT})$	521.40	15.46	< 0.001	5
16	$\Psi(.); p(\text{EFFORT} + \text{C90} + \text{ELE90} + \text{DE90})$	523.90	17.92	< 0.001	6
17	$\Psi(\text{C1020} + \text{DE1020}); p(\text{DE90} + \text{ELE90} + \text{EFFORT})$	524.30	18.35	< 0.001	7
18	$\Psi(\text{C1020} + \text{CAR1020}); p(\text{DE90} + \text{ELE90} + \text{EFFORT})$	524.70	18.73	< 0.001	7
19	$\Psi(.); p(\text{C90} + \text{ELE90} + \text{TPI90} + \text{SHA90} + \text{DE90} + \text{PFor75} + \text{PD90} + \text{SEASON} + \text{EFFORT})$	529.70	23.68	< 0.001	11
20	$\Psi(.); p(\text{EFFORT} + \text{C90} + \text{ELE90} + \text{DE90})$	533.00	26.98	< 0.001	4
152	$\Psi(.); p(.)$	587.82	84.23	< 0.001	2

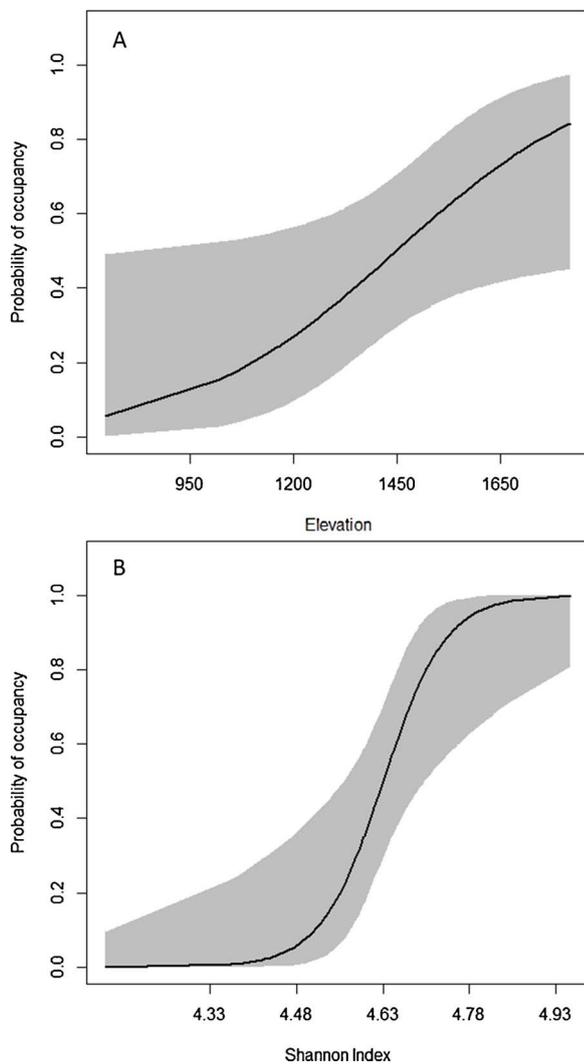


Fig. 2. Relationship between occupancy by Baird’s tapir in the Sierra Madre de Chiapas and A) the elevation (ELE1020); and B) the Shannon topographic index (SHA240).

connectivity between the SMC tapir population with that in the Ocote Biosphere Reserve. Triunfo & Frailescana-Sierra Morena (Fig. 4) is the only corridor that was protected by a Natural Protected Area (La Sepultura Biosphere Reserve). Meanwhile, the corridor Jaltenango-Triunfo & Frailescana (a) was completely unprotected (Fig. 4). Although Sierra Morena-El Ocote was the corridor that connected the SMC with the Ocote Biosphere Reserve through the Chimalapas region in Oaxaca, it was only partially protected by the Sepultura Biosphere Reserve

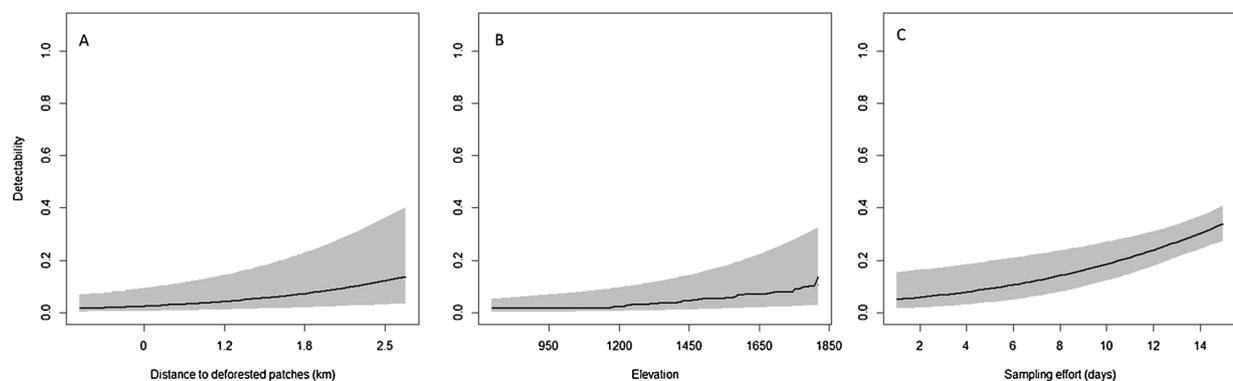


Fig. 3. Relation between detectability of Baird’s tapir and A) the distance to deforested patches > 0.5 km²(DE90); B) elevation (ELE90); and C) sampling effort measured by the number of active days for camera trap stations grouped in sampling intervals of 15 consecutive days (EFFORT).

Table 3

Baird’s tapir habitat patches in the Sierra Madre de Chiapas, their total percentage of primary forest, and the percentage that is protected.

Habitat patche name	Total area covered (km ²)	Area covered with primary forest (km ²)	Percentage of area protected (km ²)
1. Sierra Morena	49.2	34.06 (69%)	43.2 (87%)
2. El Triunfo & Frailescana	4,081. 2	3,324.6 (81%)	2,411.9 (59%)
3. Jaltenango	107.9	96.1(89%)	0 (0%)

(Fig. 4). Our analysis revealed that all potential corridors that we identified were partially covered with primary forest, which indicated that they would likely be used by tapirs (Table 4). However, all these corridors were crossed by paved or dirt roads 1–4 times, which suggests that roads could be a severe threat to maintain the connectivity in the SMC landscape (Table 4).

4. Discussion

We used occupancy models to identify suitable habitat for Baird’s tapir to establish conservation priorities for the species in the SMC. This is the first study to propose priority conservation areas and corridors for the species that integrates occupancy models and landscape information at a local scale. Our results showed that the landscape variables that best describe occupancy of Baird’s tapir in the SMC were elevation and the heterogeneity among the landform terrain (Shannon Topographic Index), which indicated that the higher sites in the mountains with rugged and hilly terrain were more suitable for the species. On the other hand, elevation, distance to deforested patches, and sampling effort were the best covariates to predict the detectability of Baird’s tapirs.

These results supported our predictions that tapir occupancy was positively associated with higher elevations and rugged terrain. In this case, our results suggested that Baird’s tapir were limited to the most remote and inaccessible sites of the SMC as a consequence of their high persecution by subsistence hunting and habitat destruction due to colonization of the region (Ferreguetti et al., 2017; Gonzalez-Maya et al., 2009; Naranjo, 2009; Tobler, 2002). Despite the fact that the species is enlisted as Endangered by the Mexican NOM-59 and is protected by the Mexican Federal Government (SEMARNAT, 2010), poaching is still a common practice in the SMC (Naranjo, 2009); we documented two cases of tapir poaching in the Frailescana Natural Reserve. Other studies carried out with other species of tapirs (*Tapirus terrestris*) have shown that occupancy and abundance of this species is correlated negatively with the level of poaching (Cruz, Paviolo, Bó, Thompson, Di Bitetti, 2014; Fa, Peres, & Meeuwig, 2002; Ferreguetti et al., 2017; Peres, 2000).

Table 4

Baird’s tapir corridors in the Sierra Madre de Chiapas and their total percentage of primary forest, percentage protected, and number of paved roads that cross the corridors.

Habitat patche name	Total area covered (km ²)	Area covered with primary forest (km ²)	Percentage of area protected (km ²)	Number of paved roads that corridor cross
a. Jaltenango-Triunfo & Fraileskana	46.6	36.1 (77%)	7.9 (16%)	2
b. Triunfo & Fraileskana-Sierra Morena	35.8	19.0 (53%)	35.8 (100%)	3
c. Sierra Morena-El Ocote	1,245.6	811.3 (65%)	75.9 (6%)	2

The covariates related to forest cover (FCov, PFor75, PFor90) were not included in the best candidate occupancy models, although forests were maintained within this landscape at higher elevations (Table 3). Meanwhile, sites in the SMC which encompassed elevations below 900 ma.s.l. were deforested almost completely. According to our results, Baird’s tapirs occupied 3455 km² of area that was covered with forest. If we extrapolate the density estimations for Baird’s tapirs, which were obtained for the SMC (lower 0.07/km², upper 0.12/km² – Carbajal-Borges et al., 2014; Lira-Torres et al., 2004), to our estimation of occupancy area, the population size of this species in the SMC could be 241 – 414 individuals. However, this extrapolation should be considered cautiously, especially because these density estimates were obtained from localized sites, and because there could be areas within the SMC landscape where tapirs have been extirpated completely by poaching. To obtain a more realistic population estimate in the SMC, it is essential to have reliable density estimates of Baird’s tapirs in several sections of the SMC using a standardized protocol.

Several studies carried on in other regions have documented that the occupancy of tapirs is associated with areas near water (Ferregueti et al., 2017; Pérez-Cortez et al., 2012). In this study, we did not evaluate the association of Baird’s tapirs with the main water sources in our study area, but the main rivers and other water sources are mostly limited to lowland areas, and the occupancy models indicated clearly that tapirs were not associated with these areas. Though, sites at higher altitudes within the mountains in the SMC were covered by mountain

cloud forest, which retain moisture almost the entire year due to the horizontal rain that originates from the breeze that comes from the Pacific Ocean. Although, we have found some ponds at the top of the mountain ranges that contained water all year that were used by tapirs. Baird’s tapirs used sites closest to water as places for resting, defecation, or cooling off during the hottest hours of the day and to prevent ectoparasites (Algers, Vaughan, & Foerster, 1998; Martinez, 2016; Naranjo, 1995; Terwilliger, 1978).

The elevation and the distance to deforested patches also may influence the detectability of Baird’s tapir in the SMC. The high degree of human activity in the lowlands could be associated with the lowest rates of occupancy and detectability of tapirs. Additionally, detectability of tapirs increased as the distance to deforested patches increased, which indicated that tapirs avoided the sites nearest to deforested patches. Tapirs prefer habitat with cover forest, and they usually avoid areas with human activity (Cove et al., 2013; Foerster et al., 2008; Naranjo, 2009; Tobler, 2002). All deforested patches in our study area were associated with human activity, and these areas included cropland, open pastures for livestock, and sites near roads and towns. In these areas, Baird’s tapirs were more vulnerable to poaching, and other studies have shown that tapirs and other ungulate species avoided areas with higher hunting activity (Cruz et al., 2014; Espinosa et al., 2014; Ferregueti et al., 2017). Furthermore, detectability of Baird’s tapirs increased as the number of effective sampling days increased (Si, Kays, & Ding, 2014).

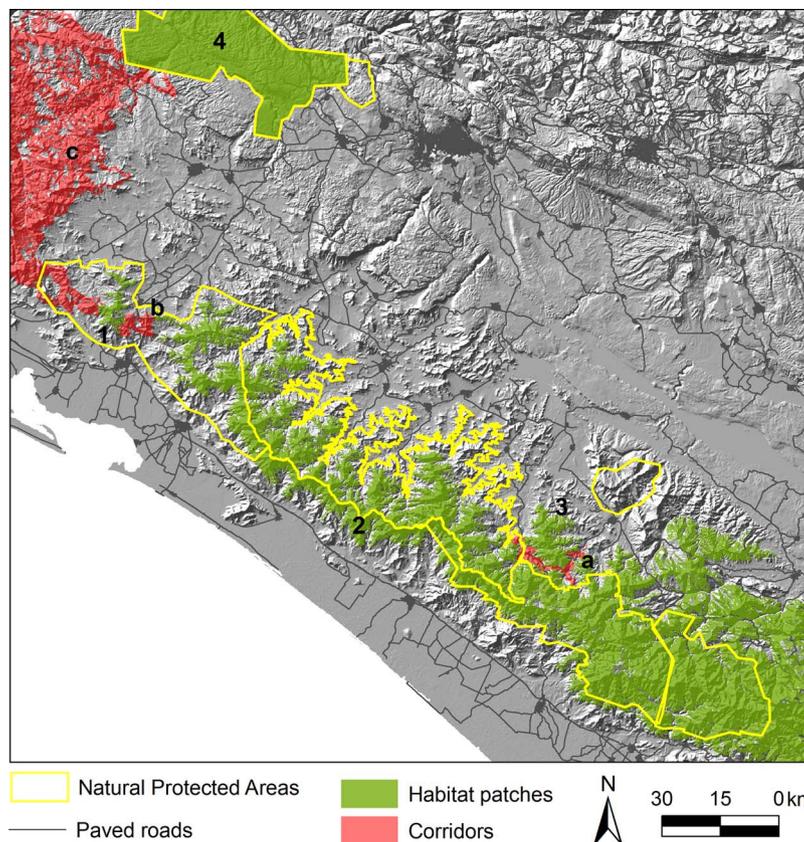


Fig. 4. Focal habitat patches (1. Sierra Morena; 2. Triunfo & Fraileskana; 3. Jaltenango; 4. El Ocote) and corridors (a. Jaltenango-Triunfo & Fraileskana; b. Triunfo & Fraileskana-Sierra Morena; c. Sierra Morena-Ocote) identified that link the Baird’s tapir population in the Sierra Madre de Chiapas.

We identified three patches of suitable habitat for Baird's tapirs and three priority corridors to maintain the viability of this population in the SMC. Most of the potential habitat for the species in the region is protected by the Selpultura Biosphere Reserve, the NRPAF, and the El Triunfo Biosphere Reserve. These are protected areas administrated by the Mexican Federal Government, and by the Pico del Oro Pascal Reserve which is a protected area administrated by the Government of Chiapas (Table 3). These natural reserves protect approximately 2455 km² of potential habitat for tapirs in the region (58%), and these areas should be the core of the species' conservation policy and practice in the SMC. However, there are some gaps in the protection of the key habitat for tapirs. For instance, next to the NRPAF, there is a large tract of potential habitat for tapirs that is unprotected, and there is another unprotected habitat patch next to the El Triunfo Natural Reserve that could provide 107 km² for tapirs (Table 3; Fig. 4). The protection of these areas is important to ensure the integrity of this ecosystem and to maintain the long term conservation of Baird's tapir in the region. However, if deforestation and human colonization increase in these areas, conservation of tapirs and other species in the region would be compromised.

We identified three crucial areas to maintain the connectivity for Baird's tapir population in the SMC. However, all these corridors are crossed by dirt and paved roads that interrupt the connectivity between suitable habitat areas. This indicates that the integrity of the SMC landscape could be threatened by the interruption of the connectivity by roads (Fig. 4). The corridor that connects the largest habitat patch with Sierra Morena is interrupted by paved roads MEX-200 and MEX-190, and the corridor that connects Sierra Morena with the Ocote Biosphere Reserve is interrupted by paved road MEX-190 in one location (Fig. 4). Roads increase mortality by collisions, facilitate access to prime tapir habitat by humans, and accelerate habitat fragmentation (Colchero et al., 2011; Conde et al., 2010; Contreras-Moreno, Hidalgo-Mihart, Pérez-Solano, & Vázquez-Maldonado, 2013; Cullen et al., 2016; Espinosa et al., 2014).

4.1. Implication for conservation

We present a proposal to specifically maintain the connectivity for Baird's tapirs in the SMC. Thus, this information should guide conservation and development agencies, and decision makers, that are involved in this region to direct conservation efforts to the most vulnerable sites identified by this study. One priority action is to ensure the complete protection of suitable areas for tapirs in this region. Our analysis suggested that most of the potential habitat for the species in the SMC is protected. However, some areas next to NRPAF and El Triunfo Biosphere Reserve should be incorporated into the conservation strategy of the region in conjunction with the local communities to guarantee its long term persistence. This could be achieved by implementing Payments for Ecosystem Services (PES) in communities that maintain tapir habitat or critical areas for connectivity. The PES is a conservation scheme used by the Mexican Government that provides economic compensation to local communities for conserving their land with natural forest. Two of the corridors identified in this analysis still contain significant amounts of primary forest. This implies that an urgent action to maintain the connectivity for Baird's tapirs should be the conservation of primary forest and habitat restoration in cleared areas. These actions are decisive to ensure long term connectivity for this population of tapirs. To improve the connectivity in the region, it is necessary that corridors for tapirs that cross paved roads include mitigation measures to avoid wildlife collisions. Mitigation measures to reduce collisions should include the construction of wildlife crossings, and installation of road signs and speed bumps.

Another fundamental component for the long term conservation of tapirs in the SMC is the involvement and participation of local communities in wildlife monitoring and surveillance activities. Since 2016, a group of 35 persons have been trained in the use and management of camera traps and collection of tapir spoor. Currently, this group of

people is identified by the local communities of the region as the volunteer community monitors of Baird's tapir in NRPAF. Their participation in these activities encourages local communities to understand the importance of having a monitoring program within their lands. Their participation allows for closer communication between communities and reserve administrators, and it promotes the protection of wildlife species and conservation of their habitats by the inhabitants of the communities.

Finally, one of the main threats for the species in the region is poaching by subsistence hunters (Naranjo, 2009). One critical need for conserving this population of Baird's tapirs over the long term is to work in conjunction with local communities to establish an agreement to ban completely the poaching of tapirs in the SMC. The first step was done in December 14th of 2016 when the administration of the NRPAF and Bioconciencia A. C. signed an agreement with 14 local communities (ejidos), which are located within NRPAF, to completely prohibit poaching of Baird's tapir within their lands. This agreement is a great advancement toward the conservation of Baird's tapir in the SMC. Because of the commitment of these local communities, there may be a future for this species in the SMC, but it is crucial to extend this effort to ensure the persistence of one of the most charismatic species of southern Mexico.

Acknowledgements

We greatly appreciate the financial support of the Conservation Program of Endangered Species (PROCER-Mexico) of the National Commission of Protected Areas (CONANP-Mexico). We would like to thank our field assistants from the NRPAF for their help and hard work. We are very grateful to the administration of NRPAF (CONANP-Mexico), especially to S. Nañez and R. Diaz-Velazquez, for supporting this research. We thank SNIB-CONABIO for providing valuable information for this study. We thank R. A. Medellín and all the members of the Laboratory of Ecology and Conservation of Terrestrial Vertebrates of the Institute of Ecology UNAM for their technical support, especially to A. Ibarra and P. Arroyo. We would also like to thank to L. Garcia-Gutierrez for their assistance during field work. Throughout the analysis, we had the assistance of the Centro de Investigación en Geografía y Geomática "Ing. Jorge L. Tamayo A.C.", and we especially thank J. M. Nuñez. We would like to thank T. A. Gavin, Professor Emeritus, Cornell University, for help with editing the English in this paper. We are very thankful to the following communities of the Frailesca region for their commitment to the conservation of Baird's tapirs: San Pedro Buenavista, Ocotal Maravillas, San Marcos, La Nueva Unión, Francisco Murguía, Ignacio Zaragoza, Plan de Ayala, San Juan de los Ángeles, Reforma Agraria, La Unión, Joaquín Miguel Gutiérrez, 24 de Febrero, Tierra Santa, and Belisario Domínguez. This work was supported by the Conservation Program of Endangered Species (PROCER-Mexico) of the National Commission of Protected Areas (CONANP-Mexico), The Natural Resources Protection Area La Frailesca, and Bioconciencia A.C. We appreciate the helpful comments of two anonymous reviewers.

References

- Algers, S., Vaughan, C., & Foerster, C. R. (1998). Resting site microhabitat selection by *Tapirus bairdii* during the dry season in Corcovado National Park, Costa Rica. *Vida Silvestre Neotropical*, 7, 136–138.
- Beier, P., Majka, D. R., & Spencer, W. D. (2008). Forks in the road: choices in procedures for designing wildland linkages. *Conservation Biology*, 22(4), 836–851. <http://dx.doi.org/10.1111/j.1523-1739.2008.00942.x>.
- Bolaños-Citalán, J. E., & Naranjo, E. J. (2001). Abundancia: Densidad y distribución de las poblaciones de ungulados en la cuenca del río Lacantún. *Revista Mexicana De Mastozoología*, 5, 45–57.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York: Springer-Verlag.
- CEIEG (2010). *Región VI. frailesca. Comité estatal de información estadística y geográfica de chiapas, gobierno del estado de chiapas*. Tuxtla Gutiérrez, Chiapas: Gobierno del Estado de Chiapas1–12.
- Carbajal-Borges, J. P., Godínez-Gómez, O., & Mendoza, E. (2014). Density, abundance

- and activity patterns of the endangered *Tapirus bairdii* in one of its last strongholds in southern Mexico. *Tropical Conservation Science*, 7(1), 100–114. <http://dx.doi.org/10.1177/194008291400700102>.
- Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., et al. (2005). Multiple causes of high extinction risk in large mammal species. *Science*, 309(5738), 1239–1241. <http://dx.doi.org/10.1126/science.1116030>.
- Carrillo-Reyna, N., & Reyna-Hurtado, R. (2015). Abundancia relativa y selección de hábitat de *Tapirus bairdii* en las reservas de Calakmul y Balam Kú, Campeche, México. *Revista Mexicana De Biodiversidad*, 86, 202–207.
- Colchero, F., Conde, D. A., Manterola, C., Chávez, C., Rivera, A., & Ceballos, G. (2011). Jaguars on the move: Modeling movement to mitigate fragmentation from road expansion in the Mayan Forest. *Animal Conservation*, 14(2), 158–166. <http://dx.doi.org/10.1111/j.1469-1795.2010.00406.x>.
- Conde, D. A., Colchero, F., Zarza, H., Christensen, N. L., Sexton, J. O., & Manterola, C. (2010). el al. Sex matters: modeling male and female habitat differences for jaguar conservation. *Biological Conservation*, 143(9), 1980–1988. <http://dx.doi.org/10.1016/j.biocon.2010.04.049>.
- Contreras-Moreno, F. M., Hidalgo-Mihart, M. G., Pérez-Solano, L. A., & Vázquez-Maldonado, Y. A. (2013). Nuevo registro de Tapir centroamericano (*Tapirus bairdii*) atropellado en el Noroeste del estado de Campeche, México. *Tapir Conservation*, 22(30), 22–25.
- Cove, M. V., Pardo Vargas, L. E., de la Cruz, J. C., Spínola, R. M., Jackson, V. L., Saénz, J. C., et al. (2013). Factors influencing the occurrence of the Endangered Baird's tapir *Tapirus bairdii*: potential flagship species for a Costa Rican biological corridor. *Oryx*, 48(3), 402–409. <http://dx.doi.org/10.1017/S0030605313000070>.
- Cruz, P., Paviolo, A., Bó, R. F., Thompson, J. J., & Di Bitetti, M. S. (2014). Daily activity patterns and habitat use of the lowland tapir (*Tapirus terrestris*) in the Atlantic Forest. *Mammalian Biology*, 79(6), 376–383. <http://dx.doi.org/10.1016/j.mambio.2014.06.003>.
- Cullen, L., Stanton, J. C., Lima, F., Uezu, A., Perilli, M. L. L., & Resit Akcakaya, H. (2016). Implications of fine-grained habitat fragmentation and road mortality for jaguar conservation in the Atlantic forest, Brazil. *Public Library Of Science*, 11(12), 1–17. <http://dx.doi.org/10.1371/journal.pone.0167372>.
- Dillon, A., & Kelly, M. J. (2007). Ocelot *Leopardus pardalis* in Belize: The impact of trap spacing and distance moved on density estimates. *Oryx*, 41(4), 469–477. <http://dx.doi.org/10.1017/S0030605307000518>.
- ESRI (2013). *ArcGIS desktop: release 10.2*. [Redlands CA].
- Espinosa, S., Branch, L. C., & Cueva, R. (2014). Road development and the geography of hunting by an Amazonian indigenous group: Consequences for wildlife conservation. *Public Library of Science*, 9(12), <http://dx.doi.org/10.1371/journal.pone.0114916>. [e114916].
- Fa, J. E., Peres, C. A., & Meeuwig, J. (2002). Bushmeat exploitation in tropical forests: an intercontinental comparison. *Conservation Biology*, 16(1), 232–237. <http://dx.doi.org/10.1046/j.1523-1739.2002.00275.x>.
- Ferreguetti, Á. C., Tomas, W. M., & de Bergallos, H. G. (2017). Density, occupancy, and detectability of lowland tapirs, *Tapirus terrestris*, in Vale Natural Reserve, south-eastern Brazil. *Journal of Mammalogy*, 98(1), 114–123. <http://dx.doi.org/10.1093/jmammal/gyw118>.
- Fiske, I., Chandler, R., Miller, J., Royle, A., Kery, M., Hostetler, D., et al. (2017). *Unmarked: models for data from unmarked animals. r* ($\geq 2.12.0$). [Retrieved from <https://cran.r-project.org/web/packages/unmarked/index.html>].
- Foerster, C. R., Vaughan, C., & Sep, N. (2008). Home range, habitat use, and activity of Baird's tapir in Costa Rica. *Biotropica*, 34(3), 423–437.
- García, M., Jordan, C., O'Farrill, G., Poot, C., Meyer, N., Estrada, N., et al. (2016). *Tapirus bairdii*. The IUCN red list of threatened species 2016: e.T21471A4517334013.
- Gonzalez-Maya, J. F., Schipper, J., & Rojas-Jiménez, K. (2009). Elevational distribution and abundance of Baird's tapir (*Tapirus bairdii*) at different protection areas in Talamanca region of Costa Rica. *Tapir Conservation*, 18(25), 29–35.
- Grand, J., Buonaccorsi, J., Cushman, S. A., Griffin, C. R., & Neel, M. C. (2004). A multiscale landscape approach to predicting bird and moth rarity hotspots in a threatened pitch pine-scrub oak community. *Conservation Biology*, 18(4), 1063–1077. <http://dx.doi.org/10.1111/j.1523-1739.2004.00555.x>.
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., et al. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, 342(6160), 850–853. <http://dx.doi.org/10.1126/science.1244693>.
- Jordan, C. A. (2015). *The dynamics of wildlife and environmental knowledge in a bioculturally diverse coupled natural and human system in the caribbean region of Nicaragua*. Doctor of Philosophy Thesis. Michigan State University.
- Kinnaird, M. F., Sanderson, E. W., Brien, T. G. O., Wibisono, H. T., & Woolmer, G. (2010). Deforestation trends in a tropical landscape and implications for endangered large mammals. *Conservation Biology*, 17(1), 245–257.
- Lapointe, S., Gallery, P., Wikelski, M., & Kays, R. (2013). Animal behavior, cost-based corridor models, and real corridors. *Landscape Ecology*, 28, 1615–1630. <http://dx.doi.org/10.1007/s10980-013-9910-0>.
- Lira-Torres, I., Naranjo, E. J., Güirris-Andrade, D. M., & Cruz-Aldán, E. (2004). Ecología de *Tapirus bairdii* (Perissodactyla: tapiridae) en la reserva de la biosfera el triunfo (Polígono I) chiapas, México. *Acta Zoológica Mexicana*, 20(1), 1–21.
- Mackenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when the detection probabilities are less than one. *Ecology*, 83(8), 2248–2255.
- Mackenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2006). *Occupancy Estimation and Modeling. Inferring patterns and dynamics of species occurrence*. New York, New York, USA: Academic Press [http://dx.doi.org/10.2981/0909-6396\(2006\)12\[450:OEAMIP\]2.0.CO;2](http://dx.doi.org/10.2981/0909-6396(2006)12[450:OEAMIP]2.0.CO;2).
- Martinez, W. E. (2016). *Abundancia relativa y ocupación del tapir (Tapirus bairdii) en cuerpas de agua en la Selva Maya*. Master in Sciences Thesis. Campeche, Mexico: El Colegio de la Frontera Sur.
- Mateo-Sánchez, M. C., Balkenhol, N., Cushman, S., Peréz, T., Domínguez, A., & Saura, S. (2015). Estimating effective landscape distances and movement corridors: comparison of habitat and genetic data. *Ecosphere*, 6(April), 1–16.
- McClure, M. L., Hansen, A. J., & Inman, R. M. (2016). Connecting models to movements: testing connectivity model predictions against empirical migration and dispersal data. *Landscape Ecology*, 31(7), 1419–1432.
- McRae, B. H., Dickson, B. G., Keitt, T., & Shah, V. B. (2008). Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology*, 89(10), 2712–2724.
- McRae, B. H., Shah, V. B., & Mohapatra, T. (2013). Circuitscape 4 user guide. *The Nature Conservancy*. http://docs.circuitscape.org/circuitscape_4_0_user_guide.html.
- Mendoza, E., Fuller, T. L., Thomassen, H. A., Buermann, W., Ramírez-Mejía, D., & Smith, T. B. (2013). A preliminary assessment of the effectiveness of the Mesoamerican Biological Corridor for protecting potential Baird's tapir (*Tapirus bairdii*) habitat in southern Mexico. *Integrative Zoology*, 8(1), 35–47. <http://dx.doi.org/10.1111/1749-4877.12005>.
- Naranjo, E. J., & Bodmer, R. E. (2002). Population ecology and conservation of Baird's tapir (*Tapirus bairdii*) in the Lacandon Forest, Mexico. *Tapir Conservation*, 11(2), 25–33.
- Naranjo, E. J., Amador-Alcalá, S. A., & Reyna-Hurtado, R. (2015). Distribución, abundancia y amenazas a las poblaciones de tapir centroamericano (*Tapirus bairdii*) y pecarí de labios blancos (*Tayassu pecari*) en México. *Therya*, 6(1), 227–249. <http://dx.doi.org/10.12933/therya-15-246>.
- Naranjo, E. J. (1995). Abundancia y uso de hábitat del tapir (*Tapirus bairdii*) en un bosque tropical húmedo de Costa Rica. *Vida Silvestre Neotropical*, 4, 20–31.
- Naranjo, E. J. (2009). Ecology and conservation of Baird's tapir in Mexico. *Tropical Conservation Science*, 2(2), 140–158.
- O'Farrill, G., Calmé, S., Sengupta, R., & Gonzalez, A. (2012). Effective dispersal of large seeds by Baird's tapir: A large-scale field experiment. *Journal of Tropical Ecology*, 28(1), 119–122. <http://dx.doi.org/10.1017/S0266467411000599>.
- O'Farrill, G., Galetti, M., & Campos-Arceiz, A. (2013). Frugivory and seed dispersal by tapirs: An insight on their ecological role. *Integrative Zoology*, 8(1), 4–17. <http://dx.doi.org/10.1111/j.1749-4877.2012.00316.x>.
- Pérez-Cortez, S., Enríquez, P. L., Sima-Panti, D., Reyna-Hurtado, R., & Naranjo, E. J. (2012). Influencia de la disponibilidad de agua en la presencia y abundancia de *Tapirus bairdii* en la selva de Calakmul Campeche, México. *Revista Mexicana De Biodiversidad*, 83(3), 753–761. <http://dx.doi.org/10.7550/rmb.25095>.
- Pérez-Farrera, M. A., Meléndez-López, E., Sarmiento, O. F., Moreno, N. L., & Najjarro, F. H. (2006). *Inventario florístico de la zona de protección forestal la frailesca, chiapas, México*. México D.F: Sistema Nacional de Información sobre Biodiversidad-Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (SNIB-CONABIO).
- Pearce, J., & Ferrier, S. (2000). Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling*, 133(0), 225–245.
- Peres, C. A. (2000). Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conservation Biology*, 14(1), 240–253. <http://dx.doi.org/10.1046/j.1523-1739.2000.98485.x>.
- R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Reyna-Hurtado, R., & Tanner, G. W. (2005). Habitat preferences of ungulates in hunted and nonhunted areas in the Calakmul. *Biotropica*, 37(4), 676–685.
- Reyna-Hurtado, R., Sanvicente-López, M., Pérez-Flores, J., Carrillo-Reyna, N., & Calmé, S. (2016). Insights into the multiannual home range of a Baird's tapir (*Tapirus bairdii*) in the Maya Forest. *Therya*, 7(2), 271–276. <http://dx.doi.org/10.12933/therya-16-348>.
- Riley, S. J., DeGloria, S. D., & Elliot, R. (1999). A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences*, 5, 23–27.
- Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., et al. (2015). Collapse of the world's largest herbivores. *Science Advances*, 1(4), <http://dx.doi.org/10.1126/sciadv.1400103> [e1400103].
- Ripple, W. J., Chapron, G., López-Bao, J. V., Durant, S. M., Macdonald, D. W., Lindsey, P. A., et al. (2017). Conserving the world's megafauna and biodiversity: The fierce urgency of now. *Bioscience*, 63(3), 197–200. <http://dx.doi.org/10.1093/biosci/biw168>.
- Ripple, W. J., Abernethy, K. A., Betts, M. G., Chapron, G., Dirzo, R., Galetti, M., et al. (2016). Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science*, 3(January 2016), <http://dx.doi.org/10.1098/rsos.160498> [160498].
- Ripple, W. J., Chapron, G., López-Bao, J. V., Durant, S. M., Macdonald, D. W., Lindsey, P. A., et al. (2016). Saving the world's terrestrial megafauna. *Bioscience*, 66(10), 807–812. <http://dx.doi.org/10.1093/biosci/biw092>.
- Robin, A. X., Turk, N., Hainard, A., Lisacek, F., Sanchez, J., Müller, M., & Xavierrobinunigech, M. X. R. (2013). Package PROC 2012-09-10 09:34:56, (1), 1–71. <http://doi.org/10.1186/1471-2105-12-77>.
- Rudnick, D. A., Ryan, S. J., Beier, P., Cushman, S. A., Dieffenbach, F., Epps, C. W., et al. (2012). The role of landscape connectivity in planning and implementing conservation and restoration priorities. *Issues in Ecology, Fall, 2012*(16), 1–20.
- SEMARNAT (2007). *Acuerdo por el que se recategoriza como Área Protegida con la categoría de Área de Protección de Recursos Naturales, a la Zona de Protección Forestal en los terrenos que se encuentran en los municipios de La Concordia, Ángel Albino Corzo y Villa Flores*. Mexico: Diario Oficial de La Federación.
- SEMARNAT (2010). *Norma oficial mexicana. NOM-059-SEMARNAT-2010*. Mexico: Diario Oficial de la Federación.
- Schank, C., Cove, M. V., O'Farrill, G., Estrada, N., Poot, C., Meyer, N., et al. (2015). Integrating current range-wide occurrence data with species distribution models to map the potential distribution of Baird's tapir. *Tapir Conservation*, 24(August), 15–25. <http://dx.doi.org/10.5281/zenodo.23417>.
- Schipper, J., Chanson, J. S., Chiozza, F., Cox, N. A., Hoffmann, M., Katariya, V., et al. (2008). The status of the world's land and marine mammals: Diversity, threat, and knowledge. *Science*, 322(5899), 225–230. <http://dx.doi.org/10.1126/science>.

- 1165115.
- Si, X., Kays, R., & Ding, P. (2014). How long is enough to detect terrestrial animals? Estimating the minimum trapping effort on camera traps. *PeerJ*, 2, e374. <http://dx.doi.org/10.7717/peerj.374>.
- Tan, C. K. W., Rocha, D. G., Clements, G. R., Brenes-Mora, E., Hedges, L., Kawanishi, K., et al. (2017). Habitat use and predicted range for the mainland clouded leopard *Neofelis nebulosa* in Peninsular Malaysia. *Biological Conservation*, 206, 65–74. <http://dx.doi.org/10.1016/j.biocon.2016.12.012>.
- Terwilliger, V. (1978). Natural history of baird' tapir on barro colorado island, Panama canal zone. *Biotropica*, 10, 211–220.
- Tobler, M. W. (2002). Habitat use and diet of Baird's tapirs (*Tapirus bairdii*) in a montane cloud forest of the Cordillera de Talamanca, Costa Rica. *Biotropica*, 34(3), 468–474. [http://dx.doi.org/10.1646/0006-3606\(2002\)034\[0468:HUADOB\]2.0.CO;2](http://dx.doi.org/10.1646/0006-3606(2002)034[0468:HUADOB]2.0.CO;2).
- Vazquez-Bautista, D. (2002). *Mastofauna de la zona de protección forestal La frailesca, Chiapas, México*. Bachelors thesis. Universidad de Ciencias y Artes de Chiapas.
- Zeller, K. A., Mcgarigal, K., & Whiteley, A. R. (2012). Estimating landscape resistance to movement: A review. *Landscape Ecology*, 27(6), 777–797. <http://dx.doi.org/10.1007/s10980-012-9737-0>.
- Zeller, K. A., McGarigal, K., Cushman, S. A., Beier, P., Vickers, T. W., & Boyce, W. M. (2016). Using step and path selection functions for estimating resistance to movement: Pumas as a case study. *Landscape Ecology*, 31(6), 1319–1335. <http://dx.doi.org/10.1007/s10980-015-0301-6>.