El Colegio de la Frontera Sur

Estimando densidades del tapir centroamericano (*Tapirus bairdii*) en la Sierra Madre de Chiapas

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Por

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Anexo 9

PORTADILLA DE TESIS DE MAESTRÍA

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Las personas abajo firmantes, miembros del jurado examinador de:

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Resumen

El tapir centroamericano (*Tapirus bairdii*) es una especie que se encuentra en peligro de extinción en toda su área de distribución. En México, una de las poblaciones más importantes se encuentra en la región de la Sierra Madre de Chiapas (SMC). Sin embargo, se conoce poco acerca de su estado de conservación y las densidades que presenta en dicha región. Actualmente, los estudios realizados con fototrampeo, en combinación con diferentes modelos como captura recaptura y marcaje recaptura espacialmente explícitos (SCR y SMR), así como los modelos de encuentro aleatorio (REM) se han vuelto una herramienta muy popular para estimar densidades de especies que no presentan un patrón de marcaje natural, como es el caso del tapir centroamericano. El objetivo principal del proyecto fue proporcionar una estimación de densidad estadísticamente robusta para el tapir centroamericano en el área natural protegida La Frailescana, situada en la Sierra Madre de Chiapas, por medio de un análisis comparativo para evaluar el comportamiento de tres modelos diferentes (SCR, SMR y REM) para estimar densidades. Además, se identificaron las limitaciones y requerimientos metodológicos de cada uno de estos modelos para su aplicación y se propuso un tamaño poblacional para la Sierra Madre de Chiapas basado en los resultados de densidad obtenidos. La estimación de la densidad fue más alta y menos precisa al usar el REM en comparación con los modelos espacialmente explícitos. El modelo SCR proporcionó la estimación de densidad más baja en comparación con la SMR, pero SMR tuvo los intervalos de confianza más pequeños, lo que representa la estimación de densidad más precisa. Creamos modelos de ocupación para extrapolar la densidad a las áreas con mayor probabilidad de ocupación del tapir centroamericano para obtener un tamaño poblacional robusto para la SMC. Nuestro estudio es el primero en estimar la densidad de una población de tapir centroamericano bajo diferentes enfoques y nos permitió definir prioridades de conservación enfocados a dichos resultados.

Palabras clave: *Tapirus bairdii*, tamaño poblacional, ocupación, modelos de captura-recaptura espacialmente explicitos; random encounter model

Introducción

El tapir centroamericano (*Tapirus bairdii*) es el mamífero nativo más grande que habita en el Neotrópico. La distribución histórica de esta especie incluía desde el sureste de México hasta el norte de Colombia (García et al. 2016), sin embargo, ahora se encuentra limitada a sitos con grandes remanentes de bosque tropical y humedales que van desde los 0 a los 3,700 msnm (Matola et al. 1997; González-Maya et al. 2009). La especie se encuentra catalogada como en Peligro en la lista roja de especies de la Unión Internacional para la Conservación de la Naturaleza (UICN; García et al. 2016) ya que se encuentra amenazada en todo su área de distribución por la pérdida de hábitat y la cacería furtiva (Jordan et al. 2010; Cove et al. 2013).

La UICN estima que existen alrededor de 3,000 individuos en vida silvestre para toda su área de distribución (García et al. 2016), aunque algunos registros sugieren que puede haber un número mayor en algunos países (Jordan et al. 2010; Meyer et al. 2013), como es el caso de México, donde previamente se había estimado que quedaban alrededor de 2,600 individuos (Naranjo 2009). Por lo tanto, contar con una estimación precisa de la densidad en las distintas poblaciones es fundamental para conocer su estado de conservación y entender aspectos básicos de la ecología de la especie (Sollmann et al. 2013; Rich et al. 2014). A su vez, esta información permite definir las prioridades de conservación y evaluar la eficacia de las políticas de manejo dirigidas a sus poblaciones (Oliveira-Santos et al. 2010; Whittington y Sawaya 2015).

Existen diversos métodos y técnicas que permiten estimar las densidades de mamíferos terrestres medianos y grandes, como la captura-marcaje-recaptura (Otis et al. 1978), transectos lineales (Trolle et al. 2008), conteos de huellas y excretas (Lizcano y Cavelier 2000; Mandujano 2014), observación directa (Fragoso 1991) y conteos aéreos (Mourão et al. 2000). Sin embargo, no todos pueden utilizarse para especies que son raras, crípticas y elusivas como el tapir centroamericano (Zero et al. 2013; Dénes et al. 2015).

El foto-trampeo es una técnica no invasiva que permite obtener registros fotográficos de especies que son raras o elusivas pudiendo abarcar grandes áreas con un esfuerzo de muestreo relativamente bajo (Srbek-Araujo y Chiarello 2005; Tobler et al. 2008). Esta técnica, combinada con diferentes modelos de captura-recaptura (Karanth y Nichols 1998), es considerada una herramienta muy robusta e importante para estimar parámetros demográficos de las poblaciones silvestres, principalmente de aquellas que presentan marcas naturales que permiten su identificación individual, como la mayoría de los felinos silvestres (Soisalo y Cavalcanti 2006).

Los modelos tradicionales de captura-recaptura (Otis et al. 1978; Karanth 1995; Karanth y Nichols 1998), consideran que la población es cerrada y utilizan la información generada de las trampas cámara para construir un historial de captura de los individuos identificados para estimar su abundancia. Posteriormente, se agrega un área de amortiguamiento alrededor del polígono de las cámaras con base en el promedio de las distancias máximas en que se movieron los individuos capturados en más de una cámara (MMDM: *mean maximum distance moved*, por sus siglas en inglés), el cual estima un área efectiva de muestreo (A_e), para finalmente obtener la densidad de la población en el área de interés $D=N/A_e$ (Noss et al. 2012). Sin embargo, el modelo de CR presenta ciertas limitaciones. La primera es que la estimación de A_e es imprecisa, y muchos autores han cuestionado su eficacia (Soisalo y Cavalcanti 2006). La segunda limitación es que no se considera la información espacial disponible obtenida de las ubicaciones de las trampas cámara. Esta información es importante porque la probabilidad de que un individuo sea capturado en la trampa cámara, depende de que exista un traslape en su área de actividad y la localización de las trampas cámara (Gopalaswamy et al. 2012). Por último, estos modelos requieren que los animales puedan ser identificados individualmente; sin embargo, en la mayoría de los estudios realizados con trampas cámara, solo un pequeño porcentaje de las especies registradas presentan algún tipo de marca natural (Carbone et al. 2001), por lo que este tipo de metodología no es la mejor para el resto de las especies.

Para abordar varias de estas limitaciones, se desarrollaron los modelos de captura-recaptura espacialmente explícitos (SCR, por sus siglas en inglés; Efford 2004; Borchers y Efford 2008; Royle et al. 2009). Estos modelos estiman la densidad de animales incorporando la información del historial de captura junto con la información espacial contenida en las trampas cámara donde se registraron los individuos (Noss et al. 2012) bajo dos posibles esquemas de análisis, bayesiano (Royle et al. 2009) o de máxima verosimilitud (Efford 2004; Borchers y Efford 2008). De tal manera que la probabilidad de encuentro se modela como una función de la distancia entre las trampas cámara y el centro de actividad de un animal s_i. Con base en lo anterior, los modelos SRC estiman dos parámetros, λ_0, que es la tasa de encuentro de la trampa cámara en el centro de actividad del individuo, y σ, parámetro escalar asociado al área de actividad, que describe la disminución de la tasa de encuentro conforme aumenta la distancia desde el centro de actividad (Tobler et al. 2013; Srivathsa et al. 2015). Sin embargo, estos modelos aun requieren que todos los individuos fotografiados puedan ser identificados individualmente.

En los últimos años, se han desarrollado modelos que permiten estimar densidades para especies que no pueden ser identificadas individualmente o que solo algunos de los miembros de la población pueden ser identificados como es el caso del tapir centroamericano (Chandler y Royle 2013; Sollman et al. 2013; Rich et al. 2014). Estos modelos, llamados marcaje-recaptura espacialmente explícitos (*mark-resight*, SMR, por sus siglas en inglés) están basados en los métodos de SCR, sin embargo, utilizan conteos espacialmente referenciados obtenidos de una o varias ocasiones de muestreo, y en donde las unidades de muestreo (ej. trampas cámara) se encuentran en un arreglo compacto o muy pegadas unas de otras, de tal manera que los individuos puedan ser registrados en múltiples sitios (Chandler y Royle 2013). Estos modelos utilizan la correlación espacial en los conteos como información acerca de la distribución espacial y el tamaño de la población (Chandler y Royle 2013). El modelo estima la densidad a partir de fotografías de individuos identificados con certeza, fotografías con animales marcados pero que no pueden ser identificados como un individuo *per se*, y fotografías de animales no identificados (Rich et al. 2014).

Paralelo a los modelos de SCR, se desarrolló un método, llamado Modelo de Encuentro Aleatorio (*Random Encounter Model,* REM por sus siglas en inglés) que permite estimar la densidad de individuos sin la necesidad de su identificación individual (Rowcliffe et al. 2008). El REM incorpora la información de las trampas cámara y ecología de movimiento de la especie de estudio y se basa en tres supuestos para su aplicabilidad. El primero es que los animales se comportan como partículas de gases ideales, moviéndose azarosa e independientemente uno de otro. Por otro lado, las fotografías representan contactos independientes entre los animales y las cámaras y finalmente, el modelo se aplica dentro de una población cerrada (Zero et al. 2013; Carbajal-Borges et al. 2014).

Estudios recientes han podido estimar la densidad del tapir centroamericano utilizando los modelos de captura-recaptura tradicionales (Mejía-Correa et al. 2010; González-Maya et al. 2012) y del tapir de tierras bajas (*Tapirus terrestris*), con los modelos SCR (Trolle et al. 2008; Noss et al. 2012; Tobler et al. 2013). Sin embargo, aunque se ha cuestionado la asertividad para identificar a los individuos en las fotografías a partir de cicatrices, manchas, sexo o tamaño (Oliveira-Santos et al. 2010), en todos los casos, los investigadores consideraron que hubo consistencia entre los observadores que determinaron el número de individuos de la especie (González-Maya et al., 2012; Tobler et al., 2013). Por otro lado, el REM ha sido utilizado principalmente en México para determinar la densidad de tapires (Carbajal-Borges et al. 2014; Lavariega-Nolasco et al. 2016). Los autores sugieren que es una buena alternativa a los modelos de captura-recaptura, ya que no es necesario la identificación individual, sin embargo, existen limitaciones, sobre todo, asociadas a la estimación de la velocidad de movimiento de la especie (Carbajal-Borges et al. 2014).

Aunque los modelos anteriormente mencionados se han probado independientemente con diferentes poblaciones de tapir, no existe un estudio que compare las diferentes metodologías para conocer su asertividad y determinar las ventajas y desventajas de su aplicación, especialmente en una especie donde los individuos no pueden ser reconocidos con certeza. Es por ello que uno de los objetivos de este trabajo de tesis fue realizar una comparación entre los tres métodos antes mencionados, para estimar la densidad del tapir centroamericano (*Tapirus bairdii).*

Por otro lado, los modelos de ocupación han sido ampliamente utilizados para hacer inferencias respecto a los factores que afectan los patrones de distribución de las especies (Hines et al. 2010; Karanth et al. 2011; Ferreguetti et al. 2017). Estos modelos de ocupación estiman la probabilidad de que una especie se encuentre presente en un área en particular (probabilidad de ocupación= ψ) y su probabilidad de detección (p), a partir de historiales de detección/no detección, obtenidos de un muestreo repetitivo, es decir, diferentes sitios de muestreo visitados repetidamente (MacKenzie et al. 2006). Además, los modelos de ocupación permiten evaluar cuáles variables del paisaje son las que más se asocian con la probabilidad de ocupación de una especie. De esa manera, los resultados obtenidos de estos modelos pueden ser utilizados para generar información respecto a las áreas que pueden estar siendo ocupadas por una especie, y enfocar los esfuerzos de manejo y conservación a dichas áreas (Jathanna et al. 2015). Con base en lo anterior, se utilizaron los modelos de ocupación para conocer las áreas de mayor probabilidad de ocupación del tapir centroamericano en la región de la Sierra Madre de Chiapas y esta información se utilizó para extrapolar los resultados de las estimaciones de densidad para obtener una aproximación del tamaño actual de su población en dicha región. El estudio se realizó en el Área de Protección de Recursos Naturales La Frailescana (APRNF), región que alberga una de las poblaciones más importantes en México (Naranjo 2009), y de la cual se conoce poco acerca de su estado de conservación (Naranjo y Cruz 1998; Mendoza y Carbajal-Borges 2011; Mendoza et al. 2013; Carbajal-Borges et al. 2014), además de que la región es un corredor importante para esta y otras especies hacia las reservas de la Selva El Ocote en Chiapas y Los Chimalapas en Oaxaca.

Considerando lo anterior este trabajo de tesis tuvo como objetivo principal proporcionar una estimación de densidad estadísticamente robusta para el tapir centroamericano en el área natural protegida La Frailescana, situada en la Sierra Madre de Chiapas, por medio de un análisis comparativo para evaluar el comportamiento de los tres modelos mencionados anteriormente para estimar densidades (SCR, SMR y REM). Además, se identificaron las limitaciones y requerimientos metodológicos de cada uno de estos modelos para su aplicación. El objetivo final es que esta información pueda ser utilizada como una herramienta que permita estandarizar la metodología para estimar la densidad de una especie de la cual se carece de información respecto al estado de conservación de sus poblaciones para gran parte de su distribución geográfica. Finalmente, se identificaron las áreas de mayor probabilidad de presencia de la especie para la región de la Sierra Madre de Chiapas, a través de modelos de ocupación, para realizar una extrapolación de las estimaciones de densidad obtenidas para contar con un tamaño poblacional de la especie en dicha región. Esta información es extremadamente importante para elaborar estrategias de conservación de esta especie en peligro de extinción.

Article

Comparing methods for estimating Baird´s tapir densities in the Sierra Madre de Chiapas, Mexico

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Abstract Knowledge of size and density of a population is fundamental to assess the recovery of any endangered species. However, these parameters are challenging to estimate, especially for unmarked species such as the Baird´s tapir. Spatial capture recapture (SCR) models have been widely used to estimate densities of species where individuals can be uniquely identified, but in recent years alternatives have been developed to obtain density estimates for unmarked populations. In this study we used photographic records to estimate Baird´s tapir densities in the Sierra Madre de Chiapas. We compared the performance of SCR with newer modeling including spatial mark-resight (SMR) and random encounter model

(REM). Baird´s tapir density did not differ significantly among statistical techniques. Density estimation (ind/km^2) was higher and less precise using the REM (0.12-0.41) compared to spatially explicit models. The SCR model provided the lowest density estimation (0.039-0.16) in comparison with the SMR (0.08-0.14), but SMR had the smallest confidence intervals, representing the most precise density estimation. We create occupancy models to extrapolate density to areas with greater probability of occurrence of Baird's tapir to obtain a more reliable estimation population size for the SMC. Our study is the first to estimate Baird's tapir density of a population under different approaches, which allowed to compare their limitations for the study and effectiveness for their applicability in other studies. Our findings support the need to strengthen surveillance and monitoring programs in the natural protected areas of southern Mexico and to develop actions that promote Baird's tapir conservation.

Key words *Tapirus bairdii*, density, spatial capture-recapture, spatial mark-resight, random encounter model, Mexico, maximum likelihood analysis

Introduction

The Baird´s tapir (*Tapirus bairdii*) is one of the last representatives of the megafauna that survived the Pleistocene extinctions (Koch & Barnosky, 2006) and is considered a living fossil because of its unique morphological and behavioral characteristics resembling those of primitive ungulates (Janis, 1984). Nowadays, tapirs are the largest native terrestrial mammals inhabiting the Neotropics (Naranjo, 2009), and because of their size and feeding habits, they provide important ecosystem services as seed dispersers and predators, as well as seedling controllers (Tobler et al., 2006; O'Farrill et al., 2013).

The historic distribution of the Baird´s tapir ranged from southeastern Mexico to northwestern Colombia (García et al., 2016). Today, its presence is limited to areas with large remnants of tropical forest and wetlands ranging from 0 to 3,620 meters above the sea level (masl; Matola et al., 1997; González-Maya et al., 2012). Populations are declining mainly because of poaching, droughts and habitat loss as consequence of land use changes, logging, plantations and fires (García et al., 2016). However, the extent of its decline is not well known because there is no reliable information on its population density and size for most of the

Baird's tapir distribution (Naranjo, 2009; Mejía-Correa et al., 2010; González-Maya et al., 2012; Carbajal-Borges et al., 2014; Lavariega-Nolasco et al., 2016; Botello et al., 2017). The Red List of Threatened Species of the International Union for the Conservation of Nature (IUCN) estimates that there are around 3,000 individuals left in the wild throughout the entire distribution range (García et al., 2016). Nevertheless, some recent studies suggest that there may be a greater number of tapirs in some countries (García et al., 2016; Schank et al., 2017), as is the case of Mexico, which has an estimate of around 2,600 tapirs for the entire country (Naranjo, 2009).

In order to have a better understanding of the conservation status of the Baird´s tapir, it is fundamental to have accurate estimates of its populations densities, which will allow to define conservation priorities and evaluate the effectiveness of management policies directed towards these populations (Oliveira-Santos et al., 2010; Whittington & Sawaya, 2015). There are several methods and techniques for estimating densities of medium-large-sized terrestrial mammals including line transects, capture-recapture methods, telemetry and sign counts (Johnson et al., 2005; Srivathsa et al., 2015; Howe et al., 2017; Popescu et al., 2017). Although not all of these can be used for rare, unmarked and elusive species such as the Baird´s tapir (Zero et al., 2013; Dénes et al., 2015). Camera-trapping constitutes a non-invasive technique to obtain photographic records from large areas for long periods of time with a relatively low cost (Srbek-Araujo & Chiarello, 2005). This technique combined with different density models is considered a very robust and valuable tool for estimating wildlife population and distribution parameters including elusive and unmarked species (O'Connell et al., 2011).

One of the most commonly used method to estimate density is the spatially explicit capture-recapture model (SCR). The SCR model estimate animal densities by incorporating capture history information along with the spatial information of where individuals were recorded (Efford, Borchers, et al., 2009; Royle et al., 2009). However, these models require the animals to be identified individually which is problematic for species that lack natural markings and thus are difficult to distinguish (e.g., tapirs; Carbone et al., 2001).

In recent years, additional models have been developed to allow estimating densities for species that cannot be individually identified or that only some members of the population can be identified (Royle et al., 2013, 2014; Sollmann et al., 2013; Rich et al., 2014). These models, called spatially explicit mark-recapture (SMR), are based on SCR models. However, individual encounter histories are partially latent only for the marked animals (Royle et al., 2014), whereas it uses accumulated counts for unmarked individuals (Sollmann et al., 2013; Rich et al., 2014). Therefore, the SMR model estimates the density from records of individuals identified with certainty, records of animals that are marked but cannot be identified individually, and records of unidentified animals (Rich et al., 2014).

Parallel to the SCR models, Rowcliffe et al., (2008) developed the Random Encounter Model (REM) a modification on the gas collision theory. REM allows estimating densities without the need of individual recognition based on information related to the speed of movement and sensor detection parameters (Lucas et al., 2015).

Each of these models (SCR, SMR and REM) has been independently tested in different wildlife populations (Royle et al., 2011; Sollmann et al., 2013; Cusack et al., 2015). However, few studies have focused on comparing these different methodologies to know their effectiveness and applicability, especially for species that cannot be easily identified individually (Noss et al., 2012; Zero et al., 2013; Anile et al., 2014; Rich et al., 2014; Kane et al., 2015; Whittington & Sawaya, 2015).

On the other hand, occupancy models have been widely used to make inferences regarding the factors affecting the spatial distribution patterns of species (Hines et al., 2010; Karanth et al., 2011; Ferreguetti et al., 2017). Occupancy models estimate the probability that a species is present in a particular area (ψ) and its probability of detection (p), based on detection/non-detection histories obtained from repetitive sampling (MacKenzie et al., 2006). Occupancy models allow to evaluate which landscape variables are mostly associated with the occupancy of a species. Therefore, the results obtained from these models can be used to generate information about species habitat preferences to create species potential distribution maps in order to prioritize management and conservation efforts on these particular areas (Jathanna et al., 2015).

In this study, we aimed to estimate Baird's tapir population size in the Sierra Madre de Chiapas (SMC) using camera traps. We first compared the performance of several density estimation models, (1) SCR, (2) SMR and (3) REM. Subsequently, we extrapolated the density to areas with greater probability of occurrence of Baird's tapir. With this approach we obtained a more reliable estimation of the species population size for the SMC with a more realistic and detailed scheme than previous studies. We expect this information to be useful to develop standardized protocols to systematically evaluate Baird's tapir population across its distribution range.

Study Area

The Sierra Madre de Chiapas (SMC), in southwestern Mexico bordering with Guatemala is a rugged mountain range with elevations ranging from 200 to 2900 masl (CEIEG, 2010). The region covers an area of around 5,000 km^2 and currently has four protected areas under different categories: a State Reserve, Pico el Loro-Paxtal, and four Federal Reserves, El Triunfo and La Sepultura Biosphere Reserves and the Natural Resources Protected Area La Frailescana (Fig. 1). The SMC has at least seven vegetation types including coniferous forest, oak forest, semi-deciduous forest, dry forest, evergreen forest and cloud forest (Pérez-Farrera et al., 2006).

Land tenure in the SMC is under control of small landowners and ejidos, which are peasant communities owning large extensions of land for farming and other uses. The use of land is mainly for agriculture and livestock production, which are causing the growth of the agricultural frontier and the consequent deforestation and habitat loss for many wildlife species (CEIEG, 2010). These phenomena, together with subsistence hunting and fires, are the main threats for wildlife in the region, especially for tapirs and other large mammals (Naranjo, 2009).

Methods

We conducted camera trapping surveys in the middle of the SMC complex, in the Natural Resources Protected Area La Frailescana (NRPAF). The area was divided into two blocks of 29 camera trap stations each. The first block was active from April 3 to May 31, 2018 and the second block from May 31 to July 29, 2018. A total of 58 camera-trap stations were placed covering an area of 70 km^2 (Figure 2). Forty-eight stations were set in pairs facing one another to photograph both sides of the tapirs to increase reliability to assign unique identities to individuals, and the remaining 10 stations only had one camera trap each. The simple stations were decided based on the safety of the equipment, since they were located very close to human settlements or where the risk of theft was high. Two doubles and one simple station were lost to robbery. The stations were active 53 ± 2 days to ensure demographic enclosure and the sampling effort was 2,975 camera days. The camera trap stations were placed at an average distance between stations of 813 ± 227 m at 50 cm from the ground. Distance between cameras was defined based on the movements and home range reported for tapirs in other studies (Foerster and Vaughan 2002, Trolle et al., 2008) and with the aim of increasing the probability of capture different individuals in each camera trap station (Chávez et al., 2014). Camera traps were programmed to be active 24 hours a day and without delay between captures to maximize photo-captures.

We performed tapir density estimate under a spatial capture-recapture framework. The SCR model consider that each individual of the population has an activity center (*s*) on which the movements of the individual are concentrated. The SCR estimates the density by modelling the number and location of activity centers s_i within the space state S. Therefore, the probability of encounter is modelled as a function of the distance between the camera traps and the center of activity (home range) of an animal s_i. Based on the above, the SCR models estimate two parameters, λ_0, which is the encounter rate of the camera trap at the center of activity of the individual, and σ, a scalar parameter related to the area of activity, which describes the decrease of the encounter rate as distance increases from the center of activity (Royle et al., 2009). The assumptions of these models (Royle et al., 2014) are: 1) each individual of the population has a fixed point associated with it, its center of activity; 2) (S) is an area large enough to include the s_i of all individuals potentially exposed to the traps; 3) capture probability is a function of the distance between the trap and the s_i of the animal; 4) the population is geographically closed; 5) animals are correctly identified and; 6) individuals can be detected in multiple locations. For this, all tapir photographs obtained from the camera traps survey were analyzed to identify tapir individuals from unique marks such as spots, scars, notches on the ears, body structure and sex (Oliveira-Santos et al., 2010; González-Maya et al., 2012). To improve the accuracy of individual identification, two researchers independently classified all tapir individuals obtained during the survey and results were then compared and a consensus reached (Kelly et al., 2008; Foster & Harmsen, 2012).

We analyzed the SCR models in a maximum likelihood framework (Efford et al., 2009) using the secr package version 3.2.0 for R (Core Team, 2016; Efford, 2019). We define our state-space as the size of the camera array polygon plus a buffer of 2.3 km, this distance was chosen based on the theory that the buffer should be wide enough to have zero probabilities of animals present at the edge appear in our sample (Efford, 2019). We fit the null model using the half-normal detection function with a Poisson distribution. This was done to set the same model in SMR to allow for direct comparison of the results.

We implemented the spatial mark-resight (SMR) model by using the encounter history data from marked individuals and the counts of the unmarked individuals to estimate Baird´s tapir density. The assumptions for this model (Sollmann et al., 2013; Royle et al., 2014; Efford, 2019) are: 1) marked individuals represent a random sample from a defined population with a uniform and known area, the state space (S); 2) the number of remaining marked individuals at the time of re-sighting maybe known or unknown; 3) no marks are lost between marking or resighting and; 4) all individuals are correctly identified as marked or unmarked. In this model, sampling events are either marking or sighting occasions. For this study we used sighting only-data with unknown individuals pre-marked, using the function addSightings and the special attributes markocc and Tu of the package secr 3.2 for R (Efford, 2019). We used the same buffer size and input files as for the SCR models, plus an additional capture history data set, which included the counts of unmarked animals in a binary form (1/0). We used the half-normal detection function to fit the model, and due to the overdispersion of the pooled counts, we re-fitted the model using an overdispersion-adjusted pseudo-likelihood.

The REM incorporates information from camera traps and the speed of movement of the species and detection of the species. It is based on three assumptions: 1) animals behave like particles of ideal gases, moving randomly and independently from each other; 2) the photographs represent independent contacts between animals and cameras and; 3) the model is applied within a closed population. The REM estimate density (D) using the following model (Rowcliffe et al., 2008; Eq. 1):

$$D = \frac{y \quad \pi}{t\big(vr(2+\theta)\big)}$$

Where y= number of tapir detections, t= survey effort in hours, v=speed of movement (distance travelled in 24 h), r= radial distance to the animal (in meters), and θ= zone of detection.

For the REM analysis, we used the formula mentioned above (Eq. 1) and considered the following parameters: *y* as independent photographic tapir detections, defined as one or a set of photographs of the same species separated by 24 h (Lavariega-Nolasco et al., 2016). For the variable *v* we considered available information regarding the average speed of movement of three tapir species (*T. bairdii*, *T. terrestris* and *T. pinchaque*) since these data is not currently available for the Baird´s tapir in the study site. For the Baird´s tapir we use information from a study conducted in Indio Maíz, Nicaragua using only pre-Hurricane data (Jordan et al., 2019), with a movement average speed of 4.06 km/day (ranging from 2.04 to 7.6 km/day; Jordan, pers com). For *T. pinchaque*, the estimated speed was 0.6 km/hr (Lizcano & Cavelier, 2000) considering that the species walked an average of 10 hr a day, we obtained a daily speed of 6 km/day. Finally, the average speed for *T. terrestris* was 5.2 km/day (range 3.6-6.7 km; Tobler, 2008). Based on the above, we used 6 km/day for the *v* parameter. The detection zone parameters, distance *r* and arc θ, were estimated for each camera trap. The parameter θ was obtained through a series of perpendicular approaches on each side of the camera trap (10 per side), at distances of 3 and 6 meters. The distance obtained between the two detection points was used to calculate θ by the Cosine Law. The resulting θ angles were transformed to radians and averaged to obtain a single measurement per camera trap. Finally, *r* was obtained by performing approximations at different distances and angles until the camera trap did not detect movement. We used 10,000 bootstraps and performed the analysis using the personal Rowcliffe script for R (Carbajal-Borges et al., 2014).

Finally, we compared density estimation models using the 95% of confidence intervals and considered estimates to be different if the 95% confidence intervals did not overlap.

Occupancy models. We used likelihood-based occupancy modelling to identify variables that best explain the occupancy and detectability, hence tapir habitat preferences in the SMC. We spatialized the best occupancy model to the entire Sierra Madre de Chiapas to identify areas with higher probability of occurrence. We then extrapolated the density obtained from our study to these areas in order to estimate the population size in the region.

For this, we used de la Torre et al. (2018) theoretical framework and camera trap dataset but scaled only for the SMC. We used the information gathered from 55 camera trap stations covering an area of 400km^2 in the PA La Frailescana (Figure 2). The stations were functioning between August 2015 to December 2016. Sampling effort was 9,274 trap days and the stations where active from 34 days to 15 months. We compiled a geospatial dataset of environmental and anthropogenic variables that where both biologically meaningful and not correlated to each other (Table 1).We generate raster layers with each pixel of 30 m resolution and used circular moving window radius of 30, 90, 510, and 1020 m to evaluate all variables at five spatial scales because species are likely to be influenced by resources and factors distributed at potentially different scales (Johnson et al., 2002; Irvin et al., 2013). We developed tapir detection histories based on the photographic records using binary values, where 1 represented the capture of the species in a specific day and camera trap station and 0 represented the lack detection of the species. We used 15 days intervals as a sampling period to increase detection probability, based on the information that Baird´s tapir can cycle its home range every 10-12 days (Jordan, 2015). We extracted the values of each covariate from the location of the camera trap and rescaled them using the mean value for each covariate and dividing it by the standard deviation. We analyzed all the variables with a Pearson test for multicollinearity and we did not include those variables that were correlated at >0.6 in the same candidate model.

Detection and occupancy probabilities were estimated through 35 sampling occasions following the single season model, assuming both closed population and that tapir occupancy of the tapirs was constant through the sampling period (MacKenzie et al., 2006). We built 171 candidate models assuming the following criteria: 1) variation in the occupancy probability as function of the covariates and detectability remained constant [(P.) + ψ]; 2) variation in detectability and occupancy as a function of covariates [P+ ψ];3) detectability and occupancy remained constant across all sites [(P.)+(ψ.)]. For the candidate models that included variation in detectability we used only the landscape covariates with a radii of 90 m scale, and we included the categorical covariates season of the year and sampling effort; and for the candidate models that included variation in the occupancy, we first identified the most informative scale for each of the covariates (30, 90, 240, 510, 1020 m radius) and test all models including additive combinations and used only the covariates that had the strongest influence on the occupancy with a summed model weigh (w_i) <50%.

We fitted occupancy models in the package Unmarked version 3.1.1. for R (Fiske et al., 2011), using the logit link function and 2000 bootstraps to assess the adjustment fit (P). We only consider those candidate models for which their confidence intervals did not include 0 in their informative predictors. Models were compared using AIC scores and weighs, and we only considered competitive models those with a $\Delta AIC \leq 2$ (Burnham & Anderson, 2004).

We evaluated the accuracy of our best candidate model by calculating the receiver operator characteristic (ROC) curve. The area under the ROC curve is obtained by plotting sensitivity (number of true positive predictions) vs 1-specificity (number of false positives; Hanely & McNeil, 1982); therefore, it estimates the probability that a randomly chosen pair of occupied and unoccupied sites are correctly ranked. Usually, values of 0.5-0.7 indicate low accuracy, 0.7-0.9 indicate useful application and values >0.9 indicate high accuracy (Manel et al., 2001). Additionally, we determined the optimal threshold value for assigning occupancy (Liu et al., 2005). Therefore, we defined occupancy areas with probabilities ≥ to the threshold optimal value as potential habitat, and areas < to the optimal threshold value as non-habitat. To implement the analysis, we used a database of 58 Baird´s tapir records from the region obtained from biological data-sets (National System of Information on Biodiversity-CONABIO-Mexico), other researchers (Mendoza et al., 2013) and records collected by us through camera traps and sights (footprints and scats). We used the package pROC for R (Robin et al., 2011) for the analysis.

Population size in the Sierra Madre de Chiapas. To calculate the tapir occupancy probability in each cell (30m pixel) of the study area, we used the inverse logit function applying the information of the best occupancy model in the Raster Calculator tool of ArcGIS 10.2 (ESRI, 2013). We used the forest cover with values >75% as an input mask data to extract the values of the occupancy raster. Using the new raster of occupancy, we classify the values of the occupancy probability into three intervals: 1) low occupancy: from the upper confidence interval threshold to discriminate habitat from no habitat obtained from the ROC analysis (0.2) to 0.59; 2) medium occupancy: from 0.6 to 0.89; and 3) high occupancy: from 0.9 to 1.0. We converted the raster into polygons and calculated the surface area for each classification. In order to provide an estimate of the population size of Baird´s tapir in the Sierra Madre de Chiapas, we extrapolated density estimations using the mean density of each model and extrapolate to each interval.

Results

During a total sampling effort of 2,975 camera days, we obtained 426 photographs of Baird´s tapir. Of these 38 were independent records, considering 24h as an independence criterion, which results in a relative abundance of 1.3 photographs/100 camera days. We were able to identify 9 different individuals, including one calf (Table 2). However, for the purpose of the study, we did not consider juveniles for the density estimations. Additionally, we had 9 independent tapir photographs that could not be assigned to any identified individual (Table 2).

The estimated density for Baird´s tapir using SCR model was 0.08 ind/km^2 (IC: 0.039-0.16). Capture probability at home-range center (g0) was estimated at 0.04 ± SE 0.01 and sigma value of 655.2 m ±SE 77.9 m. For the density estimation using the SMR model, we obtained a density of 0.10 ind/km^2 (IC:0.08-0.14), with an estimate of 0.04 ± SE 0.01 for g0 and a sigma of 655.2 m ±SE 77.9 m. For the REM we obtained a density estimation of 0.26 ind/km^2 (IC:0.12-0.41).

Occupancy models. We obtained 154 independent detections of Baird´s tapir over 25 of the 55 sampling sites that produced a naive occupancy estimates of 0.45 and 0.40 for detectability. According to the Akaike Information Criterion (ΔAIC), the first two candidate models had strong support (<2) to explain the occupancy and detectability of Baird´s tapir in the SMC (Table 3). Both models included the covariates SHA240 and ELE1020 for the occupancy and DE90, ELE90 and EFFORT for detectability. In the case of the second-best candidate model, the covariate TPI90 was included, however, it was not a good predictor because the 95% of the confidence intervals overlapped.

For the best candidate model, both covariates, ELE1020 and SHA240, had positive relationship with tapir occupancy, which means that occupancy increase in higher elevation sites (probability of occupancy and the probability of detectability ψ=0.05-0.84) and when topographic heterogeneity was greater (ψ=0.00-0.99). For detectability, the three covariates, ELE90, DE90 and EFFORT had positive correlations, where detectability increased at higher elevations (p=0.01-0.10), when distance to deforested patches increased (p=0.01-0.13) and when the sampling effort was greater (p=0.05-0.33).

The Area under the Receiver Operating Characteristic Curve (AUC) for the best occupancy model was 79.7% (CI 95%: 75.4-84%). Model sensitivity (ability to correctly predict species presence) and specificity (ability to correctly predict species absent) were 81% (CI: 72.8%-96.5%) and 30.5% (CI: 19.7%-47.17%) respectively. The optimum threshold value to discriminate habitat from no habitat of Baird´s tapir was 0.02% (0.01% – 0.2%).

Population size in the Sierra Madre de Chiapas. Using the best occupancy model, we calculated the area of occurrence for tapirs in the SMC, which encompassed a maximum area of 2,305 km^2 (considering the 3 occupancy intervals; Fig 4).

Table 4 shows the estimated population size for each occupancy interval and table 5 the estimated population size for each Natural Protected Area in the SMC. Considering the medium and high occupancy intervals (1660 km^2) combined with the SMR density estimates we obtained a population size of 166 (IC: 133-232) individuals for the SMC and using the three occupancy intervals (2305 km^2) 231 (IC: 184-323) tapir individuals for the entire region.

Discussion

Mean tapir density estimation was higher using the REM model compared to the spatially explicit models. The SCR model provide the lowest density estimation, in comparison with the SMR (Fig. 3). However, the three models overlapped their 95% confidence intervals (CI), indicating no significant differences between them. SMR had the smallest CI, representing the most precise density estimation from the three models.

Considering density estimates of Baird´s tapir from the SCR model, we obtained one of the lowest tapir densities for the entire distribution range, only above the lower density value calculated for the Sierra Madre de Oaxaca, and between 1 and 36 times lower than any other recent studies (Table 6).

Although our low densities may be due to some conservation issues including poaching and habitat loss (de la Torre et al. 2018), it is more likely that the large variations seen across previous studies are related to data quality and methods used for data analysis. For example, in studies that used traditional capture-recapture models (TCR) which resulted in the highest density values (Mejía-Correa et al., 2010; González-Maya et al., 2012; Botello et al., 2017; Camacho, 2018), most studies deployed ≤10 camera trap stations with an effective sampling area (ESA) values between 7-19 km^2 (Table 6) estimated through the ½ Mean Maximum Distance Moved (MMDM), which have been proven to an overestimate densities of different species (Soisalo & Cavalcanti, 2006; Noss et al., 2012; Tobler & Powell, 2013). Therefore, it is important to meet all the criteria, including camera traps polygons several times larger than the average species home range and sufficient number of camera traps to ensure recaptures of different individuals, to obtain a reliable density estimate (Obbard et al., 2010; Gerber et al., 2012; Noss et al., 2012). TCR can provide accurate density estimates, however, it requires to estimate the sampled area based on empirical approaches (Parmenter et al., 2003; Sharma et al., 2010) which has been proven to have recognized statistical disadvantages (Efford, 2004; Soisalo & Cavalcanti, 2006; Gopalaswamy et al., 2012). Additional deficiencies include the fact that although spatial information related to the animal home range and movement obtained from camera trap locations is available, it is not fully exploited, which is important because the probability of an individual being captured in the camera trap depends on an overlap in their activity area and the location of camera traps (Gopalaswamy et al., 2012). Therefore, the spatially explicit capture recapture models can be a better approach to estimate densities (Noss et al., 2012).

Our REM density estimate was higher but not significantly different (i.e. overlapping 95% CI) than those obtained with the SCR and SMR models (Fig 3). However, their CI were the largest of the three models. This was probably because gas model does not represent accurately how animals move in space and the speed of movement parameter was not available for our study site which produced a bias in the estimation since the model is very sensitive to this parameter (Rovero & Marshall, 2009). Additionally, the script we used only considered the mean of r and θ values of the set of camera traps and not the individual value for each camera trap, which can lead to a skewed density estimate (Rovero & Marshall, 2009).

We also found that our REM mean density estimate (0.26 ind/km^2) was higher than that obtained by Carbajal-Borges et al., (2014) for the same region (Table 6). However, as we mentioned above, one of the main limitations of this model is its sensitivity to the speed of the species movement. In this case, we used 6 km/day and Carbajal-Borges et al (2014) used 14.4 km/day. If we re-calculate density using 14.4 km/day, our estimate decreases to 0.10 ind/km^2 (IC:0.05-0.17), lower than Carbajal Borges et al. (2014) and closer to those obtained with the SCR and SMR models. Other authors (Lavariega-Nolasco et al., 2016; Camacho, 2018) had difficulties for finding a speed parameter for their study area, so they used a range of speeds (7-21.6 km/day). Nevertheless, this could lead to estimations become unreliable and inaccurate (Table 6).

Other studies that compared REM against other models (e.g. SCR, line transect), found similar density estimates and more precise results than line transects (Zero et al., 2013; Anile et al., 2014). However, these studies used available data from GPS collars from the same study site to estimate movement speed (Zero et al., 2013). Therefore, REM can be a very promising model to estimate densities for unmarked populations, because it does not require the individual identification, but unless accurate speed of movement is available for the study site, it would be challenging to estimate a reliable and unbiased density values.

Spatially explicit models have proven to be very effective to estimate densities of natural marked and in recent years, unmarked animals (Anile et al., 2014; Rich et al., 2014; Kane et al., 2015; Srivathsa et al., 2015). In our study, although both had similar results, SMR produced a slightly higher density estimate with smaller confidence intervals than SCR. This is likely because SMR uses all the available information, including the encounter data from the marked individuals which provide movement and detection information and the count data of unmarked individuals (Chandler & Royle, 2013; Royle et al., 2014). The inclusion of data from unmarked individuals could help improve density estimates that would be biased low if a large proportion of photographs cannot be attributed to individuals (Chandler & Royle, 2013).

Previous studies also showed that SMR improved density estimates for species without individual marks compared to other models including SCR, TCR and non-spatial mark-resight (Rich et al., 2014; Kane et al., 2015). Additionally, Chandler & Royle, (2013) demonstrated using simulations that SMR estimations where more precise and less biased than those using only marked individuals. Nonetheless, it is important to consider some potential limitations of the SMR assumptions, especially when camera traps are used: 1) no marks are lost between marking or resighting and; 2) all individuals are correctly identified as marked or unmarked (Royle et al., 2014). Both assumptions can be easily violated if fuzzy records are used or where only parts of the individual are shown in the photographs or if temporary marks are used (presence of ticks or botflies) which can lead to misidentification of marked and unmarked individuals. Other limitations are the time identify individuals and the uncertainty associated with the identification. However, several studies on tapirs were able to be consistent in the number of identified individuals between researchers (González-

Maya et al., 2012; Tobler et al., 2013), and identification can improve especially when results are discussed and integrated among several researchers (Tobler et al., 2013).

In this study we used the null model for SCR and SMR density estimates to allow for direct comparison. However, the advantage of spatially explicit models is that there are multiple ways to improve modeling. We can specify different sources of variation in the encounter probability including individual heterogeneity, site and individual covariates such as sex, age classes or habitat type, time variation and behavioral response to capture (Royle et al., 2014; Efford, 2019) which can affect parameter estimates (σ, λ), and if correctly applied, can improve accuracy in density estimation. Therefore, spatially explicit models can be a very flexible and versatile tool to monitor effectively populations across regions and over time (Kane et al., 2015).

This is the first study to estimate Baird´s tapir density using camera traps in combination with two spatially explicit models and REM. These comparisons allowed us to identify their limitations and, although there is no ground truth with which to compare our study estimates, the results suggest that the SMR produced the most accurate density estimate that can be used as a baseline estimates for Baird´s tapir in the SMC. Although many details of the model need to be explored and improved (Chandler & Royle, 2013; Royle et al., 2014), SMR holds a great potential to address density estimation problems from unmarked species.

Population size in the Sierra Madre de Chiapas. We applied our best occupancy model to the entire landscape of the SMC to identify the areas with the greatest likelihood of Baird´s tapir occurrence. We then used our density estimates to predict the total population size or Baird's tapir in the SMC. Although spatial extrapolations can be challenging, and their limitations should be considered, they can be a very useful resource when large-scale data collection is hampered by logistical, financial and technical limitations (Miller et al., 2004).

We chose occupancy modeling because they have proven to be efficient tools for predicting the presence of a species as a function of habitat covariates while accounting for imperfect detection (MacKenzie et al., 2006). Although results have to be taken with caution, we found convenient to extrapolate density estimates to the SMC, since the region has similar characteristics throughout its landscape, including rugged and mountainous terrain, similar vegetation types, climate, social context and Baird´s tapir facing the same threats in all parts of the SMC (Naranjo, 2009).

Our occupancy model results suggest that Baird´s tapir presence is associated with higher elevations and rugged terrain, which are found in the most remote areas of the SMC, where human presence is scarce or limited (for more discussion see de la Torre et al. 2018). However, the area of occurrence of the species turned out to be smaller than estimated by de la de la Torre et al., (2018) since occupancy models did not consider significant forest cover covariate. Consequently, we created a forest cover >75% as an input mask data to extract the occupancy values, which strongly reduced these areas.

Considering only the medium and high occupancy intervals (1660 km^2) combined with the SMR density estimates we obtained a population size of 166 (CI: 133-232) individuals for the SMC, which is lower than 225 individuals estimated by Naranjo (2009) for the same region and similar area (1,500 km^2). Yet, including the lower occupancy interval (645 km^2), population size increases to 230 (CI: 184-323) individuals. Still, lower occupancy intervals must be treated cautiously, because occurrence probability is less than 60%. Furthermore, these areas are closer to towns, roads, livestock and agricultural lands, which limits tapir presence because threats are higher in these areas. Finally, protected areas comprised around 1,700 km^2 of habitat for Baird´s tapir (including the lower occupancy interval), however, outside there are an additional 500 km^2 of unprotected habitat, which could be sustaining an important number of tapirs (Table 5).

Conservation Implications

The SMC harbours one of the six remaining Baird's tapir populations in Mexico, and the area is critical for maintaining connectivity between the mountain (Selva Zoque and Chimalapas) and the rainforest (Selva Lacandona) tapir populations (de la Torre et al., 2018; Schank et al., submitted).

Our findings support the need to strengthen the existing protection in the four protected areas of the SMC. If we compare our results with those obtained by Naranjo (2009), the SMC tapir populations have decreased by around 30% in the last 10 years, and if this trend continues there will be only around 100 individuals by 2029. Therefore, we suggest that the NRPA La Frailescana should be reclassified to a higher category of protection (e.g. Biosphere Reserve), since it is located in the middle of two Biosphere Reserves El Triunfo and La Sepultura, and the lack of national park personnel to carry out monitoring and surveillance activities and economic resources to implement conservation actions in this area, may harm the connectivity within the SMC and fragment even more Baird´s tapir and other wildlife populations that inhabit this region. Future work may focus on validating areas where there is no information on population status of this species such as the State Reserve, Pico del Loro Paxtal and unprotected areas. Additionally, it is a priority to consider the protection of the 500 km^2 of unprotected areas through different schemes including payments for ecosystem services for the communal and private lands (de la Torre et al., 2018; Schank, et al. submitted), and for national lands, including these within extant protected areas of the SMC. Throughout this process, the inclusion and participation of local communities in decision-making processes must be encouraged to strengthen strategies and conservation actions. It will be necessary to promote social organization and improve land use planning and management in local communities to identify and prioritize conservation needs.

Fostering sustainable alternatives can alleviate and reduce the impact on hunting and habitat loss in the SMC. For example, in previous years, large quantities of shade-grown coffee plantations, one of the main agricultural products in the region, were lost to coffee leaf rust (*Hemileia vastatrix*). Nowadays, producers are acquiring sun coffee trees which they believe are more resistant to plague, but this practice, is generating forest loss in sites that were previously conserved. In this way, it is important to bring new technologies and alternatives that can help solve the problems of the communities and promote conservation of Baird´s tapir habitat.

If we want to ensure Baird´s tapir conservation and protection in the SMC we will need to work together local and federal governments, civil society, NGO´s and local communities to strengthen protected areas and develop sustainable alternatives that allow the coexistence of tapirs and the development of local communities.

Author contributions MR conceptualized the study. MR, JAT, RRH, MWT and EJN design the study. MR, JAT and GC compiled the information and set camera traps. MR drafted the manuscript. JAT, MWT, EJN, CAJ, RAM and RRH, reviewed and improved the manuscript.

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Conflicts of interest None

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TABLE 1 Description of covariates used to model variation in detectability (p) and occupancy (ψ) across sites.

Type	Variable name	Abreviation	Description
Forest cover	Forest Cover	C	Percentage of forest coverage around the pixel
	Primary forest (> 75% of forest cover)	PFor75	Amount of primary forest (> 75%) around each pixel
	Primary forest (> 90% of forest cover)	PFor90	Amount of primary forest (> 90%) around each pixel
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.
	Elevation	ELE	Elevation (mals)
	Shannon Topographic Index	SHA	Differences of ranges of elevation values within a different radius.
Human	Distance to towns	DistT	The minimum distance (Euclidian) to the nearest town
	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)
	Distance to paved roads	DistR	The minimum distance to the nearest paved roads
	Distance to deforestation edge	DE	The nearest distance to the deforested patch>0.5 km2
Site covariates	Season of the year	SEASON	Season of the year when the camera trap station was active; dry or Rainy season
	Sampling effort	EFFORT	Number of active days of the camera trap stations

TABLE 2 Demography of the Baird´s tapir captures (n=9) and recaptures of marked and number of unmarked individuals obtained from camera trapping survey between April to July 2018.

Tapir capture	Number of individually marked tapir captures	Number of individually marked tapir (recaptures)	Number of unmarked (unidentifiable) tapirs
Adult males	5	4 (12)	5
Adult females	3	4 (16)	0
Juvenil	1	1 (6)	0
Sex undetermined	0	0	5

TABLE 3 Summary of our model-selection procedure examining variables affecting the probability of occupancy and detectability of the Baird´s tapir from August 2015 to December 2016. We report the model rank, Akaike’s Information Criterion (AIC_C) relative difference in AIC compared to the top-ranked model (ΔAICc), the AIC model weight (w_i) and the number of parameters in the model (K). See Table 1 for description of the covariates. Numbers after the variable represent the window area: 30m, 90m, 510m, 1020m and (.) as constant.

Rank	Model	AICc	Δ AIC	Weight (w_i)	K
1	Ψ(SHA240 + ELE1020); p(DE90+ ELE90 +EFFORT)	506.00	0.00	0.33	7
2	Ψ(SHA240 + ELE1020 +TPI90); p(DE90+ ELE90 +EFFORT)	507.50	1.57	0.15	8
3	Ψ(SHA240 + ELE1020+ PFor75); p(DE90 + ELE90+ EFFORT)	508.50	2.48	0.10	8
4	Ψ(SHA240 + ELE1020 +C1020); p(DE90 + ELE90+ EFFORT)	508.60	2.61	0.09	8
5	Ψ(SHA240); p(DE90 +ELE90 +EFFORT)	509.00	2.99	0.08	6
6	Ψ(SHA240 + C1020); p(DE90 + ELE90+ EFFORT)	509.40	3.47	0.06	7
7	Ψ(SHA240 + TPI90); p(DE90 +ELE90 +EFFORT)	509.50	3.55	0.06	7
8	Ψ(SHA240+ PFor); p(DE90 +ELE90 +EFFORT)	510.70	4.75	0.03	7
9	Ψ(C1020 + ELE1020 +TPI90 +SHA240 + RIO1020+ PFor90 + PFor75); p(DE90 + ELE90+ EFFORT)	513.00	7.03	0.01	12
10	Ψ(ELE1020); p(DE90 +ELE90 + EFFORT)	517.50	11.51	0.001	6

TABLE 4 Baird´s tapir population estimates in the Sierra Madre de Chiapas considering the contribution of each occupancy intervals: low (0.2-0.59), medium (0.6-0.89) and high (0.9-1.0) for each of the density models, SECR, SEMR and REM. ICI: Inferior Confidence Interval; UCI: Upper Confidence Interval.

Occupancy intervals	Area km^2	SECR			SEMR			REM		
		LCI	Mean	UCI	LCI	Mean	UCI	LCI	Mean	UCI
		0.4 (Ind/km^2)	0.08 (Ind/km^2)	0.16 (Ind/km^2)	0.08 (Ind/km^2)	0.1 (Ind/km^2)	0.14 (Ind/km^2)	0.12 (Ind/km^2)	0.26 (Ind/km^2)	0.41 (Ind/km^2)
Low (0.2-0.6)	645	26	**52**	103	52	**65**	90	77	**168**	264
Medium (0.6-0.9)	622	25	**50**	100	50	**62**	87	75	**162**	255
High (0.9-1.0)	1038	42	**83**	166	83	**104**	145	125	**270**	426

TABLE 5 Population estimates inside each of the Natural Protected Areas (NPA) of the Sierra Madre de Chiapas considering the contribution of each of the occupancy categories: low (0.2-0.59), medium (0.6-0.89) and high (0.9-1.0) for each of the density models, SECR, SEMR and REM. ICI: Inferior Confidence Interval; UCI: Upper Confidence Interval.

Occupancy intervals	NPA	Area km^2	**SECR**			**SEMR**			**REM**		
			ICI	Mean	UCI	ICI	Mean	UCI	ICI	Mean	UCI
			0.4 (Ind/km^2)	0.08 (Ind/km^2)	0.16 (Ind/km^2)	0.08 (Ind/km^2)	0.1 (Ind/km^2)	0.14 (Ind/km^2)	0.12 (Ind/km^2)	0.26 (Ind/km^2)	0.41 (Ind/km^2)
Low (0.2-0.6)	Sepultura	113	5	9	18	9	11	16	14	29	46
	Frailescana	106	4	8	17	8	11	15	13	28	43
	Triunfo	163	7	13	26	13	16	23	20	42	67
	Pico del Loro Paxtal	73	3	6	12	6	7	10	9	19	30
	Unprotected	190	8	15	30	15	19	27	23	49	78
	Total	*645*	*26*	*52*	*103*	*52*	*65*	*90*	*77*	*168*	*264*
Medium (0.6-0.9)	Sepultura	88	4	7	14	7	9	12	11	23	36
	Frailescana	82	3	7	13	7	8	11	10	21	34
	Triunfo	202	8	16	32	16	20	28	24	53	83
	Pico del Loro Paxtal	98	4	8	16	8	10	14	12	25	40
	Unprotected	152	6	12	24	12	15	21	18	40	62
	Total	*622*	*25*	*50*	*100*	*50*	*62*	*87*	*75*	*162*	*255*
High (0.6-1.0)	Sepultura	86	3	7	14	7	9	12	10	22	35
	Frailescana	74	3	6	12	6	7	10	9	19	30
	Triunfo	444	18	36	71	36	44	62	53	115	182
	Pico del Loro Paxtal	243	10	19	39	19	24	34	29	63	100
	Unprotected	191	8	15	31	15	19	27	23	50	78
	Total	*1038*	*42*	*83*	*166*	*83*	*104*	*145*	*125*	*270*	*426*

TABLE 6 Baird´s tapir density estimation obtained in other studies throughout its distribution range using Traditional Capture Recapture (TCR) Models and Random Encounter Model (REM). NCTS: Number of Camera Trap Stations; NCTD: Number of camera trap days; IP: Number of Independent photographs; NIT: Number of identified tapirs; SR: Speed Rate in km/day; ESA: Effective Sampled Area in km²; MDE: Mean Density Estimate in ind/km².

Study area	Method	NCTS	NCTD	IP	NIT	SR km/day	ESA (km^2)	MDE (ind/ km^2)	Source
México									
Sierra Madre de Oaxaca	REM	51	3215	65	-	7-21.6		0.07-0.24	Lavariega-Nolasco, et al, 2016
Totontepec Villa de Morelos	TCR	7	592	43	9	-	18.75	0.32	Botello, et al. 2017
Sierra Mixe	TCR	4-7	-	3-26	5-7		10-17	0.43-0.54	Vázquez Camacho, 2018
Sierra Mixe	REM	4-7	-			7-21.6	-	0.03-0.95	Vázquez Camacho, 2018
El Triunfo	REM	25	3,817	54		14.4		0.12	Carbajal-Bojorquez, et al, 2014
Costa Rica Talamanca	TCR	10	540	77	15		7.16	2.93	González-Maya, et al, 2012
Colombia Los Katios	TCR	27	1215	48	13	-	13.68	1.02	Mejía-Correa, et al, 2014

FIG. 1Study area showing the four Natural Protected Areas inside the Sierra Madre de Chiapas, and the location of the camera traps that were used to perform density estimate analysis.

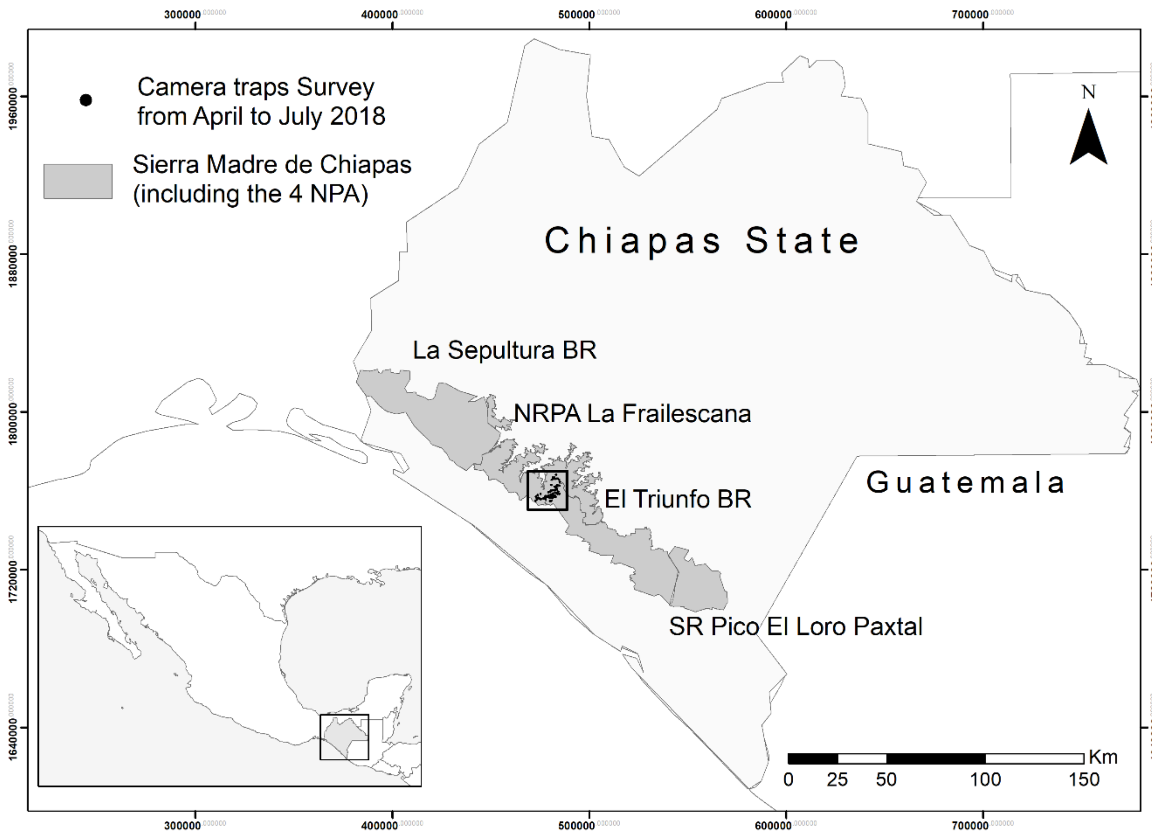


FIG. 2 Camera-trap layout used in 2015-2016 and 2018 in La Frailescana. Purple dots correspond to the 2015-2016 camera trap survey used to perform occupancy models. Green squares and triangles correspond to the 2018 camera trap survey to estimate Baird´s tapir density in the Sierra Madre de Chiapas.

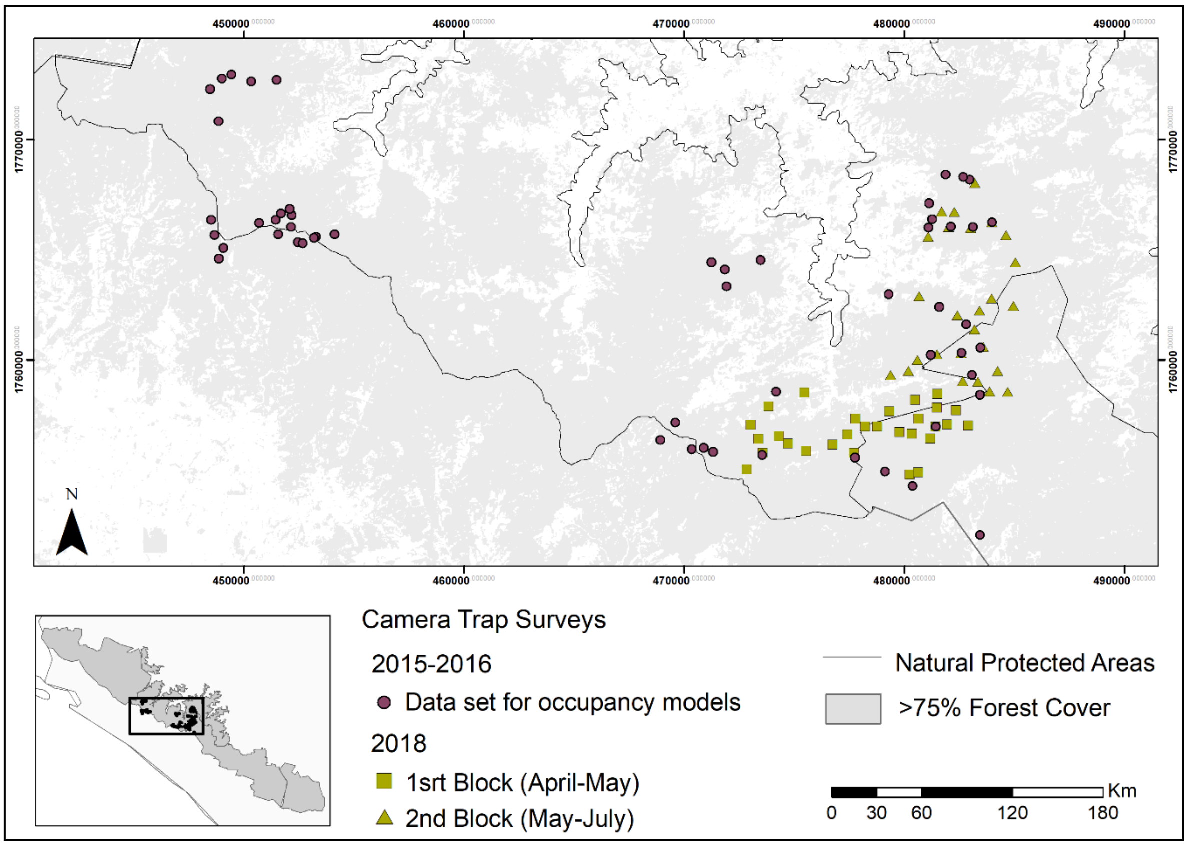


FIG. 3 Comparison of density estimates for Baird´s tapir in the Sierra Madre de Chiapas, obtained by camera trapping survey and using three different models: Spatially Explicit Capture-Recapture (SECR), Spatially Explicit Mark Resight (SEMR) and Random Encounter Model (REM). Whiskers represent the 95% confidence intervals.

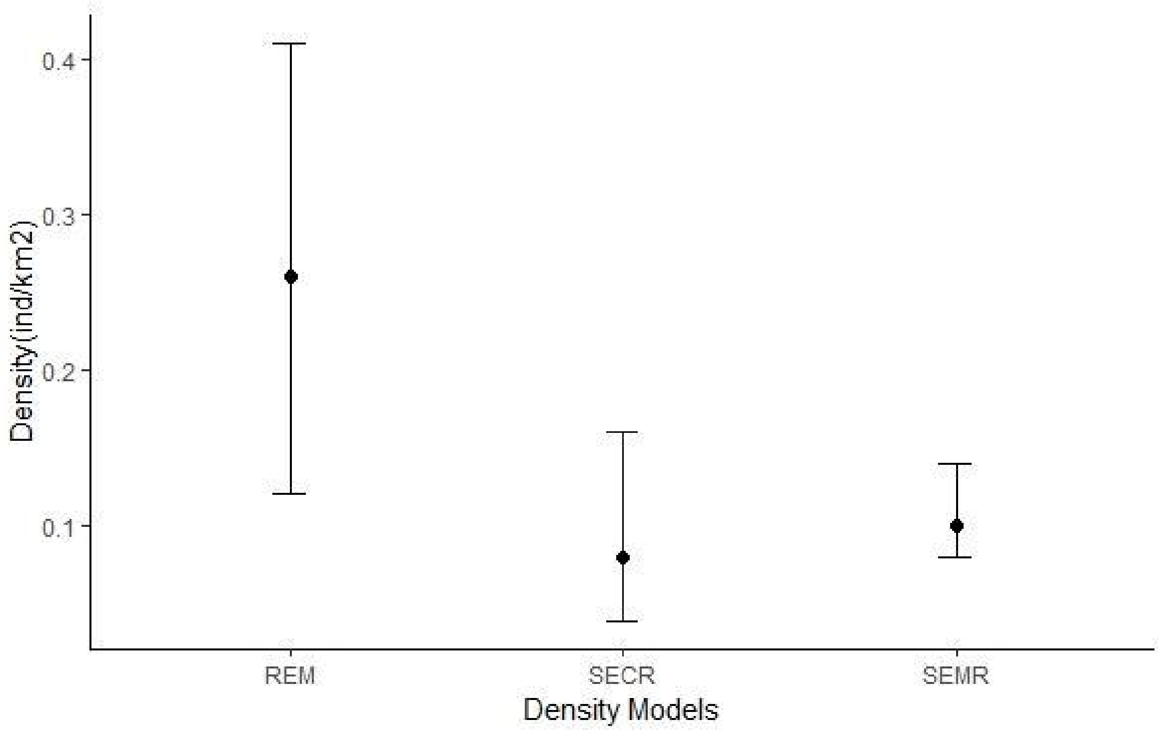
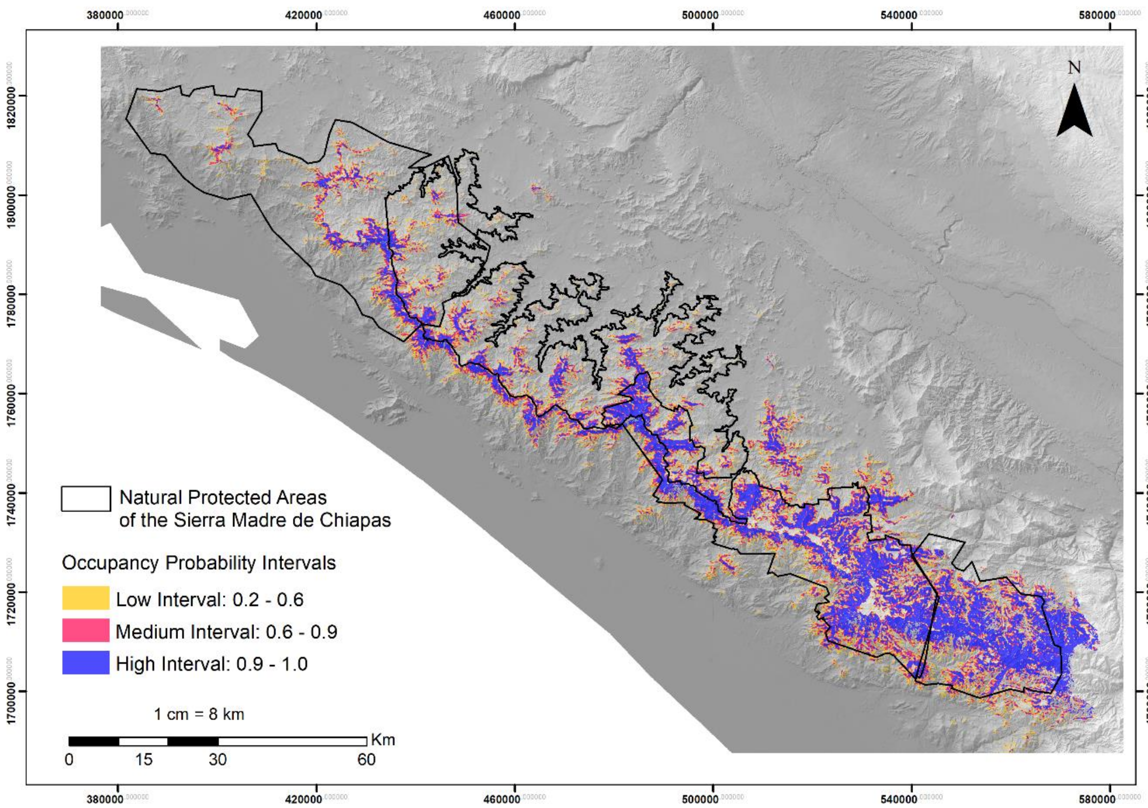


FIG. 4 Map showing the probability of occupancy of the Baird´s tapir in the Sierra Madre de Chiapas. Probability of occupancy were classified in three intervals: 1) low occupancy: from 0.2 to 0.6 (yellow); 2) medium occupancy: from 0.6-to 0.9 (red); and 2) high occupancy: from 0.9-1.0 (blue).



Conclusiones

Contar con el tamaño y densidad de individuos de una población es fundamental para evaluar el estado y las políticas de conservación enfocadas a cualquier especie en peligro de extinción. Sin embargo, estos parámetros son difíciles de estimar, especialmente para especies sin patrones de marcas naturales, como en el tapir centroamericano.

En este estudio utilizamos registros fotográficos obtenidos por trampas cámara para estimar la densidad del tapir centroamericano en la Sierra Madre de Chiapas. Utilizamos los modelos de captura-recaptura espacialmente explícitos (SCR) y comparamos sus limitaciones y requerimientos metodológicos con nuevos modelos que incluyen el de marcaje-recaptura espacialmente explícito (SMR) y el modelo de encuentro aleatorio (REM).

Los resultados demostraron que las estimaciones de densidad del tapir centroamericano no difirieron significativamente entre los tres modelos, ya que hubo un traslape entre los intervalos de confianza (IC) del 95%. La estimación de la densidad fue más alta y menos precisa al usar el REM 0.26 ind / km2 (IC: 0.12-0.41) en comparación con los modelos espacialmente explícitos. El modelo SCR proporcionó la estimación de densidad más baja 0.08 ind/km^2 (IC: 0.039-0.16) en comparación con el SMR 0.10 ind/km^2 (IC: 0.08-0.14), sin embargo, SMR tuvo los intervalos de confianza más pequeños, lo cual indica que esta estimación de densidad fue la más precisa.
Por otro lado, utilizamos los modelos de ocupación para identificar las áreas de mayor probabilidad de presencia de la especie y así poder contar con un área a la cual extrapolar las densidades obtenidas con los modelos de densidad, para poder predecir su tamaño poblacional en la Sierra Madre de Chiapas (SMC).

Utilizando el mejor modelo de ocupación, calculamos un total de 2,305 km^2 como área de ocupación para los tapires en la SMC. Sin embargo, para poder realizar la extrapolación de densidad, dividimos el área identificada en tres categorías de acuerdo con su probabilidad de ocupación: 1) probabilidad baja (0.2-0.59); 2) probabilidad media

(0.6-0.89) y; 3) probabilidad alta (0.9-1.0). Posteriormente, utilizamos el promedio de densidad obtenido del SMR, que fue el más preciso de los tres modelos y lo multiplicamos por el área de cada una de las categorías identificadas.

Teniendo en cuenta solo las áreas con intervalos de ocupación medio y alto (1660 km^2) y utilizando la estimación de densidad de SMR, obtuvimos un tamaño poblacional de 166 individuos (IC: 133-232) para toda la SMC. Si incluimos las áreas con un intervalo de ocupación más bajo (645 km^2), el tamaño de la población aumenta a 230 individuos (IC: 184-323). Sin embargo, es importante tomar en cuenta que el intervalo más bajo de ocupación tiene una probabilidad de ocupación menor al 60%, por lo que este último resultado debe de tratarse con cautela. Además, estas áreas se encuentran más cerca de ciudades, caminos, ganado y cultivos, lo cual limita la presencia de los tapires porque las amenazas son mayores.

Este es el primer estudio que estima la densidad del tapir centroamericano utilizando trampas cámara en combinación con dos modelos espacialmente explícitos (SCR y SMR) y el modelo de encuentro aleatorio (REM). Este trabajo nos permitió realizar comparaciones e identificar las limitaciones de cada uno de los modelos y, aunque no conocemos el número real de individuos que hay en la región y con la cual podamos comparar las estimaciones de nuestro estudio, los resultados sugieren que el SMR produjo la estimación de densidad más precisa. Sin embargo, aunque se deberán explorar y mejorar muchos detalles del modelo (Chandler y Royle 2013; Royle et al. 2014), tiene un gran potencial para abordar los problemas de estimación de densidad de especies sin marcas naturales como el tapir centroamericano.

Nuestros resultados respaldan la necesidad de fortalecer la protección existente en las cuatro áreas protegidas del SMC, para mantener la conectividad dentro del SMC y fomentar la recuperación de las poblaciones de tapir centroamericano y otras poblaciones de fauna silvestre que habitan en esta región.

Por otro lado, en futuros proyectos se deberá enfocar la validación de áreas donde no hay información sobre el estado de la población de esta especie, como la Reserva Estatal, el Pico del Loro Paxtal. Además, deberá ser una prioridad considerar la protección de las áreas que no se encuentran protegidas a través de diferentes esquemas, incluyendo pagos por servicios ambientales para las tierras que son comunales y privadas (de la Torre et al. 2018; Schank et al. sometido), e incluir los terrenos nacionales dentro de las áreas protegidas existentes del SMC.

Se deberá fomentar la inclusión y participación de las comunidades locales en los procesos de toma de decisiones para fortalecer las estrategias y acciones de conservación. Será necesario promover la organización social y mejorar la planificación y el uso de la tierra por medio de ordenamientos territoriales en las comunidades locales para identificar y priorizar las necesidades de conservación.

Finalmente, se deberán fomentar alternativas sostenibles que puedan reducir el impacto en la caza y la pérdida de hábitat en el SMC, por medio de nuevas tecnologías y alternativas que ayuden a mitigar los problemas sociales en las comunidades y promover la conservación del hábitat del tapir centroamericano.

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