

Research Article

Density, abundance and activity patterns of the endangered *Tapirus bairdii* in one of its last strongholds in southern Mexico

Juan Paulo Carbajal-Borges¹, Oscar Godínez-Gómez² and Eduardo Mendoza^{2*}

¹Laboratorio de Ecología de Poblaciones y Comunidades Tropicales - Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México. Antigua Carretera a Pátzcuaro 8701, Colonia Ex-hacienda de San José de la Huerta. Morelia, Michoacán, CP. 58190. México. (elcoacervado@gmail.com); ²Laboratorio de Análisis y Conservación de la Biodiversidad - Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo. Avenida San Juanito Itzicuaro s/n., Colonia Nueva Esperanza. Morelia, Michoacán, C. P. 58337, México. (oscjaguar@gmail.com)

*Corresponding author E-mail: mendoza.mere@gmail.com, Phone and fax: +52 (443) 327-2350 and 327-2351.

Abstract

Baird's tapir (*Tapirus bairdii*) is one of the most emblematic mammalian species from Mesoamerica. Due to its level of evolutionary distinctiveness and anthropogenic threat this species was recently ranked in 34th position, in terms of its urgency for conservation, among more than 4,000 species of mammals assessed by experts from the Zoological Society of London. Despite its evolutionary and conservation relevance there remain important gaps in knowledge of the basic ecology of this species. Based on camera-trapping data, we estimated Baird's tapir abundance and analyzed its patterns of daily activity and preference for different altitude intervals in El Triunfo Biosphere reserve, one of the last strongholds for this species in southern Mexico. We also applied a recently developed method (Random encounter model) to estimate tapir density without the need of individual identification. Tapir relative abundance was: 1.3 events/100 camera-trap days and density: 0.12 ind./km². Tapir activity concentrated around dusk ($\chi^2=21.18$, $P<0.01$) and use of mid-altitude areas was preferred ($\chi^2=49$, $P < 0.001$). This study provides data on the ecology of the species and insights on study methods that can have a direct positive impact on its management and conservation.

Keywords: density estimation, camera-trapping, cloud forest, mammal threat, daily activity

Resumen

El Tapir o Danta centroamericana (*Tapirus bairdii*) es una de las especies de mamífero más notables de Mesoamérica. Debido al grado de amenaza que experimenta y a que representa una línea evolutiva muy distintiva, esta especie fue recientemente colocada en el lugar 34, en términos de la prioridad de su conservación, entre más de 4,000 especies de mamíferos evaluados por expertos de la Sociedad Zoológica de Londres. A pesar de esto, persisten importantes vacíos en el conocimiento de la ecología básica de esta especie. Con base en un estudio de foto-trampeo estimamos la abundancia de *T. bairdii* y analizamos sus patrones de actividad, a lo largo del día, y de uso de sitios a lo largo de un gradiente altitudinal en la Reserva de la Biosfera de El Triunfo, uno de los últimos refugios de la especie en el sureste de México. Asimismo, aplicamos un método recientemente desarrollado (Modelo de encuentros aleatorios) para estimar la densidad del tapir sin la necesidad de realizar identificación individual. Los valores estimados de abundancia relativa de la especie y densidad fueron: 1.3 eventos/100 días cámara-trampa y 0.12 ind./km². La actividad del tapir se concentró alrededor del anochecer ($\chi^2=21.18$, $P<0.01$) y en la zonas de altitud media ($\chi^2=49$, $P < 0.001$). Este estudio presenta información sobre la ecología básica de la especie y sobre aspectos metodológicos de su estudio que pueden impactar de manera positiva las prácticas para su manejo y conservación.

Palabras clave: estimación de densidad, foto-trampeo, bosque de neblina, mamíferos amenazados, actividad diaria.

Received: 16 October 2013; Accepted 24 January 2014; Published: 24 March 2014

Copyright: © Juan Paulo Carbajal-Borges, Oscar Godínez-Gómez and Eduardo Mendoza. This is an open access paper. We use the Creative Commons Attribution 3.0 license <http://creativecommons.org/licenses/by/3.0/us/>. The license permits any user to download, print out, extract, archive, and distribute the article, so long as appropriate credit is given to the authors and source of the work. The license ensures that the published article will be as widely available as possible and that your article can be included in any scientific archive. Open Access authors retain the copyrights of their papers. Open access is a property of individual works, not necessarily journals or publishers.

Cite this paper as: Carbajal-Borges, J. P., Godínez-Gómez, O. and 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* Vol.7 (1): 100-114. Available online: www.tropicalconservationscience.org

Introduction

Nearly three quarters of the mammalian diversity worldwide is imperiled by extinction due to anthropogenic impacts [1]. Large-bodied mammal species are particularly affected by these impacts as a consequence of having: a) life history traits (e.g., extensive habitat requirements, low densities and low reproductive rates) that make them specially sensitive to anthropogenic disruption and b) representing highly valued pieces for subsistence or commercial hunting [2-5]. Knowledge of population parameters (e.g., abundance, density and activity patterns) of large-bodied mammals is scant despite being essential for assessing their conservation status and designing sound management strategies. Fortunately, the increased accessibility and sophistication of camera-traps have revolutionized the study of wildlife. Standardized rates of picture recording (e.g., number of pictures/100 camera-trap days) are increasingly used as estimators of population abundance [6-8]. Yet calls for caution have been made about the risk of confounding variations in species detectability with differences in abundance [9-11]. In mammals having distinctive marks (e.g., stripes, spots and scars) camera-trapping allows individual identification, which has enabled use of mark-recapture models to estimate abundance and density [12-13]. This approach, however, is not applicable to the many mammal species that lack any distinctive markings. On the other hand, the capacity of camera-traps to continuously monitor animal activity has enabled researchers to describe daily activity patterns with a level of detail not possible previously [14-16].

Technologies such as camera-trapping are particularly important in the case of highly threatened species such as Baird's tapir (*Tapirus bairdii* Gill, 1865). This species is the largest mammal dwelling in the Neotropics (>250 kg). Moreover, it is the only native representative of the Perissodactyla in the region and one of the few evolutionary lineages that survived the wave of extinctions that impacted mega-herbivores during the end of the Pleistocene. Historic distribution of *T. bairdii* included most of southern Mexico, Central America and the northern portion of South America [17-18]. However, its current distribution is highly reduced and fragmented due to the impacts of habitat loss and hunting. According to specialists of the International Union for the Conservation of Nature, global Baird's tapir population has decreased by 50% in the last thirty years [19]. Due to its level of evolutionary distinctiveness and level of threat *T. bairdii* was recently ranked 34th in urgency for conservation among more than 4,000 mammalian species assessed by experts from the Institute of Zoology in London [20]. Despite its level of threat and its ecological and evolutionary relevance, important gaps exist in knowledge of the basic ecology of this species [21].

Our study estimates Baird's tapir abundance and density, describes its daily activity, and assesses its use of sites along an altitudinal gradient, based on camera-trapping data. This study is carried out in one of the last strongholds of the species in southern Mexico: the Biosphere Reserve of El Triunfo (BRET), Chiapas. Southern Mexico is a critical spot for the conservation of Baird's tapir because it is estimated to support nearly one-third of the species remaining global population (roughly estimated at 5,000 individuals) [19, 22]. Populations of Baird's tapir inhabiting mountain forests, such as those of the BRET, have been less studied than those in tropical

rain forests and seasonal forests [23]. The role of the BRET as a stronghold for Baird's tapir is increasing as human impact further reduces natural habitat extent and connectivity in Southern Mexico [24].

A secondary goal of this study is to test a novel method for estimating tapir density based on camera-trapping data. Mark-recapture methods to estimate tapir density have been challenging due to uncertainty in individual identification [7, 25]. It was only recently that Rowcliffe et al. [10] proposed a way to estimate animals density based on camera-trap data without the need of individual identification. This method, called the Random Encounter Model (REM), is based on mechanistic approaches used to describe rates of collisions between gas molecules [26]. The application of this method requires data directly obtained from camera-trapping as well as independent information about the camera-traps and the species under study. The few studies that have tested the effectiveness of REM have produced promising results [10, 27-29].

Methods

Study site

The El Triunfo Biosphere Reserve (BRET) is located in the central portion ($15^{\circ} 09' 10''$ - $15^{\circ} 57' 02''$ N and $92^{\circ} 34' 04''$ - $93^{\circ} 12' 42''$ W) of the mountain range of the Sierra Madre in the state of Chiapas, southern Mexico (Fig. 1). The BRET has a total extent of 119,177.3 ha, which are divided into five core areas and a buffer zone. The buffer zone has an extent of 93,355.2 ha. This work focuses specifically on the core zone I (CZ-I) which is the largest (11,550.0 ha) among the five core areas in the BRET and the one protecting the largest tract of well-conserved cloud forest (~7,210.0 ha) [30].

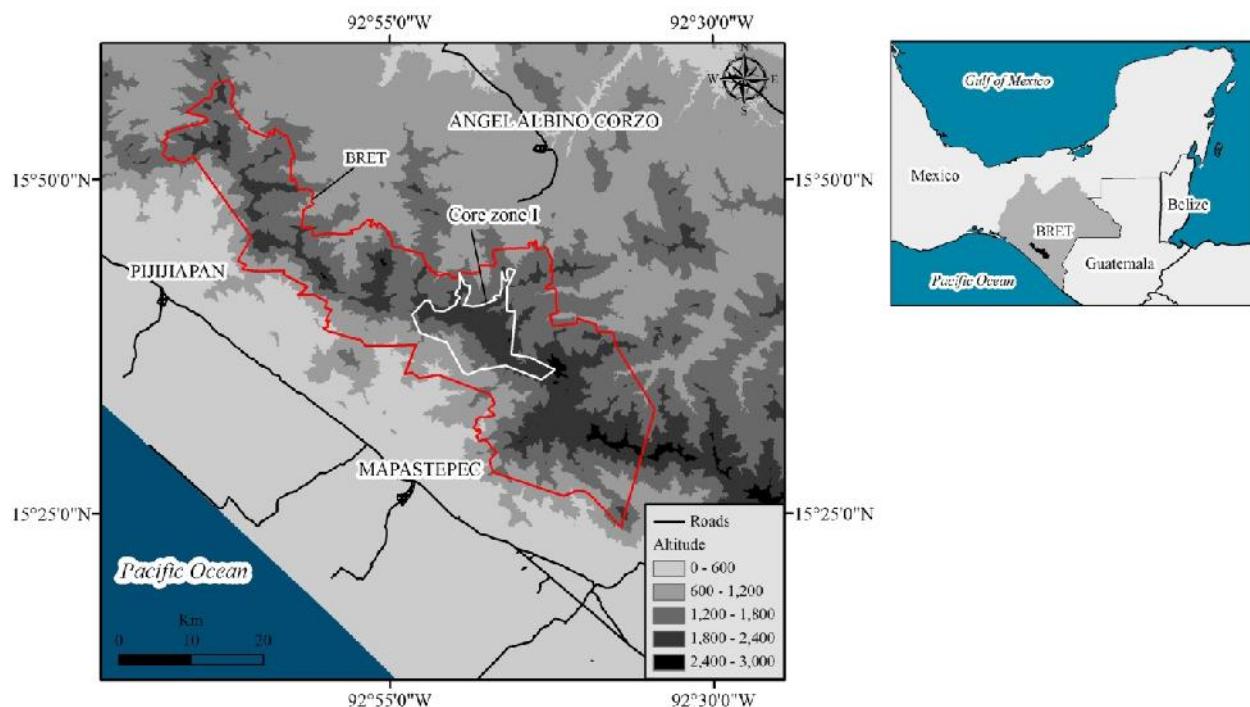


Fig. 1. Location of El Triunfo Biosphere Reserve (BRET) (red polygon) and the Core Zone I (white polygon) in the left panel.

The BRET is characterized by steep topography (with terrain slopes > 60°) and a wide altitudinal gradient (450 to 2,550 meters). Average temperature varies between 12 and 22°C, and annual precipitation ranges from 1,000 to 4,500 mm. Main vegetation types are cloud forest and semi-evergreen tropical forest. The BRET protects the largest tract of cloud forest in Mexico (48,990.0 ha), which is a habitat type globally endangered due to deforestation and climate change [30-32]. The El Triunfo Biosphere Reserve is considered the second most diverse protected area in Mexico in terms of mammalian species (112), exceeded only by the Montes Azules Biosphere in the Lacandon forest, Chiapas. Moreover, the BRET constitutes one of the last strongholds in the country for large mammalian herbivores such as the tapir, the Central American Red brocket (*Mazama temama*), collared peccary (*Pecari tajacu*) and felids such as Jaguar (*Panthera onca*), Ocelot (*Leopardus pardalis*) and Margay (*L. wiedii*) [30, 33]. Therefore, the BRET plays a key role in conservation of large mammals in Mexico. Unfortunately, land cover change and, more recently, mining pose an increasing threat to the integrity of the reserve [24, 34, C. Guichard pers. comm.]

Camera-trapping sampling design

In December 2010 we set up 25 camera-trapping stations in the CZ-I. Each station was equipped with one camera trap (20 Bushnell 119445 and 5 Cuddeback CaptureIR). Locations of camera-trapping stations were defined taking as a guide three trails: Palo gordo, Bandera and Costa. These trails are used mainly by park guards for monitoring activities and occasionally by researchers and bird watchers (Fig. 2). We started from the field station, and every 500 m (straight line distance measured with a handheld GPS, Garmin 60Csx) we went off the trail in a perpendicular random direction (left/right) to set a camera-trap. Steepness of the terrain made it difficult to move far from the trail, but the minimum walked distance was 15 m. Cameras were set off the trails to reduce the repetitive recording of tapirs moving along them and to comply with the assumptions used to estimate animal's density (see below). Few studies have reported Baird's tapir home ranges, but one of the most comprehensive studies based on radio telemetry reports an average home range of 1.25 square km [35]. Based on this estimation, we set surveying stations 500 m apart in order to record different individuals without leaving large gaps in the area under surveillance.

In each surveying station we attached the camera-trap to a tree stem at 70 cm-height from the ground and lightly cleared the herbaceous vegetation in front of it to avoid interferences (false positives). Camera traps were checked every month until May 2011 to download pictures and replace batteries.

Camera-trapping data base

Pictures were organized in a database with the help of the specialized software Camera Base v1.5.1 [36]. All tapir pictures were identified with corresponding camera-trapping station, date and time of collection data. To avoid sequences of pictures of a particular individual, we grouped pictures in one-hour periods for a given site (hereafter picture events).

Density estimation

The Random Encounter Model (REM) has three main assumptions: (i) animals conform adequately to the model used to describe the detection process; (ii) photographs represent independent contacts between animals and cameras; and (iii) the population is closed [10]. The first assumption basically means that animals behave like ideal gas particles, moving randomly and independently of one another. This assumption is clearly unrealistic because animals respond to each other as well as to their physical environment. However, preliminary research indicates that this method is insensitive to slight violations of this assumption [10]. On the other hand, placement of the camera traps off trails and at regular distances would increase independence between movement of tapirs and the locations of the camera-traps (assumption no. 2). This way to set cameras contrasts with the common

practice of setting cameras in spots where the target species is known to frequent (e.g., water ponds). Finally, restriction of our study to a five-month period would fulfill the assumption of population closure.

We applied the REM using the following equation:

$$D = \frac{y}{t} \frac{f}{vr(2 + \theta)}$$

Where y = number of tapir events, t = sampling effort (i.e., camera-trap days), v = animal's average daily speed of movement (km), r = radius of the camera trap detection zone (km) and θ = angle of the camera trap detection zone (radians). We obtained information on the angle of the camera-trap detection zone directly from camera manuals. The radius of the camera-trap detection zone was estimated in the field by walking in front of each camera trap at increasingly greater distances until no event was recorded. We averaged radius and angles of all the cameras to get a single value that was used in the calculations. We carried out a literature review to search for studies on tapir movement. We used the value reported by Lizcano & Cavelier [37] for the Andean tapir = 14.4 km/day (0.6 km/h) because: 1) it was obtained through the use of GPS collars and 2) it corresponds to a study area with similar characteristics (climatic and topographic) to our study area. We used an R script [38] kindly provided by M. Rowcliffe to carry out the calculation of density and generate its corresponding 95% confidence intervals.

We compiled the few available estimates of Baird's tapir density to compare with our resulting density estimation. Due to the scarcity of information we included density estimations derived from both camera-trapping and trail walks.

To estimate the sensitivity of density estimations to variations in the value of tapir's speed of movement, we repeated the calculation, in progressive steps, up to alternatively reducing and increasing the speed of movement by 50% in relationship to that obtained by Lizcano & Cavelier [37]. Sensitivity analysis focused on this parameter because it had greater uncertainty, regarding its real value, in comparison to the other parameters used in the calculation of density.

Abundance estimation

We applied the following equation to get an estimator (encounter rate) of Baird's tapir abundance:

$$ER = \frac{\text{number of picture events}}{\text{sampling effort (camera - trap days)}} * 100$$

This abundance estimator has been used in a number of studies and therefore bears comparative interest [39]. We compiled the available estimates of Baird's tapir relative abundance, based on camera-trapping, to compare with our estimation.

Daily activity patterns

We grouped the number of tapir events per hour of the day and tested the null hypothesis that tapir activity was uniform throughout the day, applying the Rayleigh test [40]. We used the program Oriana V4.05 [41] to apply this test and to generate circular histograms.

To complement this analysis we grouped tapir events in three periods: diurnal, nocturnal, and crepuscular (dawn and dusk). Dusk and dawn times were obtained for our particular area and season of study using program Sun Times v7.1 [42]. We defined the crepuscular period as including one hour before and one hour after the corresponding dawn/dusk time. We tested for differences in the frequency of events per period applying a goodness of fit Chi-square test [43]. To calculate the expected frequency of events for each period, we divided

the total number of tapir events by 24 hours and then multiplied by the number of hours included in each period (e.g., four hours in the case of crepuscular).

Tapir activity across an altitudinal gradient

We took advantage of the altitudinal heterogeneity existing in the area covered by the camera-traps to analyze the relationship between tapir activity and altitude. We grouped camera-trapping stations in three sets according to the following altitude intervals: 1,474m-1,746m (four camera-traps); 1,746m-2,019m (11 camera-traps); 2,019m-2,291m (10 camera-traps). Altitudinal variation in these intervals encompassed 75% of extent of the CZ-I. Width of the altitude interval was defined simply by dividing by three the altitudinal range covered by the camera-trapping stations. This choice was made because mountain cloud forest dominated most of the locations in which camera-traps were set and distinguishing among different habitat types in the remaining locations was difficult, given variations of vegetation, topography, and slope exposure.

We followed the approach proposed by Neu et al. (1974) [44] to assess whether the observed number of picture records was greater than expected for any given altitude interval. To calculate the expected number of records per altitude interval we multiplied the total number of tapir records by the proportion of the sampling effort (camera-trapping days) made in each of them. To compare observed vs. expected frequencies we applied a Chi-square test. When null hypothesis was rejected we calculated Bonferroni confidence intervals [44] to determine which observed frequencies were different from the expected, using the following expression:

$$P_i - Z_{\alpha/2k} \sqrt{\frac{P_i(1-P_i)}{n}} \leq p_i \leq P_i + Z_{\alpha/2k} \sqrt{\frac{P_i(1-P_i)}{n}}$$

where P_i = proportion of pictures recorded in the altitude interval i , k = number of altitude intervals, $Z_{\alpha/2k}$ = limit value of the standardized normal distribution corresponding to a probability of $\alpha/2k$ and n = total number of picture records.

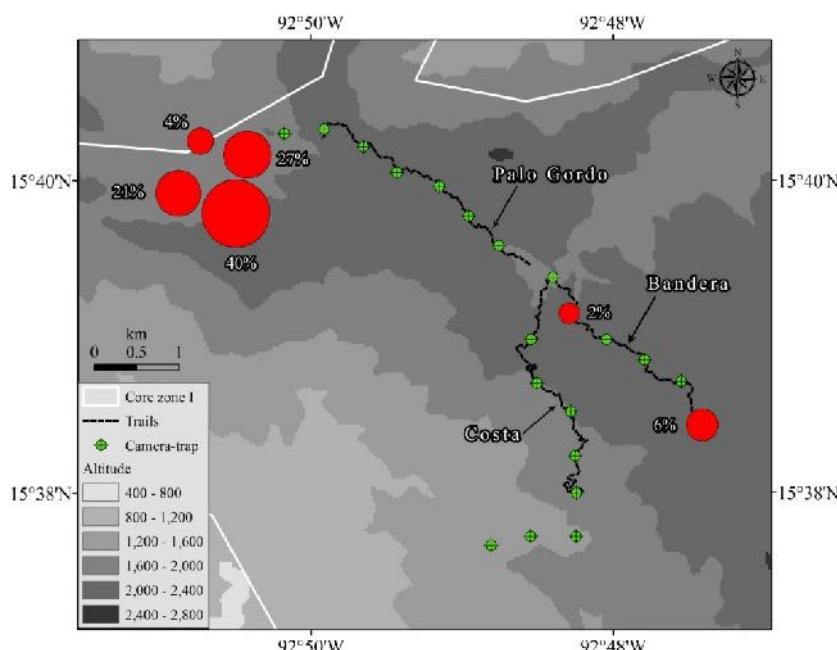


Fig. 2. Location of camera-trapping stations in the Core Zone I of El Triunfo Biosphere Reserve. Red globes indicate camera trap stations in which tapir activity was recorded. Size of the globes is related to the number of tapir events recorded.



Fig. 3. Baird's tapir crossing in front of one the camera-trapping stations in the Core Zone I of El Triunfo Biosphere Reserve.

Results

Evidence of tapir presence in the Core Zone I of the El Triunfo Biosphere Reserve

From December 2010 to May 2011 we accumulated 3,817 camera trap days and recorded 54 tapir pictures (Fig. 2 and 3). When we grouped these pictures within one-hour intervals the resulting number of events was 48. We found that 92% of the tapir events were concentrated in only four of the surveying stations (Fig. 2). In total only six of the surveying stations recorded tapir activity (Fig. 2).

Daily tapir activity

We rejected the null hypothesis that tapir activity was distributed uniformly throughout the day ($Z = 7.82$, $p < 0.01$). Tapirs were active throughout most of the day, but an activity peak occurred during dusk (Fig. 4A). Likewise, results of Chi-square's goodness of fit test showed that there was an excess of activity during the crepuscular period and a shortage of activity during day time ($\chi^2 = 21.18$, $p < 0.01$, Fig. 4B).

Tapir presence across an altitudinal gradient

We rejected the null hypothesis that tapir presence occurred randomly at different altitudes ($\chi^2 = 49$, $p < 0.001$). Based on Bonferroni confidence intervals we found that frequency of tapir records was greater than expected for the medium altitude interval, whereas the number of observed records was less than expected for high altitudes (Table 1).

Table 1. Analysis of Baird's tapir habit preferences applying Chi-square test and Bonferroni confidence intervals (see text for details).

Habitat (masl)	Sampling effort (camera-trap days)	Expected proportion of use	Observed ± 95% confidence Bonferroni intervals	Overall statistic and p-value
Low (1,474-1,746)	611	0.16	0	
Medium (1,746-2,019)	1679	0.42	0.86≤0.94≤1.0	$\chi^2 = 49.0$ $p < 0.001$
High (2,019-2,291)	1527	0.38	0≤0.06≤0.17	

Density and abundance estimation

The application of the REM resulted in an estimated density of 0.12 tapirs/km² and an associated 95% confidence interval = 0.03-0.25 tapirs/km². Our sensitivity analysis showed that halving tapir's speed of movement doubled the estimated density (0.24 ind./km²) (Table 2). Increasing tapir's speed of movement had less impact on the calculated density (Table 2). As mentioned before, most of the tapir records concentrated in a small subset of the camera-traps. Calculation of density averaging the number of tapir events recorded in these camera-traps greatly reduced the estimated overall density (0.04 ind./km²). However, because we detected the presence of different tapir individuals in that area (based on body size variation), we use for the following discussion the density estimation obtained considering all the camera traps as independent. Tapir's relative abundance was equal to 1.3 events/100 camera-trap days. This estimation ranged between 0.7 and 1.9 events/100 camera-trap days among months.

Table 2. Density estimations using the REM with values of tapir speed of movement lower than and greater than reported by Lizcano and Cavalier (2006)*.

Speed (km/day)	Density Ind./km ²	Lower 95% confidence interval	Upper 95% confidence interval
7.2	0.239	0.491	0.031
9.6	0.179	0.375	0.023
12	0.143	0.297	0.021
14.4*	0.119	0.237	0.015
16.8	0.102	0.209	0.016
19.2	0.090	0.185	0.013
21.6	0.080	0.166	0.014

Discussion

Effectiveness of camera-trapping to monitor tapir activity

Use of camera-traps allowed us to get a relatively abundant number of tapir records, as we obtained 48 tapir picture events over the course of our study while a team of highly trained park guards monitoring the same trails, during the same period, recorded no direct tapir sightings. Differences in the effectiveness of the two methods are likely due to: 1) camera-traps being active 24 hour a day whereas trails are only walked three days per month, and 2) camera-traps are nearly undetectable and silent, whereas people walking alert tapirs of human presence, particularly when the forest floor is covered with dry litter.

Daily tapir activity

It has been suggested that tapirs tend to become more nocturnal in response to human disruption [22]. In our study we found that tapir activity clearly concentrated around dusk, yet there was activity, with less intensity, throughout most of the day. This finding might suggest that our study area provides highly protected habitat for tapirs. However, a definitive testing of this assumption requires documenting tapir activity patterns in other areas more exposed to human impact, such as those located outside and on the border of the El Triunfo Biosphere Reserve. Regarding the study of daily activity patterns, we emphasize the importance of using all the data generated by camera-traps instead of grouping picture records in just three categories (crepuscular, diurnal and nocturnal). One of the most valuable features of camera traps is their capacity to monitor continuously an animal's activity. Methods of analysis should accordingly take full advantage of this capacity in order to avoid losing some information by lumping together data into coarse categories.

Use of the REM as an alternative method to estimate Baird's tapir density

Use of the REM resulted in an estimated tapir density within the range of known Baird's tapir densities (Fig. 5) and is relatively close to a previous estimate (0.07 ± 0.03 ind./km²) obtained in our study area, using a different methodology based on tapir detection along trails [46]. These findings lend some support to the use of the REM as an alternative method to generate Baird's tapir density estimations.

Some previous attempts used camera-trapping in combination with mark-recapture models to estimate tapir density [7, 23]. In contrast to the REM, use of mark-recapture models requires identification of individual tapirs, which needs high quality pictures to distinguish each animal's distinctive spots [47]. Such high quality pictures require monitoring stations equipped with paired camera-traps, which limit the area under surveillance per

sampling season. Moreover, there remain some unresolved issues regarding the effects of being able to identify only a fraction of the total population studied and the impact of individual misidentification [25].

In comparison, an attractive aspect of the REM method is that it does not require individual identification, paired camera-traps, or high quality pictures. Moreover, the REM is a method under continuous improvement [48]. Yet the REM is not free of some complications, such as the need for accurate independent estimations of animal's population parameters (e.g., speed of movement). These estimations are hard to obtain, even using very specialized techniques such as telemetry [49]. Likewise, further testing is needed to verify REM assumptions. For this, the use of other non-invasive techniques to independently estimate density, such as DNA extraction from feces, telemetry to estimate an animal's movement, can play an important role [50].

Patterns of Baird's tapir abundance and density

There are still few available studies providing estimations of Baird's tapir abundance or density based on camera-trapping. This, together with the existence of methodological differences in the sampling design used prevents a comprehensive analysis of habitat-related patterns of tapir abundance/density. Studies are particularly scarce in mountain habitats like the BRET [23]. Here we compare the estimations obtained in this study with those reported in other studies and habitats. Due to its scarcity, particularly in the case of density estimations, we include estimations generated with different methods (e.g., telemetry), not just camera-trapping.

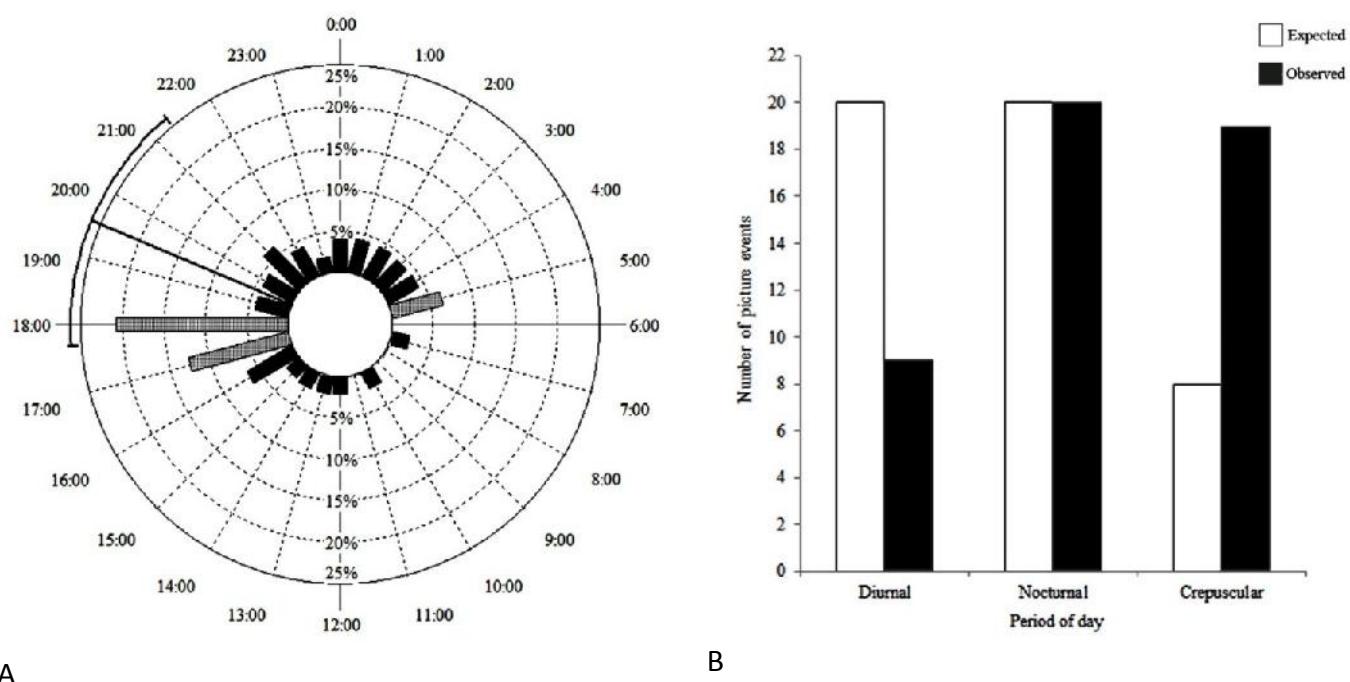


Fig. 4. A) Pattern of daily activity of Baird's tapir in the Core Zone I in El Triunfo Biosphere Reserve. Lighter gray bars indicate peaks of activity. Radius and arc indicate, respectively, location of average hour of activity and its 95% confidence interval. **B)** Differences between expected and observed frequencies of Baird's tapir activity in El Triunfo Biosphere Reserve for different periods of the day ($\chi^2=21.18$, $P<0.01$).

Our tapir density estimation (0.12 ind./km^2) is 24 times lower than density (2.93 ind./km^2) calculated by González-Maya et al. [23] in a similar mountain forest from the Talamanca Cordillera in Costa Rica (Fig. 5). Estimation generated by Gonzalez-Maya et al. [23] is the highest density reported for the species. On the other hand, tapir density estimated in this study is higher than that calculated in some disturbed rain forest [51] but clearly lower than that observed in some conserved rain forest or even some disturbed rain forest [51-52](Fig. 5).

In a wider sense, it is interesting to notice that tapir density calculated in this study is close to that reported for the Andean tapir (*T. pinchaque*), 0.17 ind./km^2 and 0.18 ind./km^2 by Downer [53] and Lizcano and Cavelier [54], respectively. The Andean tapir is a species that inhabits regions topographically similar to the ETBR. In contrast, density of the Brazilian tapir (*T. terrestris*) seems to be clearly greater ($0.07\text{-}3.7 \text{ ind./km}^2$) [7, 55-57].

Relative abundance (1.3 events/100 camera-trap days) calculated for Baird's tapir in this study is close to the value reported by Gonzalez-Maya et al. [58] for two protected areas in the Talamanca Cordillera in Costa Rica (Fig. 5). On the other hand, tapir's relative abundance in the Core zone I of the BRET is greater than that estimated for the species in anthropogenically disturbed forests and even in other preserved forests [59-60] (Fig. 5). In comparison, Baird's tapir abundance in the BRET is much lower than that reported in more seasonal tropical forests from the Yucatan peninsula [61-62] (Fig. 5). However, this strong contrast might result, at least in part, from the fact that surveys in the Yucatan peninsula were carried out near temporal water holes ("aguadas") where tapirs concentrate their activity.

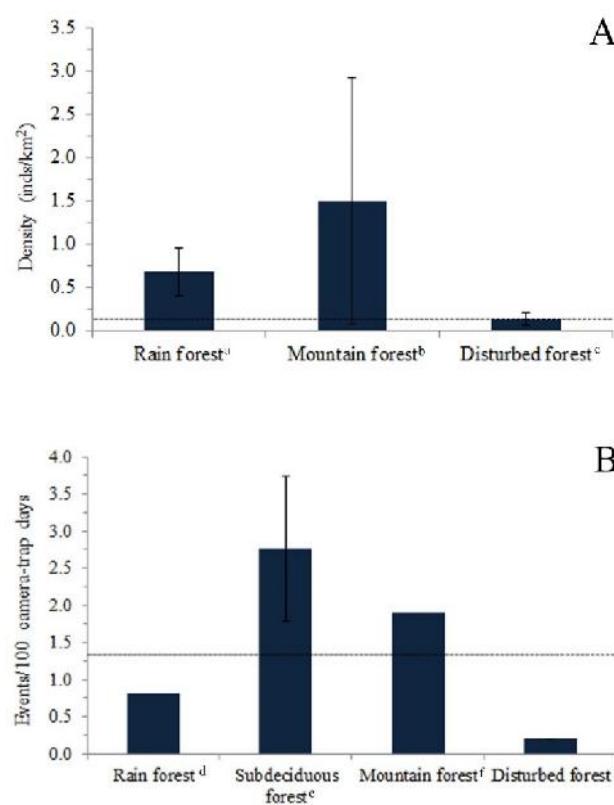


Fig. 5. A) Average Baird's tapir density and **B)** Relative abundance estimated for different habitat types in different studies. Horizontal dotted lines in both panels indicate the respective values estimated in this study for comparison.
Sources of information: a = [45, 51, 66]; b=[23,46], c= [51-52]; d=[60]; e=[59, 61-62]; f=[58] and g=[58, 67].

Patterns of Baird's tapir spatial activity

We found that tapir activity concentrated in the northwest portion of the study area (Fig. 2). In this portion of the CZ-I of the BRET, secondary vegetation is common, which might be providing an important food source for tapirs. Moreover, this area tends to flood during high rains, which might create water holes that are preferred habitat for tapirs [45]. This finding has management implications for the species because this area is located between the core zone and the buffer zone and falls beyond the area that is regularly monitored by park-guards. Special attention should be paid to this area to avoid any conflict between people and fauna.

Tapir activity in the surveyed area concentrated in medium altitudes. A study by Gonzalez-Maya et al. [58] carried out in the mountain ridge of the Talamanca region, Costa Rica, found a similar pattern of concentration of Baird's tapir activity in mid-elevations (2,000-2,600 m asl). Mid-elevations might offer some conditions (e.g., shelter against bad weather and greater variety of food resources) that make them an important habitat for tapirs dwelling in mountain forests.

Implications for Conservation

Estimation of population and demographic parameters of Baird's tapir is one of the priorities of the species' Action Plan coordinated by the Group of Tapir Specialist from the International Union for the Conservation of Nature [21, 63]. The effectiveness of camera traps to document the activity of highly secretive species is greatly increasing the type of evidence needed to advance our understanding of Baird's tapir ecology and conservation status, paving the way for more sophisticated analyses such as those designed to estimate population viability [64]. It is important to keep in mind, however, that defining best practices for tapir camera-trapping studies and for analyses of their results would require the coordinated effort of all relevant stakeholders. This should include local people, park managers and guards, tapir specialists, and also statisticians.

The REM adds to the set of available tools to estimate animal population density based on camera-trapping [10, 65]. However, wider implementation of the REM to estimate density in species lacking natural distinctive marks, such as Baird's tapir, would require further testing of its assumptions and limitations. If the REM proves to be immune to slight violations of its assumptions this method can be a very powerful tool to increase our knowledge of Baird's tapir patterns of population density. Likewise, REM can help to reduce bias in tapir density estimations caused by varying abilities of field workers and researchers to detect the species in its natural habitat. Standardized protocols to estimate Baird's tapir density and abundance and to quantitatively describe its activity patterns throughout its distribution range, are essential to develop necessary baseline data for assessing negative impacts of anthropogenic perturbation, as well as the positive effects of management actions in key tapir areas such as El Triunfo Biosphere reserve.

Acknowledgements

We thank the all the staff of the National Commission for Protected Areas (CONANP) assigned to the ETBR, in particular C. Guichard Romero and J. C. Castro Hernández, for providing critical support during all the stages of this project. Funding for this study was provided by the Scott Neotropical Fund from the Cleveland Metroparks Zoo and UC Mexus-CONACyT. Fellowships from the National Council of Science and Technology (CONACyT) and the Program for Teacher's Improvement from the Ministry of Public Education (PROMEP-SEP) were awarded to JP Carbajal-Borges and O. Godinez-Gomez, respectively. Comments by E. Brenner and A. Camargo Sanabria and three anonymous reviewers greatly improved an earlier draft of this paper.

References

- [1] Baillie, J. E. M., Griffiths, J., Turvey, S. T., Loh, J. and Collen, B. 2010. *Evolution Lost: Status and trends of the world's vertebrates*. U.K. Zoological Society of London.
- [2] Kelt, D.A. and Vuren, D.H. V. 2001. The ecology and macroecology of mammalian home range area. *The American Naturalist* 157: 637-645.
- [3] Jerozolimski, A. and Peres, C. A. 2003. Bringing home the biggest bacon: A cross-site analysis of the structure of hunter-kill profiles in Neotropical forests. *Biological Conservation* 111: 415-425.
- [4] Kinnaird, M. F., Sanderson, E. W., O'Brien, T. G., Wibisono, H. T. and Woolmer, G. 2003. Deforestation trends in a tropical landscape and implications for endangered large mammals. *Conservation Biology* 17: 245-257.
- [5] Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R., Sechrest, W., Orme, C. D. L. and Purvis, A. 2005. Multiple causes of high extinction risk in large mammal species. *Science* 309: 1239-1241.
- [6] O'Brien, T. G., Kinnaird, M. F. and Wibisono, H. T. 2003. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation* 6: 131-139.
- [7] Trolle, M., Noss, A. J., Cordeiro, J. L. P. and Oliveira, L. F. B. 2008. Brazilian tapir density in the Pantanal: A comparison of systematic camera-trapping and line-transect surveys. *Biotropica* 40: 211-217.
- [8] Tobler, M. W., Carrillo-Percastegui, S. E., Leite Pitman, R., Mares, R. and Powell, G. 2008. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Animal Conservation* 11: 169-178.
- [9] Jennelle, C. S., Runge, M. C. and MacKenzie, D. I. 2002. The use of photographic rates to estimate densities of tigers and other cryptic mammals: A comment on misleading conclusions. *Animal Conservation* 5: 119-120.
- [10] Rowcliffe, J. M., Field, J., Turvey, S. T. and Carbone, C. 2008. Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology* 45: 1228-1236.
- [11] Rovero, F. and Marshall, A.R. 2009. Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology* 46: 1011-1017.
- [12] Karanth, K. U. and Nichols, J. D. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79: 2852-2862.
- [13] Mendoza, E., Martineau, P. R., Brenner, E. and Dirzo, R. 2011. A novel method to improve individual animal identification based on camera-trapping data. *The Journal of Wildlife Management* 75: 973-979.
- [14] Gómez, H., Wallace, R. B., Ayala, G. and Tejada R. 2005. Dry season activity periods of some Amazonian mammals. *Studies on Neotropical Fauna and Environment* 40: 91-95.
- [15] Ridout, M. S. and Linkie, M. 2009. Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological and Environmental Statistics* 14: 322-337.
- [16] Akbaba, B. and Ayaş, Z. 2012. Camera trap study on inventory and daily activity patterns of large mammals in a mixed forest in north-western Turkey. *Mammalia* 76: 43-48.
- [17] Nolasco, A. L., Lira-Torres, I. and Ceballos, G. 2007. Ampliación del área de distribución histórica del tapir (*Tapirus bairdii*) en el Pacífico Mexicano. *Revista Mexicana de Mastozoología* 11: 91-94.
- [18] Matola, S., Cuarón, A. D. and Rubio-Torgler, H. 1997. Status and action plan of Baird's tapir (*Tapirus bairdii*). In: *Tapirs: status survey and conservation action plan*. Brooks, D. M., Bodmer, R. E. and Matola, S. (Eds.), pp.29-45. IUCN/SSC Tapir Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.
- [19] Castellanos, A., Foerester, C., Lizcano, D. J., Naranjo, E., Cruz-Aldán, E., Lira-Torres, I., Samudio, R., Matola, S., Schipper, J. and González-Maya. J. F. 2008. *Tapirus bairdii*. In: IUCN 2013. *IUCN Red List of Threatened Species*. Version 2013.1. www.iucnredlist.org
- [20] Isaac N. J. B., Turvey S. T., Collen, B., Waterman, C. and Baillie, J. E. M. 2007. Mammals on the EDGE: Conservation priorities based on threat and phylogeny. *PLoS ONE* 2(3): e296.
- [21] García, M. J., Medici, E. P., Naranjo, E. J., Novarino, W. and Leonardo, R. S. 2012. Distribution, habitat and adaptability of the genus *Tapirus*. *Integrative Zoology* 7: 346-355.
- [22] Naranjo, E.J. 2009. Ecology and conservation of Baird's tapir in Mexico. *Tropical Conservation Science* 2: 140-158.

- [23] González-Maya, J. F., Schipper, J., Polidoro, B., Hoepker, A., Zárrate-Charry, D. and Belant, J. L. 2012. Baird's tapir density in high elevation forests of the Talamanca region of Costa Rica. *Integrative Zoology* 7: 381-388.
- [24] Mendoza, E., Fuller, T. L., Thomassen, H. A., Buermann, W., Ramírez-Mejía, D. and Smith, T. B. 2013. Preliminary assessment of the effectiveness of the Mesoamerican Biological Corridor for protecting potential Baird's tapir (*Tapirus bairdii* Gill, 1865) habitat in southern Mexico. *Integrative Zoology* 1: 35–47.
- [25] Oliveira-Santos, L. G. R., Zucco, C. A., Antunes, P. C. and Crawshaw Jr., P. G. 2010. Is it possible to individually identify mammals with no natural markings using camera-traps? A controlled case-study with lowland tapirs. *Mammalian Biology* 75: 375-378.
- [26] Hutchinson, J.M.C. and Waser, P.M. 2007. Use, misuse and extensions of "ideal gas" models of animal encounter. *Biological Reviews* 82 : 335-359.
- [27] Rovero, F. and Marshall, A.R. 2009. Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology* 46: 1011-1017.
- [28] García, P., Arévalo, V. and Mateos, I. 2009. Using sightings for estimating population density of Eurasian otter (*Lutra lutra*): A preliminary approach with Rowcliffe et al's Model. *IUCN Otter Specialist Group Bulletin* 26: 50-59.
- [29] Suselbeek, L. 2009. Mammal density estimation from camera trapping data using gas models; a test with the paca (*Agouti pacificus*). Master thesis. University of Groningen, Netherlands.
- [30] INE (Instituto Nacional de Ecología), SEMARNAP (Secretaría del Medio Ambiente, Recursos Naturales y Pesca). 1998. *Programa de manejo: Reserva de la Biosfera El Triunfo*. Instituto Nacional de Ecología - Secretaría del Medio Ambiente Recursos Naturales y Pesca. México.
http://www2.ine.gob.mx/publicaciones/consultaPublicacion.html?id_pub=168
- [31] Bubb, P., May, I., Miles, L. and Sayer, J. 2004. *Cloud Forest Agenda*. The United Nations Environment Programme and World Conservation Monitoring Centre. Cambridge, U.K.
- [32] CONABIO. 2010. *El Bosque Mesófilo de Montaña en México: Amenazas y oportunidades para su conservación y manejo sostenible*. Comisión Nacional para el Conocimiento y uso de la Biodiversidad, México.
- [33] Espinoza, E., Anzures, A. and Cruz-Aldán, E. 1998. Mamíferos de la Reserva de la Biosfera El Triunfo, Chiapas. *Revista Mexicana de Mastozoología* 3: 79-94.
- [34] Ramírez-Mejía, D., Cuevas, G. and Mendoza, E. 2011. Escenarios de cambio de cobertura y uso de suelo en el Corredor Biológico Mesoamericano-Méjico. Sociedad Latinoamericana de Percepción Remota y Sistemas de Información Espacial (SELPER). *Proceedings of the 19th National Meeting of the Latin American Society of Remote Sensing and Systems of Spatial Information (SELPER)*. October 2011 Morelia, Michoacán, México.
http://www.ciga.unam.mx/publicaciones/images/abook_file/MemoriasSelper2011.pdf
- [35] Foerster, C. R. and Vaughan, C. 2002. Home range, habitat use, and activity of Baird's tapir in Costa Rica. *Biotropica* 34: 423–437.
- [36] Tobler, M. W. 2010. Camera Base. Microsoft Office Access. Ver. 1.5.1. USA. <http://www.atrium-biodiversity.org/tools/camerabase/>
- [37] Lizcano, D. J. and Cavelier, J. 2004. Using GPS collars to study mountain tapirs (*Tapirus pinchaque*) in the Central Andes of Colombia. *Tapir Conservation* 13: 18–23.
- [38] R Core Team., 2012. R: A Language and Environment for Statistical Computing. Version 2.15.0. R Foundation for Statistical Computing, Austria. <http://www.R-project.org>
- [39] Jenks, K. E., Chanteap, P., Damrongchainarong, K., Cutter, P., Redford, T., Lynam, A. J., Howard, J. and Leimgruber, P. 2011. Using relative abundance indices from camera-trapping to test wildlife conservation hypotheses – an example from Khao Yai National Park, Thailand. *Tropical Conservation Science* 4: 113-131.
- [40] Zar, J. H. 2010. *Biostatistical Analysis*. Pearson Prentice-Hall. Massachusetts, USA.
- [41] Kovach Computing Services. 2012. Oriana. Version 4.01. Kovach Computing Service, USA.
- [42] Kay, S. and Du Croz, T., 2008. Sun Times. Version 7.1. <http://www.apl72.dsl.pipex.com/suntimes.htm>
- [43] Manly, B.F.J., McDonald, L. and Thomas, D.L. 1993. *Resource selection by animals: Statistical design and analysis for field studies*. Springer, U.K.

- [44] Neu, C. W., Byers, C. R. and J. M. Peek. 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* 38:541-545.
- [45] 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.
- [46] Lira-Torres, I., Naranjo, E.J., Güiris, D.M. and Aldán-Cruz, E. 2004. Ecología de *Tapirus bairdii* (Perissodactyla: Tapiridae) en la Reserva de la Biosfera El Triunfo (Polígono I), Chiapas, México. *Acta Zoológica Mexicana* (nueva serie) (1): 1-21.
- [47] Noss, A.J., Cuéllar, R.L., Barrientos, J., Maffei, L., Cuéllar, E., Arispe, R., Rúmiz, D. and Rivero, K. 2003. A camera trapping and radio telemetry study of lowland tapir (*Tapirus terrestris*) in Bolivian dry forests. *Tapir Conservation* 12 : 24-32.
- [48] Rowcliffe, M.J., Carbone, C., Jansen, P. A., Kays, R. and Kranstauber, B. 2011. Quantifying the sensitivity of camera traps: an adapted distance sampling approach. *Methods in Ecology and Evolution* 2: 464–476.
- [49] Rowcliffe, M.J., Carbone, C., Kays, R., Kranstauber, B. and Jansen, P.A. 2012. Bias in estimating animal travel distance: the effect of sampling frequency. *Methods in Ecology and Evolution* 3: 653–662.
- [50] Sánchez, A., de Figueiredo, M. G., Hatanaka, T., de Paula, F. F. P., Silveira, L., Jácomo, A. T. A. and Galetti Jr, P. M. 2009. Microsatellite loci isolated from the lowland tapir (*Tapirus terrestris*), one of the largest Neotropical mammal. *Conservation Genetics Resources* 1: 115-117.
- [51] Naranjo, E. J. and Bodmer, R. E. 2002. Population Ecology and Conservation of Baird's Tapir (*Tapirus bairdii*) in the Lacandon Forest. *Tapir Conservation* 11: 25-33.
- [52] Bolaños, J. B., and Naranjo, E. J. 2001. Abundancia, densidad y distribución de las poblaciones de Ungulados en la cuenca del río Lacantún, Chiapas, México. *Revista Mexicana de Biodiversidad* 5: 45-57.
- [53] Downer, C. C. 1996. The mountain tapir, endangered 'flagship' species of the high Andes. *Oryx* 30: 45-58.
- [54] Lizcano, D. J., and Cavelier, J. 2000. Daily and seasonal activity of the mountain tapir (*Tapirus pinchaque*) in the Central Andes of Colombia. *Journal of Zoology* 252: 429-435.
- [55] Mendes Pontes, A. R. 2004. Ecology of a community of mammals in a seasonally dry forest in Roraima, Brazilian Amazon. *Mammalian Biology* 69: 319-336.
- [56] Medici, E. P. 2010. Assessing the viability of lowland tapir populations in a fragmented landscape. Doctoral dissertation, University of Kent, U. K.
- [57] Noss, A. J., Gardner, B., Maffei, L., Cuéllar, E., Montaño, R., Romero-Muñoz, A., Sollman, R. and O'Connell, A. F. 2012. Comparison of density estimation methods for mammal populations with camera traps in the Kaa-lya del Gran Chaco landscape. *Animal Conservation* 15: 527-535.
- [58] González-Maya, J.F., Schipper, J. and 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: 29-35.
- [59] Kelly, M. J. 2003. Jaguar Monitoring in the Chiquibul Forest, Belize. *Caribbean Geography* 1 : 19-32.
- [60] Lira-Torres, I. and Briones-Salas, M. 2012. Abundancia relativa y patrones de actividad de los mamíferos de los Chimalapas. Oaxaca, México. *Acta Zoológica Mexicana* 28:556-585.
- [61] Pérez-Cortéz, S. and Matus-Pérez, E. S. 2010. El tapir *Tapirus bairdii* en la región sureste del Área de Protección de Flora y Fauna Bala'an Ka'ax, Quintana Roo, México. *Therya* 2: 137-144.
- [62] Pérez-Cortéz, S., Enriquéz, P. L., Sima-Panti, D., Reyna-Hurtado, R. and 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: 753-761.
- [63] Medici, E. P., Carrillo, L., Montenegro, O. L., Miller, P.S., Carbonell, F., Chassot, O. Cruz-Aldán, E., García, M., Estrada-Andino, N. Shoemaker, A. H. and Mendoza, A. 2006. Baird's tapir conservation workshop: Final report. IUCN/SSC Tapir Specialist Group & IUCN/SSC Conservation Breeding Specialist Group. Apple Valley, Minnesota, USA.
- [64] Medici, E. P. and Desbiez, A. L. J. 2012. Population viability analysis: using a modeling tool to assess the viability of tapir populations in fragmented landscapes. *Integrative Zoology* 7: 356–372.

- [65] Tobler, M. W., Hibert, F., Debeir, L., & Richard-Hansen, C. 2013. Estimates of density and sustainable harvest of the lowland tapir *Tapirus terrestris* in the Amazon of French Guiana using a Bayesian spatially explicit capture-recapture model. *Oryx*, 1-10. (doi:10.1017/S0030605312001652)
- [66] Foerster, C. R. 1998. Ecología de la danta centroamericana *Tapirus bairdii* en un bosque tropical húmedo de Costa Rica. Tesis de Maestría, Universidad Nacional de Costa Rica.
- [67] Portillo, H. O. and Hernández, J. 2011. Densidad del Jaguar (*Panthera onca*) en Honduras: Primer estudio con trampas-cámara en la Mosquita Hondureña. *Revista Latinoamericana de Conservación* 2: 45-50.