

Habitat use and activity patterns of ungulates in a tropical rainforest of southern México

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Baird's tapir (*Tapirella bairdii*), white-lipped peccary (*Tayassu pecari*), and collared peccary (*Dicotyles tajacu*) sympatrically occur in the Lacandon Forest of Chiapas, México. These species contribute to maintain ecosystem dynamics through herbivory, seed dispersal, and seed predation, constituting important prey for large carnivores and hunters. We analyzed activity patterns and habitat use of the three focal species to assess the degree of temporal and spatial habitat segregation among them in Montes Azules Biosphere Reserve (REBIMA) and surrounding communities. Between February and October 2015 we deployed camera-traps during 8,463 camera-trap days to estimate the presence and activity of tapirs and peccaries in two habitat types: "conserved" (REBIMA), and "transformed" (community forests; AFC). Habitat use and activity patterns of tapirs and peccaries were assessed through logistic regression models. We found that Baird's tapir was almost exclusively nocturnal with a trend towards crepuscular activity, while both peccary species were diurnal, therefore showing a high daily temporal segregation from the tapir. Both peccary species were similarly active in the two study sites, while tapirs were more active in continuous forest within the protected area. The occurrence of tapirs and white-lipped peccaries depended on the presence and proximity of water sources and roads. Our results suggest that spatial segregation of the habitat allows coexistence of both peccary species in the study area. AFC have potential for maintaining populations of tapirs and peccaries in the Lacandon Forest. Conserving these forests by local communities is essential to ensure the persistence of these mammals.

El tapir centroamericano (*Tapirella bairdii*), el pecarí de labios blancos (*Tayassu pecari*) y el pecarí de collar (*Dicotyles tajacu*) habitan en la Selva Lacandona, Chiapas, México, los cuales contribuyen a mantener la dinámica de los ecosistemas a través de la herbivoría, la dispersión y la depredación de semillas, además de constituir presas importantes para grandes carnívoros y cazadores locales. Analizamos el uso de hábitat y los patrones de actividad de las tres especies para evaluar su grado de segregación espacio-temporal en un paisaje con selva continua y en un paisaje modificado en el área de estudio. Entre febrero y octubre de 2015 utilizamos cámaras-trampa durante 8,463 días- cámara para estimar la presencia y actividad de las especies focales analizando dos tipos de hábitat: "conservado" (Reserva de la Biosfera Montes Azules; REBIMA), y "transformado" (bosques comunitarios; AFC). Evaluamos el uso de hábitat de las especies mediante modelos de regresión logística. Encontramos que el tapir fue casi exclusivamente nocturno con una tendencia hacia la actividad crepuscular, mientras que ambas especies de pecaríes fueron diurnas, mostrando una alta segregación temporal diaria, respecto al tapir. Ambas especies de pecaríes tuvieron una actividad similar en los dos sitios de estudio, mientras que los tapires fueron más activos en el bosque continuo dentro del área protegida. La presencia del tapir y el pecarí de labios blancos dependió de la presencia y cercanía del agua, caminos y carreteras. Nuestros resultados sugieren que la segregación espacial del hábitat permite la coexistencia de ambas especies de pecaríes en el área de estudio. AFC tiene potencial para mantener poblaciones de estas especies; su conservación por las comunidades locales es esencial para asegurar la persistencia de estos mamíferos.

Keywords: Coexistence; habitat use; Maya forest; resource partitioning; ungulates.

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Introduction

The Lacandon Forest of Chiapas hosts one of the largest remnants of humid tropical forest in Mexico, inhabited by numerous species of wild flora and fauna ([Carabias et al. 2015](#); [Carrara et al. 2015](#)), many of which are also natural resources for the inhabitants of rural communities ([Naranjo et al. 2010](#)). However, it has been shown that habitat deterioration, fragmentation, and loss in these tropical forests have resulted in the local and regional disappearance and

isolation of populations of white-lipped peccary (*Tayassu pecari*) and tapir (*Tapirella bairdii*; [Tejeda-Cruz et al. 2009](#); [Schank et al. 2017](#); [Meyer et al. 2019](#); [Thornton et al. 2020](#)). These two species, along with the collared peccary (*Dicotyles tajacu*), live in sympatry in southern Mexico ([Naranjo et al. 2015](#)). Tapir and white-lipped peccary are threatened of extinction in Mexico ([SEMARNAT 2010](#)). Both species currently face reductions in their population sizes and distribution ranges in southern Mexico, Central America, and

South America, as a consequence of changes in plant cover and land use, poaching, and disease transmissions (Naranjo *et al.* 2015; Moreira-Ramírez *et al.* 2019).

Tapir and peccary populations (orders Perissodactyla and Cetartiodactyla, respectively; hereafter referred to as ungulates) play important ecological roles (Eisenberg 1989; Bodmer 1991; Reyna-Hurtado *et al.* 2014; Naranjo 2018). As primary consumers, they contribute to the dynamics and structuring of the ecosystems where they thrive through herbivory, seed dispersal or seed predation, and are also important prey of large Neotropical carnivores (Naranjo 2009; Reyna-Hurtado *et al.* 2014; Malhi *et al.* 2016). Conservation actions for these threatened species require reliable information on the ecology and spatio-temporal dynamics of their populations. For this reason, the need to accurately estimate variables related to habitat use and the relationships between these large herbivores is now greater than ever. Considering the current effects of various environmental stressors such as climate change and habitat loss (Frey *et al.* 2017) and the pressures from human activities (Naranjo 2009), it is important to understand the relationships between the local fauna and its habitat, how they use the habitat (Pianka 1983; Dirzo *et al.* 2014), and their responses to these emerging effects (*e.g.*, loss of biodiversity and changes in abundance and distribution; Schaefer *et al.* 2008).

Closely related sympatric species tend to differ ecologically to coexist, so that they become segregated in some niche dimensions (Gause 1934; Schoener 1974). The tapir and peccary species inhabiting the Lacandon region live in sympatry and, although differing in how they use the local habitat (Tejeda-Cruz *et al.* 2009), they consume similar food resources such as fruits, stems, and leaves (Reyna-Hurtado *et al.* 2014; Naranjo 2019). This leads to assuming that there is clear segregation in terms of hours of activity and sites used most frequently.

A broad variety of methods have been used for analyzing how wild animals use the resources available in the local habitat (Johnson 1980; Burnham and Anderson 2004). The present study considered the use of the habitat and the analysis of activity patterns of tapir and peccaries as a proxy to assess the existence of spatio-temporal segregation in the areas inhabited by these species at the landscape scale in the Lacandon Forest. We sought to understand the relationships of the tapir and peccaries with their environment, especially to assess the influence of the landscape on the probability of habitat use of the species studied. To this end, we considered the effects of anthropic influence (*i.e.*, expansion of the farming frontier) as *a priori* variables (*i.e.*, occurrence of wildlife in relation to towns, water bodies, roads, and vegetation types; MacKenzie and Royle 2005; Kéry and Royle 2016).

This work addressed the following research questions: 1) Is there segregation in the activity patterns of the tapir the two peccary species that inhabit the Lacandon Forest? 2) Which of the *a priori* variables considered in this study are

drivers of habitat use by each species in the study area? Our overall objective was to assess the habitat use and activity patterns of the ungulates under study in the Montes Azules Biosphere Reserve and adjacent areas. In particular: 1) we compared the occurrence, distribution, and patterns of activity of these species at sites with and without frequent human presence in the study area; 2) we analyzed habitat use for the three species studied.

Materials and methods

Study area. This work was conducted from February to October 2015, in the southern portion of the Lacandon Forest (16°08'56"-16°11'58.3" N and 90°53'57"-91°18'45" W), Chiapas, Mexico. The sampling was carried out in an effective sampling area (ESA) of 150 km² within the southern sector of the Montes Azules Biosphere Reserve (REBIMA, 3,312 km²) and in community forest areas (ACF; ESA = 162.5 km²) of *ejidos* (communal land) adjacent to the REBIMA in the municipality of Marques de Comillas (Figure 1). The altitude of the study area ranges from 150 to 250 meters a.s.l. (Naranjo 2008), with approximately 50 % of the natural forest cover still present (Tejeda-Cruz *et al.* 2009; Garmendia *et al.* 2013, Muench and Martínez-Ramos 2016).

The prevailing climate in the region is warm humid with abundant summer rainfall (Am (i') gw"; García 2004). The mean annual precipitation oscillates between 2,500 and 3,500 mm, with 80 % of rains between June and November (García-Alaniz *et al.* 2010; Arce-Peña *et al.* 2019). Currently, the Lacandon region, except for the REBIMA, is dominated by heterogeneous landscapes composed of fragments of evergreen tropical forest of different sizes and successional states (Rzedowski 1978; Challenger and Soberón 2008) within a matrix of crop fields (mainly maize and oil palm), livestock ranches, and scattered human settlements (Carrara *et al.* 2015; Muench and Martínez-Ramos 2016; De La Torre and Rivero 2019).

We analyzed two types of habitats, namely "conserved areas" (the REBIMA) and a transformed landscape ("community forest areas"; ACF) as this anthropic condition is one of the key drivers of the abundance and distribution of the tapir and peccaries (Naranjo 2019). Fieldwork took place over 250 days between February and October 2015, comprising the rainy season (which peaked in September) and the dry season of the year (*i.e.*, March), as well as the maximum mean temperature (28°C) recorded in May (García and Lugo 1992). The sampling effort was 8,463 camera trap-days. Cuddeback® Black Flash E3 digital cameras were installed in 64 sampling points (hereafter camera trap stations) with a detection zone of 134 m² per camera trap, approximately. Of these, 32 camera trap stations were located in the southern REBIMA sector and 32 in ACFs. These traps were used for recording data on occurrence and frequency, sex (tapir only), and hours of activity of the ungulates of interest in the study area. Using a geographic information system (GIS), the study area was spatially delimited and the proportion of different types of coverage (for-

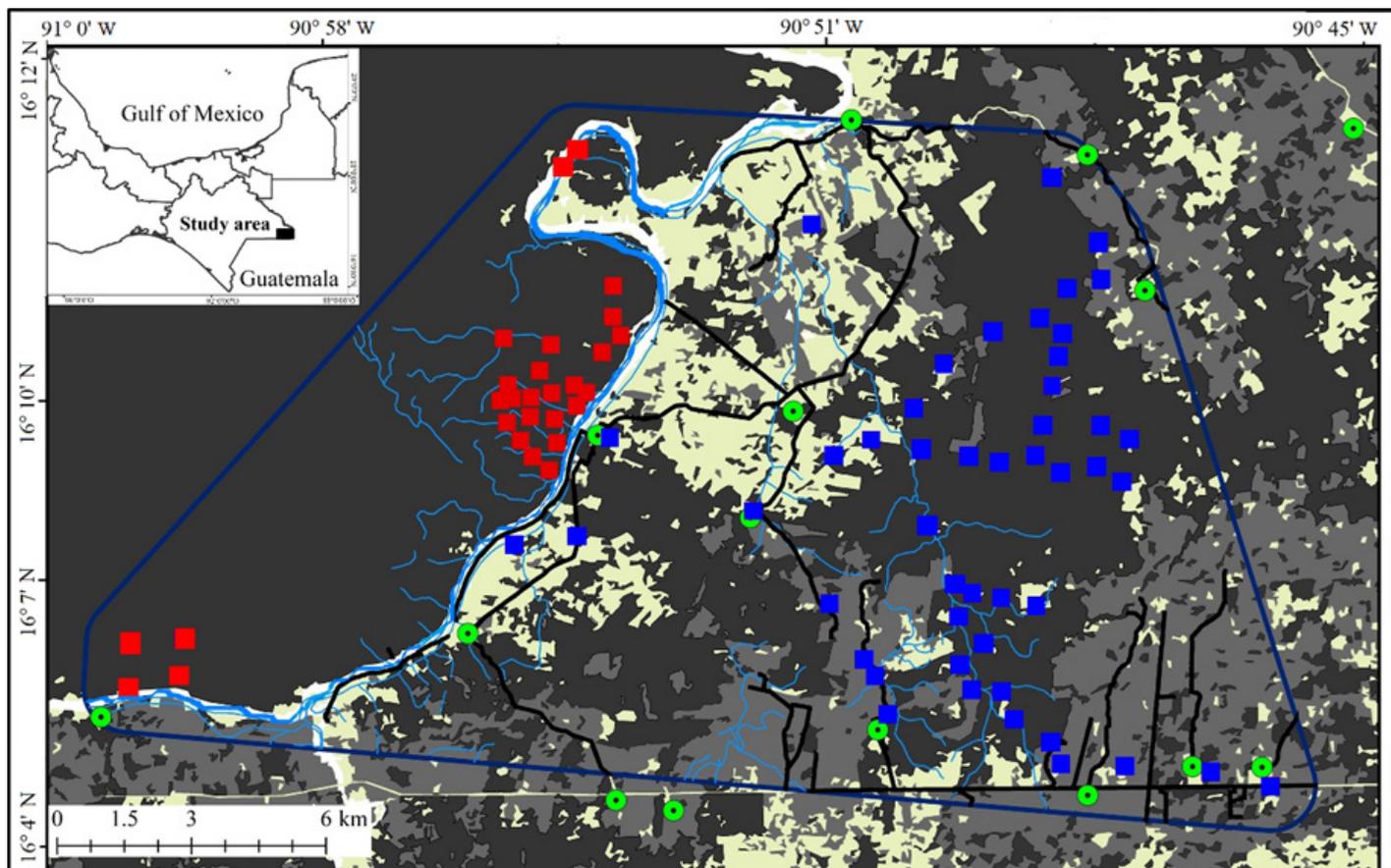


Figure 1. Study Area. Location of sampling sites, which include a portion of the southern sector of the Montes Azules Biosphere Reserve (REBIMA, red squares), and community forest areas (ACF, blue squares). Lacandon Forest, Chiapas, Mexico (February–October 2015).

est cover, land uses, and water bodies) and the proximity to anthropic elements (e.g., roads and towns) in the study area were estimated.

The spatial distribution of camera trap stations followed a grid layout in each of the study sites (REBIMA and ACF), with a minimum separation of 1 km between them to ensure the independence of records, considering the monitoring protocols applied to the study of other big mammals (modified from Silver 2004 and Chávez et al. 2013; Figure 1). Trap cameras were set to operate 24 hours a day and capture sequences of three photos per minute in case of motion detection. For each capture, the date, time, and geographic location of each camera trap station (sampling unit) were verified, as well as the number of individuals recorded. To consider a record as an independent capture and thus minimize any potential autocorrelation (Moreira-Ramírez et al. 2019), only photographs captured with a separation of more than 24 h between them were considered for each species.

Sampling was carried out on areas of dense evergreen tropical forest of various successional stages, as well as patches of riparian vegetation, which were randomly selected to record tapir and peccary individuals and their traces, and for use as sites for installing camera traps. Although pastures and meadows were excluded because they have not been mentioned in the literature as suitable

for tapir or white-lipped peccary in Mexico (March and Naranjo 2005; Carrillo-Reyna et al. 2015; Reyna-Hurtado et al. 2009), some camera-trap stations were placed in areas adjacent (~10 to 100 m) to these types of land use, considering that the collared peccary is listed as a generalist species (Sowls 1997; Reyna-Hurtado et al. 2014). Photographic records were used to construct binomial matrices (“1” to “0”, where 1 = presence and 0 = absence) for each camera-trap station. The matrix for each species was processed with the *Tidyverse* (Wickham 2017) and *SjPlot* (Lüdecke 2018) libraries in R v.4.0.2 (R Core Team 2019).

Habitat use. The use of the habitat by each species was analyzed using logistic regression models with the *Glmulti* package (Calcagno 2019); these models are suggested for their suitability to work with binomial variables (Manly et al. 2002). In addition, covariates were used to identify some of the environmental conditions (Table 1, Supplementary material) that influenced habitat use by ungulates in the study area (Manly et al. 2002; Gaillard et al. 2010). To this end, a high-resolution multi-spectral satellite image for the year 2014 (Landsat 8 Oli Tars) was used, along with the classification of plant cover and land uses previously generated in the Geographic Information Analysis Laboratory (LAIGE, in Spanish) at Colegio de la Frontera Sur (ECOSUR). This monitored classification was modified in the ArcMap program to produce a map of the study area with four lay-

ers of different types of classification of the landscape elements studied: 1) water bodies, 2) human settlements, 3) roads, and 4) vegetation and land use (evergreen tropical forest, secondary tropical forest, crops, pastures and meadows, water bodies, and roads). The logistic regression models were compared using the Akaike information criterion corrected for small sample size (AICc) and weight of each variable, to determine the relative evidence in favor of each model (Burnham and Anderson 2004; Fletcher and Fortin 2018) and the influence of each covariate on the probability of occurrence (interpreted as the probability that a given species is present or absent, and thus, that sites with certain characteristics are used). The models with the best support were selected considering those that yielded the minimum AIC score and $\Delta\text{AICc} \leq 2$ as proposed by Burnham and Anderson (2004), in addition to the weight (W_i). The models with $\Delta\text{AICc} \leq 2$ were selected and averaged to evaluate the relative importance of the variables and the significance of their values (Barton 2019).

Spatio-temporal comparisons of occurrence records for each species were performed using parametric (Student's t) and non-parametric (Mann-Whitney U) tests to evaluate the differences between frequencies of photographic records, occurrences, and relative abundances of species within and between types of conditions across sites in the study area (Sokal and Rohlf 1995).

Activity patterns. We consider the total number of photographs captured and pooled the number of capture events into one-hour intervals for the 24 hours of the day to search for patterns in the actual hours of activity of each focal species (Tobler et al. 2008). We used the "Overlap" package in R by Meredith and Ridout (2017), which allowed plotting the hours of activity of each species using the kernel density estimation, in addition to estimating the overlap coefficient (Dhat) between the patterns of one or two species in different sites.

Results

Frequency of records. Of the 64 camera-trap stations, 24 recorded tapir individuals (11 in REBIMA and 13 in ACF). Collared peccaries were recorded in 11 REBIMA and 16 ACF stations, respectively, while white-lipped peccaries were recorded in 18 stations (6 in REBIMA and 12 in ACF). According to independent photographic records, the tapir was captured more frequently in the protected area (REBIMA; $n = 59$) than in community forest areas (ACF, $n = 28$; $U = 89.5$, $P = 0.01$). The collared peccary was most frequently recorded at the ACF site, attaining statistical significance ($n = 47$; $U = 386.5$, $P = 0.04$). However, this trend was not observed for the white-lipped peccary; although it had more records in the ACF site (48 records) than in REBIMA (33), this difference between sites was non-significant ($U = 127$; $P = 0.60$). In the case of the tapir, a higher proportion of males was recorded in REBIMA versus ACF ($U = 30$; $P = 0.01$), while females showed a similar proportion between sites ($U = 66.5$, $P = 0.78$; Table 2, Supplementary material). The sex of peccary

individuals captured could not be determined based on the photographs recorded.

Habitat-use models. For each of the models generated for the species, the number of variables included, AICc, difference between each model and the model with the lowest delta AICc (Δ), and Akaike weight (W_i) are reported (Tables 2-4, Supplementary material). According to the AICc, the best models to explain the occurrence of the tapir in the study area (Table 2a, Supplementary material) included the variables *distance to permanent water bodies* and *roads* (e.g., dirt roads and roads; with weight [$W_i = 0.63$]) and the vegetation types *evergreen tropical forest* (BTP) and *secondary tropical forest* (BTS; Table 2b, Supplementary material). The best model indicated that the probability of site use by the tapir increases as the distance to water bodies decreases, especially when considering the tropical forest (BTP and BTS; Tables 2a, 2b, Supplementary material; Figure 2).

In the case of the collared peccary, the probability of habitat use increased with the presence and proximity of roads and human settlements, and with the distance from water bodies ($W_i = 0.20$; Table 3a, Supplementary material; Figure 2). However, the presence of different types of vegetation in the study landscape was relatively unimportant (Table 3b, Supplementary material). On the other hand, the probability of habitat use by the white-lipped peccary increased in sites with little anthropic intervention. The response in the probability of use was directly related to the distance to variables associated with anthropic disturbance, such as human settlements, roads and dirt roads, and inversely related to the distance to water bodies ($W_i = 0.42$; Tables 4 and 5, Supplementary material; Figure 2).

Activity patterns. A total of 235 independent photographic records were captured for the ungulates under study (tapir: $n = 87$; white-lipped peccary: 81; collared peccary: 67), including date and time. For the tapir, the photographic evidence revealed a clear preference for nighttime activity (mostly between 2:00 h and 5:00 h; Figure 3). In contrast, photographic records of collared peccary and white-lipped peccary suggested that both species are mostly diurnal, with a slight tendency to be active in the afternoon (after 16:00 h), and with virtually no activity at night (Figure 3).

The overlap coefficients allowed distinguishing the high degree of segregation between the ungulates in the study area across the time dimension. The two peccary species showed an overlap of more than 80 % (Dhat = 0.82; Figure 3). Each of these two species showed a high temporal segregation relative to the tapir. The indicators of temporal overlap between each of the peccary species and the tapir showed little overlap in their hours of activity (i.e., white-lipped peccary vs. tapir: Dhat = 0.34; collared peccary vs. tapir: Dhat = 0.42; Figure 3).

Discussion

Our results show trends in habitat use for the three ungulates studied and high levels of temporal segregation between the peccaries and the tapir in the study area. Considering

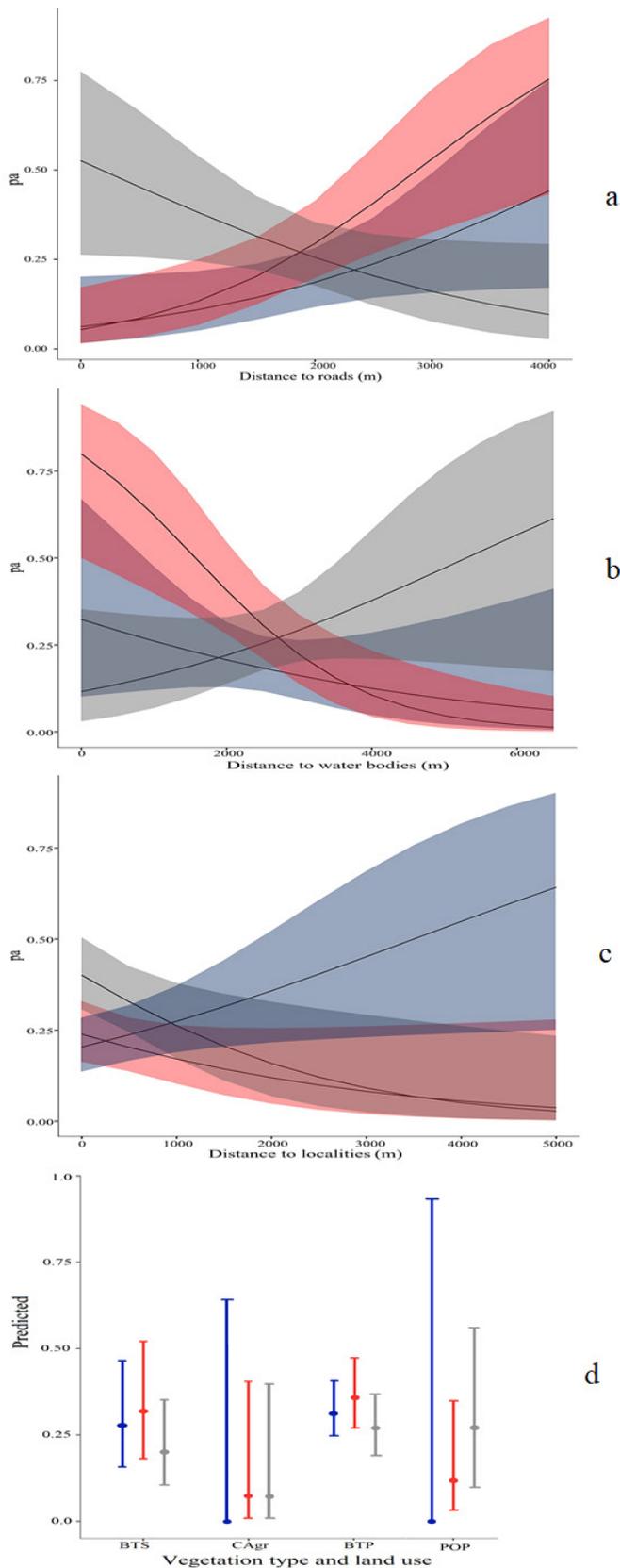


Figure 2. Logistic regression graphs considering variables predictive of habitat use by *Tapirella bairdii* (red), *Dicotyles tajacu* (gray), and *Tayassu pecari* (blue) with respect to distance to roads (a), distance to water bodies (b), distance to human settlements (c), and types of vegetation and land use (d) in community forest areas (ACF) and the protected area (Montes Azules Biosphere Reserve; REBIMA) in the Lacandon Forest, Mexico. pa: Presence-absence predictive values Aca: Mature secondary forest, BTP: Evergreen tropical forest, BTS: Secondary tropical forest, CAgr: Agricultural crops, POP: Pastures and meadows.

time as a resource (*i.e.*, something that is 'consumed', similar other resources; [Kronfeld-Schor and Dayan 2003](#); [Frey et al. 2017](#)), the tapir and peccaries have partitioned niches. It is important to highlight the difference between the habitat use by the two peccary species, as they exhibit opposite response patterns to anthropic variables, such as the presence of roads and proximity to human settlements, and to resources such as water (Figure 2). The habitat variables considered *a priori* in this study were limited; however, their assessment could be key for continuing the study of the interactions between the spatial and temporal dimensions of the ecological niches of these species ([Frey et al. 2017](#)).

Habitat use. Given the frequencies and occurrences observed in collared peccary records at both sites, our null hypothesis was validated since this species indiscriminately used both habitat types. This result has been reported in other studies conducted in America for this species, which have documented the presence of collared peccary in a wide range of habitats and environmental conditions, as well as its high tolerance to anthropic pressures ([Kiltie 1982](#); [Reyna et al. 2014](#); [Briceño-Méndez et al. 2016](#)). The similar use intensity of both habitat types by the white-lipped peccary despite the anthropic disturbance factors in the ACF is probably because the ecological conditions meet the resource requirements (*i.e.*, water, food, and shelter, among others) of this species in this site. [Muench and Martínez-Ramos \(2016\)](#) reported that the ACF preserved all species of medium- and large-sized mammals in the region. Thus, in spite of the anthropic pressures, this area still functions as a suitable habitat for peccary populations ([Fryxell et al. 2014](#); [Krausman and Morrison 2016](#)). This area also contains numerous water bodies (Figure 1), a key factor for the movement of white-lipped peccaries ([Reyna-Hurtado et al. 2009](#)). However, to determine the viability of the local populations of these ungulates in ACF, studies on age structure and population movement ecology are required, which may indicate that the species is reproducing in the area and that there is structural and functional connectivity ([Morrison et al. 2006](#); [Garrido-Garduño and Vázquez-Domínguez 2013](#)).

The fact that a higher number of tapir records were recorded in REBIMA ($n = 59$) than in ACF ($n = 28$), *i.e.*, a higher relative abundance of tapir in the former (20.9 ind/1000 camera trap-days in REBIMA vs 10.8 ind/1000 camera trap-days in ACF; Tables 3 to 5, Supplementary material) may be due to the greater surface area covered by mature forest in the protected site. Besides, the tapir tends to move away or become more elusive in areas with human presence and hunting ([Naranjo and Cruz 1998](#); [Zapata-Ríos and Branch 2015](#)). It has also been documented that the presence of domestic or feral canids can lead to changes in the habitat use of native species, thus affecting their movement and hours of activity ([Vanak and Gompper 2009](#); [Silva-Rodríguez et al. 2010](#)).

The ACF contains a large fragment of tropical forest (~5800 ha) in different successional stages that maintains some connectivity with other adjacent forest patches (Fig-

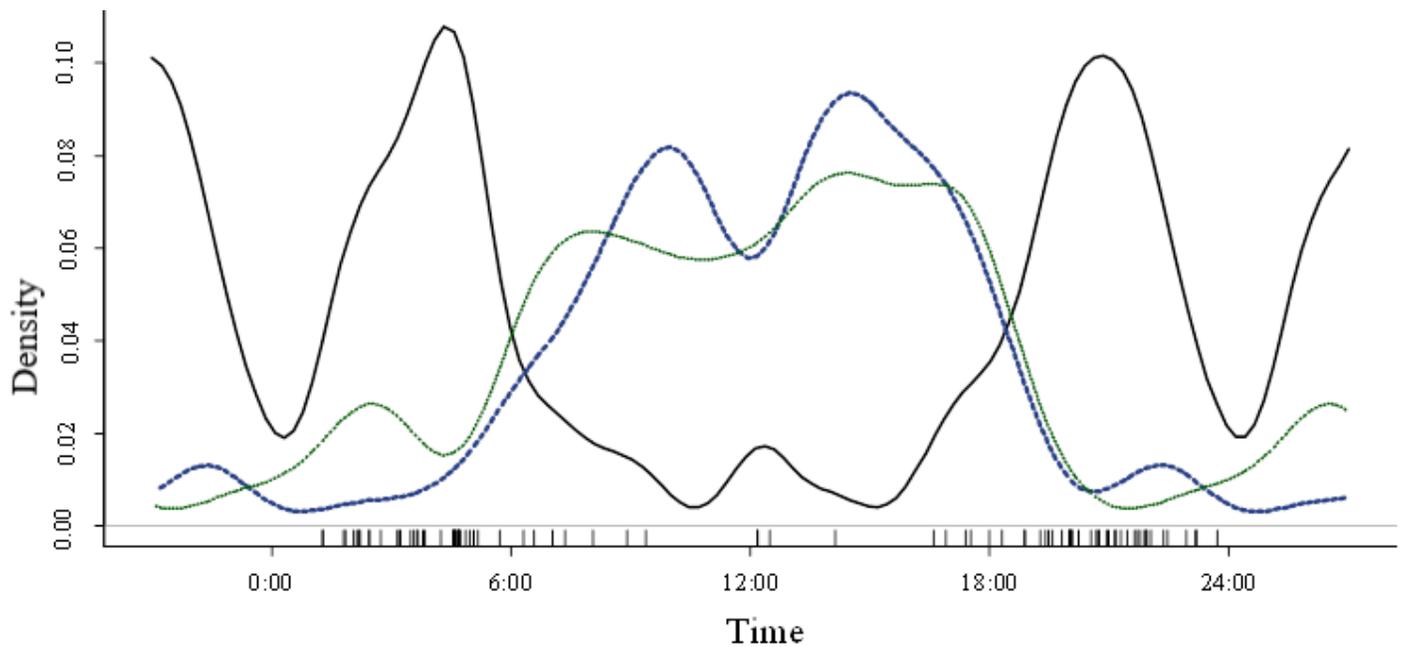


Figure 3. Overlap of activity between ungulate species in community forest areas (ACF) and the protected area (Montes Azules Biosphere Reserve; REBIMA) in the Lacandon Forest, Mexico. Black line: *Tapirella bairdii*; blue line: *Tayassu pecari*; green line: *Dicotyles tajacu* (overlap coefficient), values of the confidence interval. $D. tajacu$ - $T. bairdii$ - $T. pecari$ = 0.34 (0.17–0.37); $T. pecari$ - $D. tajacu$ = 0.82 (0.84–1.03), and $D. tajacu$ - $T. bairdii$ = 0.42 (0.22–0.44).

ure 1; [Gil-Fernández et al. 2017](#)). The white-lipped peccary was recorded more frequently in ACF than in REBIMA (Table 5, Supplementary material), likely due to migratory or episodic movements that favor their presence even in non-protected areas ([Mendes-Pontes and Chivers 2007](#); [Reyna-Hurtado et al. 2009](#)).

Habitat use models. The models constructed to evaluate habitat use by the species confirm previous reports, which describe low tolerance to anthropic effects (*i.e.*, presence of roads and infrastructure) and preference for areas with connectivity to water bodies by the tapir and white-lipped peccary ([O’Farrill et al. 2014](#); [Naranjo 2019](#); [Reyna-Hurtado et al. 2014](#); [Moreira-Ramírez et al. 2019](#)). In contrast, our results show that the collared peccary uses both types of sites (protected area and community forest areas) in a similar way. Consistent results have been reported for this species in similar Neotropical environments where food is not a limiting factor ([Terborgh 1986](#); [Peres 19946](#); [Galetti et al. 1999](#)). This helps to explain the occasional records of this species crossing roads and in agricultural areas in the present study. To note, the use of agricultural systems by *T. pecari* has been documented in dry savannas of Venezuela, the dry Chaco in Paraguay ([Mayer and Wetzel 1987](#); [Redford and Eisenberg 1992](#)), and grasslands of central and central-western Brazil, where they are even considered a pest for the damage and losses caused to farmers ([Jacomio et al. 2013](#); [Lima et al. 2019](#)). This is not the case in southeastern Mexico, since the populations of *T. pecari* rarely cause damages to agricultural systems, to the best of our knowledge ([Naranjo 2002](#); [Romero-Balderas et al. 2006](#)). This discrepancy may be related to the regional context of the areas where this

species thrives, since the great Chaco and the Amazon are characterized by large extensions of habitat (> 1.5 million km²; [Cartes et al. 2015](#); [Camino et al. 2017](#)) and low human densities, contrary to our study area, which shows smaller areas of suitable habitat and high human density and disturbance ([Naranjo 2019](#)).

Activity patterns. For the tapir, previous studies in Mexico and elsewhere report activity patterns within a specific time span (nocturnal or diurnal; [Eisenberg 1989](#); [Sanderson and Trolle 2005](#)), or with hours of activity split into two periods of the day (typically daytime and nighttime; [Matola et al. 1997](#); [Foerster and Vaughan 2002](#)). Besides, these ungulates tend to move away or become more elusive in areas with human presence and hunting ([Naranjo and Cruz 1998](#); [Zapata-Ríos and Branch 2015](#)). It has also been documented that the presence of domestic or feral canids can lead to changes in the habitat use of native mammals, affecting their movement and hours of activity ([Vanak and Gompper 2009](#); [Silva-Rodríguez et al. 2010](#)). In the study area, intrusion events of domestic dogs and hunters were recorded in the ACF; however, the current hunting rate or frequency has not been documented (Figures 2 and 4).

This study found that the tapir displays activity patterns with two marked peaks of nighttime activity (20:00 to 23:00 h and 2:00 to 5:00 h; Figure 3). This finding is consistent with reports for other tapir populations in Mexico, such as those inhabiting Los Chimalapas, Oaxaca ([Lira-Torres et al. 2014](#)) and the Calakmul Biosphere Reserve, Campeche (unimodal period of activity: 20:00 to 3:00 h; [Sánchez-Pinzón et al. 2020](#)). The bimodal pattern reported in this study has also been observed for *T. pinchaque* in the central Andes of Colombia ([Lizcano and Cavelier 2000](#)).

and *T. terrestris* in the Ecuadorian Amazon (Espinosa and Salvador 2017). In contrast, the unimodal pattern of activity of the tapir in Calakmul may be the result of monitoring associated with water bodies (open canopy areas), a vegetation structure allowing greater moonlight permeability (*i.e.*, subdeciduous tropical forest; Lizcano and Cavalier 2000), and anthropic pressures such as hunting (Oliveira-Santos et al. 2010; Sánchez-Pinzón et al. 2020). In addition, environmental heterogeneity in different habitats can influence wildlife activity patterns (Liu et al. 2017). The evergreen tropical forest of the Lacandon Forest is more exuberant and rich in food resources and moisture than other vegetation types (Rzedowski 1978; Hubbel 2001; Pennington and Sarukhan 2005), which may influence the activity pattern of this species.

The activity patterns recorded for both peccary species show that they were mainly diurnal, with peaks of activity between 14:00 and 18:00 h and sporadic activity in the evenings or nights. Our results are consistent with Briceño-Méndez et al. (2016), who reported for these peccary species diurnal patterns with peak activity between 08:00 h and 14:00 h in sites with persistent hunting in Calakmul, Mexico. However, they differ slightly from the findings in a similar ecosystem in Brazil (Galetti et al. 2015), where peaks of activity were recorded between 5:00 and 10:00 h

for the white-lipped peccary and from 17:00 to 22:00 h for the collared peccary. Other studies have shown activity patterns different from those exhibited by both peccary species in the present study, showing that they can be active throughout the day (Mayer and Wetzel 1987; Arroyo-Arce et al. 2017). Our results differ from those of Keuroghlian et al. (2004), who did not observe a temporal overlap between these species in a landscape of southeast Brazil. The differences in the hours of activity just mentioned may be due to factors associated with particular habitat characteristics, community structure, and local (hunting) or regional disturbance variables that influence the activity patterns of species (Frey et al. 2017). The hours of activity of peccaries recorded in this study suggest a mechanism to avoid predation since these are opposite to the activity peaks of their main predator in the study area, the jaguar *Panthera onca* (De la Torre and Medellín 2011), as well as to avoid hunting (Briceño-Méndez et al. 2016).

This suggests that habitat segregation (spatial dimension) rather than temporal segregation, may be one of the main mechanisms allowing the sympatric coexistence of both species of peccaries in the Lacandon Forest. Niche partitioning between these two tayassuids in the study area could be based on: 1) the differential use of food resources, with minor variations in the diet, as reported in several studies throughout its distribution range (Reyna-Hurtado et al. 2014); and 2) differences in the movement ecology of the white-lipped peccary, which, given the amplitude of its displacement, allows gaining an advantage over collared peccaries (Reyna-Hurtado and Tanner 2005; Reyna-Hurtado et al. 2009). This means that while *T. pecari* is able of traveling long distances of up to 120 km in preserved forests in search of food, forced by its metabolism, the collared peccary can meet its metabolic and ecological requirements even in disturbed areas (Reyna-Hurtado et al. 2014) and in smaller areas of suitable habitat, according to the home range of 7.3 km² reported by Naranjo (2002) in the Lacandon Forest.

The similarities and differences in the parameters evaluated in this study versus other studies were due to different causes, considering that animals can modify their spatio-temporal activity behavior, either to reduce the risk of natural predation (Oliveira-Santos et al. 2010; Lone et al. 2017) or as an effect of anthropic alterations such as habitat fragmentation and hunting (Tejeda-Cruz et al. 2009; Carreira et al. 2020). This has cascading effects on the rest of the community (Carreira et al. 2020), a potential situation that should be monitored by managers of protected and non-protected areas under the current laws and regulations seeking to preserve the viability of populations through management plans and conservation actions (Robinson et al. 2016; Dellinger et al. 2019).

Although the low tolerance of the white-lipped peccary to the effects of human activities has been documented (Reyna-Hurtado and Tanner 2007; Altrichter et al. 2012; Keuroghlian et al. 2013; Mandujano and Reyna-Hurtado



Figure 4. Evidence of firearm hunting and presence of domestic canids within the ACF, Lacandon Forest, Chiapas, Mexico (2015).

2019), the fitness of logistic regression models showed an unexpected positive projection for the use of the ACF forest area, similar to that of areas within the REBIMA (see Figure 2). The fact that white-lipped peccaries have been observed in areas with human settlements is encouraging for their conservation. We hope these results will contribute to convince decision-makers and the inhabitants of the Lacandon Forest that the coexistence between human and wildlife populations in the region is feasible.

Our results indicate that: 1) both peccary species display different habitat preferences in the study area, while tapir preferred using the protected area, as significant evidence of niche partitioning; and 2) the ACF site is an important relict of tropical forest with the potential to maintain populations of these species; therefore, the conservation of these forests by local communities is essential to ensure the persistence of these ungulates. The conservation of these populations and other natural resources in the Lacandon Forest has become urgent given the unsustainable production practices that promote deforestation (*i.e.*, extensive livestock ranching and commercial agriculture) in areas adjacent to federal and community protected natural areas. In our view, more environmentally friendly productive activity schemes such as agroforestry systems should be implemented in the region to mitigate unsustainable practices and their effects. Also, the protection and management of the remaining habitat in managed areas (ACF) are relevant and necessary, as well as the protection of wildlife from poaching.

We suggest addressing this information gap in future studies by assessing the movements of wild ungulates to better know their habitat occupation, distribution, and potential metapopulation dynamics, which may explain their presence in fragments of habitat surrounding the REBIMA (Naranjo and Bodmer 2007). Another aspect worth investigating is the influence of structural and functional connectivity, as well as habitat suitability for these species at the landscape level in the study area.

It is both convenient and relevant to generate information with spatially explicit variables that ensure greater fidelity and independence of captures of the movements of ungulates across the study area, such as the estimation of their home ranges (Frey *et al.* 2017; Mandujano and Reyna-Hurtado 2019) and approximations with occupation models, habitat preferences, and other resource selection models (*e.g.*, resource selection functions; Manly *et al.* 2002; Lele *et al.* 2013). Future research should contribute to reversing these processes, for instance, by supporting the generation of conservation strategies and strengthening management plans for the populations of wild ungulates and their habitats in the Lacandon Forest. One approach to this end would be through Wildlife Conservation Management Units with species that tolerate the sustainable use of their populations, such as the collared peccary and the lowland paca (*Cuniculus paca*).

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Supplementary material

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