

Habitat use of wild ungulates in fragmented landscapes of the Lacandon Forest, Southern Mexico

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Abstract

Habitat use of five ungulate species was assessed in two fragmented sites in the Lacandon Forest, Southern Mexico. Differential habitat use was expected according to the habitat requirements of each species. Repeated track counts were carried out from September 2005 to December 2006 along 19 line transects totaling 683 km, obtaining 2271 ungulate records. We found that Baird's tapir and the white-lipped peccary are actually rainforest specialists avoiding disturbed habitats in the Lacandon Forest, while the red brocket deer, the collared peccary, and the white-tailed deer show different degrees of success in using habitat mosaic derived from human activities. Given that fragmentation patterns have an effect on habitat use of ungulate species in our study area, more information about the effects of landscape configuration on the distribution and abundance of those species is needed. In order to favor conservation of the ungulate species array in the Lacandon Forest, we recommend enforcement of mature rainforest protection and maintenance of heterogeneous landscapes in human settlements through traditional agricultural practices, agroforestry, and intensive pastureland management.

Keywords: Chiapas; habitat management; habitat selection; Montes Azules Biosphere Reserve; Neotropical rainforest.

Introduction

The Lacandon Forest is one of the most important rainforest tracts in Mexico, which in turn constitutes a portion of the largest remaining tropical forest north of the Amazon: the Greater Maya Forest shared by Belize, northern Guatemala and southeastern Mexico (Rodstrom

et al. 1999). However, this impressive biodiversity is being threatened by factors, such as deforestation, land use change for agriculture and cattle ranching, induced forest fires, timber extraction, and wildlife overexploitation (INE 2000). In response, Mexico's federal government has decreed seven protected areas in the Lacandon region comprising approximately 4200 km² of which 3312 km² correspond to Montes Azules Biosphere Reserve (Tejeda-Cruz and Márquez-Rosano 2006).

Several authors (Vasquez and Ramos 1992, Muench 1998) state that approximately 50% of the original forest cover of the Lacandon Forest was lost particularly during the second half of the twentieth century as a result of colonization by both indigenous and "mestizo" (mixed European and indigenous origin) people from other regions of Chiapas as well as from other Mexican states (SEDUE 1992, Mariaca 2002). Colonization favored the conformation of numerous agricultural communities with diverse cultural background, whose productive activities have transformed natural ecosystems in complex landscapes constituted by a mosaic of rainforest fragments surrounded by secondary vegetation, agricultural plots, and grasslands. Different fragmentation patterns of landscape are expressed in distinct spatial arrays of its elements (patches, corridors, and the matrix; Forman 1995). These differences imply variations in habitat availability and an integral (and differential) effect on wildlife species (Ojasti 2000), which depends on their particular habitat requirements and their ability to move through the elements of the landscape (Forman 1995, Turner et al. 2001).

Information on habitat use is crucial to understand the relationship between distribution and abundance of wildlife species. This information can be helpful to assess not only habitat requirements of animals but also to: (1) predict their presence or abundance in other areas and potential effects of habitat transformation (Arthur et al. 1996, Ríos-Uzeda et al. 2006); and (2) support sound wildlife management plans (Carmiña-Cardenal 2003, Morrison et al. 2006). Several studies have focused on habitat use of Neotropical ungulates (Bodmer 1990, Naranjo 1995, 2002, Fragoso 1998, 1999, Naranjo and Cruz 1998, Foerster and Vaughan 2002, Tobler 2002, Lira et al. 2004, Reyna-Hurtado and Tanner 2005), and most of these studies have been conducted in relatively well-preserved habitat types, including secondary vegetation with no human presence. However, it is still not well understood how ungulate habitat use differ between fragmented and non-fragmented landscapes, assuming that each species may respond differently to human-induced fragmentation depending on their habitat requirements, adaptability, and tolerance to human presence.

Neotropical ungulates (deer, peccaries, and tapirs) have an important role as foliage consumers, seed dis-

persers, and seed predators, contributing to maintain rainforest ecosystem dynamics. These mammals also constitute important prey for large predators, including humans (Naranjo 2002) who have extensively used ungulates and other wildlife species as sources of food, clothes, medicine, tools, ritual objects, trophies and company for centuries (Ojasti 2000, Robinson and Bennett 2000). Ungulates still are a relevant resource for current dwellers of the Lacandon Forest, representing approximately 66.6% of the terrestrial wildlife biomass they extract (Naranjo et al. 2004).

Five native ungulate species inhabit the Lacandon Forest. These species show habitat requirements moving along an ecological gradient between strict specialists and generalists (species names according to Grubb 2005a,b).

The white-lipped peccary (*Tayassu pecari* Link 1795) is restricted to extensive tropical forests of Central and South America, including palm swamps and savannas within wetlands. It prefers dense vegetation areas with permanent water bodies, and its tolerance towards deforested habitats seems minimal. In Mexico, this peccary is found in both tropical evergreen and subdeciduous forest, and occasionally in tropical dry forest. Its optimal habitat in Mexico is constituted by primary lowland evergreen forest tracts over 300 km² (Leopold 1959, Mayer and Wetzel 1987, Bodmer 1990, Álvarez del Toro 1991, March 1993, 2005, Fragoso 1998, 1999).

Baird's tapir (*Tapirus bairdii* Gill 1865) is well adapted to live in a variety of tropical and subtropical habitats with permanent water bodies. Its distribution in Mexico and Central America is restricted to well-preserved remaining tropical forest tracts over 100 km² and with little or no human activity (Matola et al. 1997, March and Naranjo 2005). This species has been extirpated from most of its original distribution range because of habitat loss and overhunting (Leopold 1959, March and Naranjo 2005).

The red brocket deer (*Mazama americana* Erxleben 1777) lives in both mature and successional lowland and montane evergreen and subdeciduous forests, where it uses natural openings and clearings as feeding sites. It also may occupy savannas containing dense vegetation patches as refuges. This deer seems to be more abundant in well-preserved areas far from human settlements (Leopold 1959, Álvarez del Toro 1991, Naranjo 2002, Gallina 2005).

The white-tailed deer (*Odocoileus virginianus* Zimmermann 1780) habitat requirements are met in many tropical ecosystems including savannas, pine-oak forest, plantations, pasturelands, and relatively open tropical forests (Leopold 1959, Teer 1994, Galindo-Leal and Weber 2005). Some authors affirm that the white-tailed deer avoids dense tropical evergreen and cloud forests, although it may be present in secondary forest (Leopold 1959, Álvarez del Toro 1991, Naranjo 2002, Galindo-Leal and Weber 2005).

The collared peccary (*Pecari tajacu* Linnaeus 1758) inhabits a great variety of habitat types, even those with moderate disturbance. The vegetation types used by this species in Mexico includes evergreen, subdeciduous, and dry tropical forest, thorn forest, xerophitic vegetation, pine-oak forest, cloud forest, secondary vegetation,

and even farmlands surrounded by dense vegetation (Álvarez del Toro 1991, Sows 1997, Naranjo 2002, March and Mandujano 2005). Leopold (1959) points out that collared peccary populations reach their maximum densities in dry tropical forest and thorn forest, being less abundant in pristine tropical rainforest.

Considering their habitat requirements, we expected that: (1) specialist species (white-lipped peccary, tapir, and red brocket deer) would use well-preserved habitats, such as the rainforest within Montes Azules more frequently, avoiding other habitat types; (2) semi-open area species (white-tailed deer) would be more frequently found in disturbed habitat types than in other habitat types; and (3) generalist species (collared peccary) would use all habitat types according to their availability in the study area. To test these hypotheses, repeated track counts were carried out along linear transects in two fragmented sites (Rio Azul and Ixcán) of Montes Azules Biosphere Reserve and contiguous communities in the Lacandon Forest, Southern Mexico.

Materials and methods

Study area

The Lacandon Forest occupies the eastern portion of the state of Chiapas, Mexico. The topography of the area is complex, with series of parallel karstic mountain ranges of Cretacic origin separated by long valleys and creeks at altitudes of 100–1800 m. A second group of lower mountains is composed by lutites and sandstones mostly of Tertiary origin, which form gentle slopes and hills contiguous to recent alluvial plains along major watercourses (Vasquez and Ramos 1992, Muench 1998). The climate is predominantly tropical with abundant summer rainfall. Mean annual temperature and precipitation are 22°C–25°C and 2000–3500 mm, respectively (INE 2000). Natural vegetation types of the Lacandon Forest include tropical rainforest, cloud forest, pine-oak forest, riparian forest, and savannah (INE 2000). Our study sites (Figure 1) were located in the southwest part of the Lacandon Forest, including the core area of Montes Azules as well as adjacent disturbed areas within or outside this reserve (buffer zone).

The first site (Rio Azul) is entirely within Montes Azules Biosphere Reserve, comprising a mosaic of rainforest, secondary vegetation, agricultural plots (mainly cornfields), and small grasslands managed by indigenous farmers from local communities. In this site, human population is distributed in six communities with a total population of 1112 (INEGI 2006). Residents of these communities are mainly farmers cultivating corn and beans for local consumption in relatively small plots (<2 ha). These crops are produced under a slash and burn system, using specific plots for up to 2 years and then abandoning them for around 5 years, allowing secondary vegetation growth that improves soil fertility in preparation for a new agricultural cycle. The main commercial crop in the area is shade coffee in small plantations (0.5–2 ha). Cattle ranching is not well-developed and occurs on a small scale in this site, but the expansion of this production system is expected following

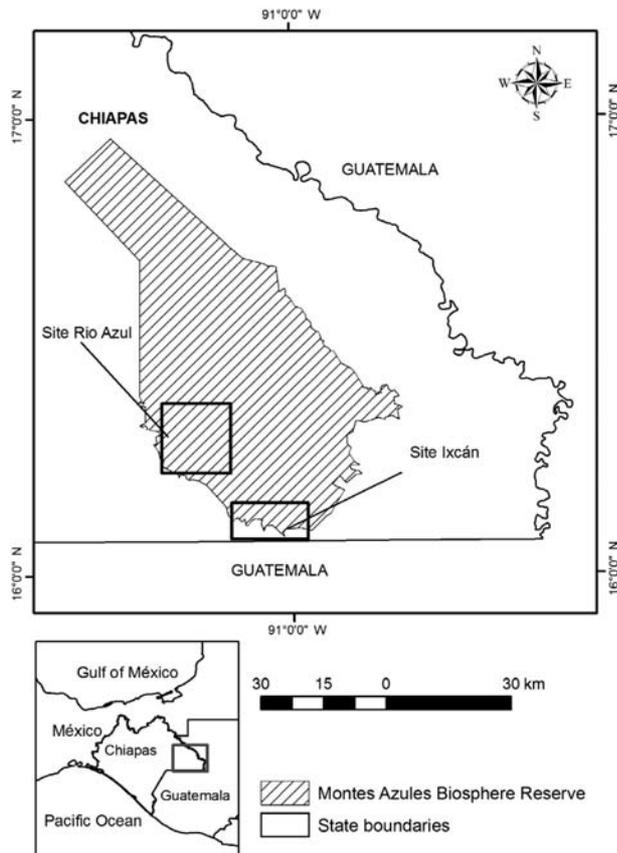


Figure 1 Study sites in the Lacandon Forest, Chiapas, México.

current land use patterns at the expense of rainforest remnants and secondary vegetation. Some people of Rio Azul occasionally extract “xate” palms (*Chamaedorea* spp.) for sale.

The second site (Ixcán) includes a well-preserved rainforest tract inside Montes Azules and adjacent lands outside the protected area owned by Ixcán communities and a private ranch. Both zones are divided by the Lacantun River and they comprise a human population of 1717 (INEGI 2006). The main economic activity is extensive cattle ranching in induced pasturelands with low productivity. The lack of pasture fields rotation derives in overgrazing and erosion problems. Consequently, current carrying capacity (1 head/ha) in those pasturelands is below the potential capacity (up to 3 heads/ha) which could be achieved if adequate management of pastures and livestock were adopted. In this scenario, the expansion of grazing areas is based on the transformation of rainforest remnants and secondary vegetation into pasturelands. Cattle ranching is complemented with commercial crops (jalapeño peppers, cacao, and bananas)

in small plots (<0.5 ha), using chemical fertilizers and pesticides, and by subsistence crops (corn and beans).

Due to the expansion of extensive cattle ranching, there is a high demand for land in Ixcán. This demand has driven many farmers to transform their plots into pasturelands, which currently is driving a shift in the landscape configuration at Ixcán, from a matrix of farmlands and secondary vegetation to a matrix of grasslands comprising forest fragments on the steepest slopes. Subsistence hunting and fishing are common practices on both sites, constituting important sources of protein for residents (Inda 2005). On both Rio Azul and Ixcán, illegal migration to the United States has increased in recent years, which has resulted in an expansion of cattle ranching by families receiving dollars sent by their migrant relatives.

Availability of habitat types

Available vegetation maps of the study area (CI 2000) are general and do not allow to distinguish the high heterogeneity associated with variations in geomorphology, soil types, plant species composition, and effects of human activities. To classify habitat types in both study sites, we used Pennington and Sarukhán’s (1998) natural vegetation criteria as tall evergreen forest (TEF), where dominant trees are over 30 m high, usually with large buttresses. Anthropogenic variability was evaluated along a habitat transformation gradient comprising three vegetation types derived from human disturbance: (1) disturbed tall evergreen forest (DTEF), similar to TEF but with evidence of human disturbance, such as cut trees, open trails, and roads; shaded coffee and cacao plantations were included in this category; (2) secondary vegetation (SV), conformed by successional shrubs or herbs growing in abandoned agricultural fields; and (3) farmlands (FLs), encompassing cornfields, pepper plantations, and grasslands with disperse trees and shrubs.

The most abundant habitat type in both sites was TEF, occupying 57.8% in Rio Azul and 54% in Ixcán of total cover along transects. This habitat type was found in areas within Montes Azules where there are no human settlements nearby. Transformed vegetation types (DTEF, SV, and FLs) were mainly observed where communities have their territories (Table 1). The most remarkable difference between sites is that the FLs of Ixcán triple in size Rio Azul FLs. The relative cover (distance) of each habitat type was quantified along the 19 transects sampled.

Habitat use

Ten transects were sampled in Rio Azul, six in undisturbed areas (TEF) and four in disturbed areas (communal

Table 1 Habitat type proportions (% of length) estimated along transects sampled in the Lacandon Forest, Mexico.

Habitat types	Site Rio Azul (%)	Site Ixcán (%)
Tall evergreen forest (TEF)	57.8	54
Disturbed tall evergreen forest (DTEF)	26.2	22.8
Secondary vegetation (SV)	11.8	10.7
Farmlands (FLs)	4.2	12.5
Total	100	100

lands). Average length of transects was 3.35 km (2.50–4.85 km). In Ixcán, nine transects were walked: five in undisturbed areas and four in disturbed areas (average length: 2.57 km; 1.30–3.35 km). All transects were marked with tape every 50 m and geo-referenced every 200 m. Ungulate track counts were done every month from September 2005 to August 2006 in Ixcán, and from January 2006 to December 2006 in Rio Azul. Track identification was supported by published field guides (Reid 1997, Aranda 2000) as well as by the authors' previous experience in the study area. Counts were carried out at a slow pace (1–1.5 km/h) between 07:00 and 11:30 h, and between 15:00 and 18:00 h (Naranjo 2002). Minimum time elapsed between two consecutive counts along the same transect was 20 days. Groups of footprints evidently left by a single individual were counted as a single track, as well as footprint accumulations of gregarious species (i.e., peccaries) were counted as a single group record. When consecutive track groups within a transect seemed to correspond to different individuals according to the researchers' experience, a minimum distance of 100 m was used to discriminate among records of a given species (Bolaños and Naranjo 2001). All tracks found were erased to prevent double counts. Each track group recorded was associated to a specific vegetation type.

Animal sign-based indices were used as estimators of population abundance (Ojasti 2000). The use of these indices is recommended to study cryptic or elusive terrestrial mammal species (Norris et al. 2008), particularly when habitat visibility is limited (Ojasti 2000), as is the case of ungulates in Neotropical rainforests, such as the Lacandon area. An additional advantage of sign-based indices is that records are often independent of activity patterns of focal species (Ojasti 2000, Naranjo and Bolaños 2003). In this regard, systematic track counts along linear transects were applied to obtain indices comparing the abundance of medium- and large-sized mammals, such as ungulates among habitat types (Naranjo 1995, 2002, Naranjo and Cruz 1998, Aranda 2000, Escamilla et al. 2000, Tobler 2002, Guzmán-Lenis and Camargo-Sanabria 2004, Lira et al. 2004, Reyna-Hurtado and Tanner 2005, 2007), as well as to assess conservation status of peccaries populations (Cascelli de Azevedo and Amorim-Conforti 2008).

Naranjo and Bolaños (2003) found a positive correlation between track encounter rates and densities of mammals estimated along 1908 km of line transects in the Lacandon Forest. These authors state that indices of abundance were considerably more cost-effective than capturing focal species.

Data analysis

There are several methods for studying habitat use by animals considering habitat as a categorical variable (see Alldredge and Griswold 2006 for a review). Most of these methods require data from direct individual sightings of marked specimens and are not applicable to sign (i.e., tracks and feces) counts. Habitat use was estimated in this study using Neu et al.'s (1974) method modified by Byers et al. (1984). This method allows the use of animal sign-based abundance indices and has been used to test

the hypothesis that habitat types are used proportionally to their availability within a given study site (Alldredge and Ratti 1992). In this method, χ^2 -tests with Bonferroni intervals are applied to compare observed and expected proportions of tracks in relation to the proportion of each habitat type (Byers et al. 1984). Concerning these χ^2 -tests, Roscoe and Byars (1971) point out that when there is a great departure of the frequencies from a uniform distribution, the average expected frequency (number of observations- n /number of habitat types- k) may be 2.0 for testing at $p=0.5$. Koehler and Larntz (1980) suggest that the χ^2 -test performs well in situations where $k \geq 3$, $n \geq 10$, and $n^2/k \geq 10$. Zar (1999) recommends its use if the data fit both the Roscoe and Byars's (1971) and Koehler and Larntz's (1980) guidelines. This method is eligible if habitat use is combined for all animals and its main assumptions are: (a) all the observations are independent; (b) habitat availability is equal for all animals; and (c) habitat availability is known (Alldredge and Griswold 2006). Calculations were done through the computer program HABUSE (Byers et al. 1984).

Byers et al.'s (1984) method has been criticized because Bonferroni's confidence intervals ignore the "unit sum constraint" derived from the sum of proportions of available habitat types (Aebischer et al. 1993, Alldredge and Griswold 2006). More criticism comes from the assumption that: (1) repeated observations of gregarious animals and their signs are not independent (Alldredge and Ratti 1992, Alldredge and Griswold 2006); and (2) type II error increases as the number of habitat types considered is higher (Alldredge and Ratti 1986). Nevertheless, this method continues to be frequently applied in habitat use analyses due to its simplicity, versatility, and low cost (Alldredge and Griswold 2006). Alldredge and Ratti (1986) recognize that many studies violate the assumption of independent observations owing to logistic and financial constraints. While this situation does not invalidate field data, it limits conclusions drawn from them. Thus, the results of these studies should be carefully interpreted and assumption violations should be reported.

Complementary, a second analysis of habitat use was done using Johnson's (1980) method, which is based on the comparison between ranks of habitat use and habitat availability, testing the hypothesis of equality of both ranks ordering. This approach does not require independence of observations (Alldredge and Ratti 1992) and it is applicable when habitat availability is estimated or known either for animal groups or for individuals (Alldredge and Griswold, 2006). This method allows the exclusion of questionable habitats and habitats without any observation. However, it is prone to information loss and lack of sensitivity when the habitat use and availability proportions are different while they have the same rank ordering (Alldredge and Ratti 1986, 1992, Alldredge and Griswold 2006). Despite Johnson's (1980) method use of averaged observations from identified individuals, it has been used in studies based on indices of abundance (Muench 2001, Reyna-Hurtado and Tanner 2005) comparing the rank ordering of observed tracks versus habitat availability. The differences between observed track ranks and habitat availability ranks was averaged across transects for each study site and species.

Results

Habitat use

During the study, 2271 records of ungulate tracks were reported along 683.4 km of line transects. Among all records, 1616 (71%) originated from Rio Azul and 655 (29%) from Ixcan (Tables 2 and 3).

White-lipped peccary Only 15 tracks of this species were observed during the study, eight in Rio Azul and seven in Ixcan, which did not allow running statistical analyses. These tracks were recorded only in TEF in or near the core area of Montes Azules Biosphere Reserve and not far from permanent water sources.

Baird's tapir A total of 394 tapir tracks were observed (214 in Rio Azul and 180 in Ixcan). Tapir tracks were more

frequently found in well-preserved habitat types with presence of permanent water bodies, such as rivers, streams, and lagoons. According to Byers et al.'s (1984) method, tapirs showed a higher-than-expected use of TEF in both sites, while the remaining habitat types were used very little or not used by this species (Rio Azul: $\chi^2=114.7$, $df=3$, $p<0.001$; Ixcan: $\chi^2=153.3$, $df=3$, $p<0.001$). The Johnson's (1980) method failed to show any difference between the frequency of observed tracks and the habitat availability ranks in Rio Azul, while this method was not applied in Ixcan because tapir tracks were observed in a single habitat type (TEF).

Red brocket deer This species recorded the highest number of track counts ($n=1146$) in the study area and was mostly observed in Rio Azul ($n=926$, 80.8%). According to Byers et al.'s (1984) method, red brocket

Table 2 Ungulate tracks observed in transects of the Lacandon Forest, Mexico.

Site	No. of transects	Distance traveled (km)	Track numbers					Total
			Tpe	Tba	Mam	Pta	Ovi	
Rio Azul	10	395.1	8	214	926	337	131	1616
Ixcan	9	288.3	7	180	220	211	37	655
Total	19	683.4	15	394	1146	548	168	2271

Tpe, white-lipped peccary (*Tayassu pecari*); Tba, Baird's tapir (*Tapirus bairdii*); Mam, red brocket deer (*Mazama americana*); Pta, collared peccary (*Pecari tajacu*); Ovi, white-tailed deer (*Odocoileus virginianus*).

Table 3 Analyses of habitat use by five ungulate species in two sites of the Lacandon Forest, Mexico, according to the analysis of track counts by two different methods.

Species	Habitat type	Rio Azul				Ixcan			
		n	n	B's	J's	n	n	B's	J's
		obs.	exp.	test ^a	test ^b	obs.	exp.	test ^a	test ^b
<i>Tayassu pecari</i>	TEF	8	4.6	+	-	7	3.7	+	-
	DTEF	0	2.1	-	-	0	1.6	-	-
	SV	0	0.9	-	-	0	0.7	-	-
	FL	0	0.3	-	-	0	0.8	-	-
<i>Tapirus bairdii</i>	TEF	201	123.7	+	0	180	97.2	+	-
	DTEF	11	56	-	0	0	41	-	-
	SV	2	25.2	-	0	0	19.2	-	-
	FL	0	9	-	Nt	0	22.5	-	-
<i>Mazama americana</i>	TEF	595	535.6	+	0	168	118.8	+	0
	DTEF	192	242.4	-	0.2	38	50	=	0
	SV	132	109	=	-0.16	11	23.5	-	-0.33
	FL	7	38.8	-	0	3	27.5	-	0
<i>Odocoileus virginianus</i>	TEF	18	75.7	-	1	10	20	-	Na
	DTEF	69	34.3	+	0	21	8.4	+	0
	SV	42	15.4	+	-1	5	4	=	0.33
<i>Pecari tajacu</i>	FL	2	5.5	=	0	1	4.6	-	Dh
	TEF	212	195	=	0.2	108	114	=	Na
	DTEF	79	88.2	=	0.2	69	48	=	1
	SV	46	39.7	=	-0.4	31	22.5	=	-1
	FL	0	14	-	Nt	3	26.4	-	0

TEF, tall evergreen forest; DTEF, disturbed tall evergreen forest; SV, secondary vegetation; FL, farmland (annual crops and grasslands); B's test, Byers et al.'s (1984) test; J'test, Johnson's (1980) test.

+, observed frequency higher than expected frequency; =, similar observed and expected frequencies; -, observed frequency lower than expected frequency; -, Johnson's test was not run due to insufficient data (tracks were observed in only one habitat type). Nt, habitat type omitted in Johnson's test because no tracks were observed.

Dh, doubtful habitat type omitted in Johnson's test because it is relatively common but rarely used (Alldredge and Ratti, 1986).

Na, habitat type omitted in Johnson's test because the tracks of collared peccary and white-tailed deer were found exclusively in a single habitat type (tropical evergreen forest) in some transects of Ixcan.

^aAll analyses but one (*Tayassu pecari*) was significant at $p<0.001$.

^bLower values (negative numbers included) indicate higher habitat use frequency.

deer used TEF more frequently than expected in both sites, used SV and DTEF according to their availability in Rio Azul and Ixcan, respectively, and used less than expected the remaining habitat types (Rio Azul: $\chi^2=47.9$, $df=3$, $p<0.001$; Ixcan: $\chi^2=51.8$, $df=3$, $p<0.001$). Johnson's method (1980) showed that SV was the most frequently used habitat type by red brocket deer in both study sites.

White-tailed deer A total of 168 tracks (131 in Rio Azul and 37 in Ixcan) were observed. In Rio Azul, Byers et al.'s (1984) method indicated that DTEF and SV were more frequently used than expected, whereas FLs were used according to their availability, and TEF was used less than expected ($\chi^2=127$, $df=3$, $p<0.001$). In Ixcan, only DTEF was used more than expected, SV was used according to its availability, and both TEF and FL were used less than expected ($\chi^2=26.8$, $df=3$, $p<0.001$). According to Johnson's (1980) method, the most frequently used habitat was SV in Rio Azul, while in Ixcan this method did not show any difference between the frequency of observed tracks and the habitat availability ranks.

Collared peccary In total, 548 were encountered, of which 337 were in Rio Azul and 211 in Ixcan. This species used TEF, DTEF, and SV according to their availability in both sites, whereas this species used FLs less than expected (Rio Azul: $\chi^2=17.5$, $df=3$, $p<0.001$; Ixcan: $\chi^2=33.2$, $df=3$, $p<0.001$). Johnson's method (1980) showed a more frequent use of SV in both sites.

Discussion

Habitat use

Byers et al.'s (1984) method was appropriate for data analyses in this study. According to Alldredge and Ratti (1986), Roscoe and Byars (1971), and Koehler and Larntz (1980), our datasets were adequate for applying χ^2 -tests to all but one (white-lipped peccary) ungulate species. We recognize that absolute independence between subsequent observations of animal signs is difficult to achieve. However, we consider that the experience of observers as well as the minimum distance criteria among consecutive track groups taken during the 12 months of fieldwork helped to mitigate this problem. This situation has been addressed by Alldredge and Ratti (1986), who suggested that the violation of the independence assumption constrains conclusions drawn from field observations, but it does not invalidate such observations.

The application of Johnson's (1980) method allowed detecting geographically restricted habitat types frequently used by ungulate species, such as brocket deer, white-tailed deer, and collared peccary, in our study area. However, we were unable to analyze observations occurring within a single habitat type, as was the case of collared peccary in both sites and Baird's tapir in Ixcan. Moreover, given that the signs of collared peccary and

white-tailed deer were found exclusively in a single habitat type (TEF) in some transects of Ixcan, these observations were omitted from the analyses run with Johnson's method. This method was also insensitive to differences in proportions of observed track groups and habitat availability when the rank order was the same for both variables (i.e., Baird's tapir in Rio Azul and white-tailed deer in Ixcan, Alldredge and Ratti 1992, Alldredge and Griswold 2006).

We consider that Byers et al.'s (1984) and Johnson's (1980) methods to assess ungulate habitat use were complementary in this study in the case of red brocket deer, white-tailed deer, and collared peccary. The first method helped to identify habitat use with precision and allowed to test the hypotheses proposed, while the second allowed to detect under-represented habitat types frequently used by these ungulates, such as SV, which covered 11.8% and 10.7% of transects sampled in Rio Azul and Ixcan, respectively. In general, habitat use of ungulate species was similar to that reported in the literature, which implied rejection of our null hypothesis (use of habitat types according to their availability). However, a complex landscape configuration (a mosaic of forest fragments with interconnecting corridors and a matrix of SV, FLs, and grasslands) seems to favor the presence of both deer species and the collared peccary.

In the case of white-lipped peccary, the number of tracks found in the study area was too small to apply statistical analyses. However, all of the observations of this species were done in mature rainforest close to permanent water bodies and in areas connected to the Montes Azules core area. This is in agreement with previous observations of white-lipped peccaries by several authors in extensive and undisturbed areas. Nevertheless, studies conducted in Amazonia have documented the preference of this ungulate for flood forest in alluvial plains (Bodmer 1990), palm swamps, and flooding savannas (Fragoso 1999), while it uses TEF on steep slopes less frequently than the collared peccary. In this regard, Naranjo (2002) found that the white-lipped peccary was one of the dominant species within the medium- and large-sized mammal community in the alluvial plains of the Lacandon Forest, not far from our study area (approximately 20 km). This supports our assumption that white-lipped peccaries are not abundant in our study sites partly due to their rugged topography.

Baird's tapir tracks were more frequently observed in well-preserved habitat types with presence of permanent water bodies, such as rivers, streams, and lagoons. Our results from analyses performed using Byers et al.'s (1984) method are in agreement with previous data from both the Lacandon Forest and other study sites, indicating frequent use of pristine habitat types by tapirs (Leopold 1959, Naranjo and Cruz 1998, Naranjo and Bodmer 2002, Lira et al. 2004, 2005, March and Naranjo 2005, Reyna-Hurtado and Tanner 2005, Tobler et al. 2006). It is interesting to note that there was no evidence of tapir presence in disturbed tropical evergreen forest or SV at Ixcan. This may be attributed to different landscape configurations between sites: a mosaic of forest patches, SV, and FLs in Rio Azul, and a matrix of extensive grasslands in Ixcan, constituting a more hostile environment

for tapir movement. Tapirs showed a less-than-expected use of the three disturbed habitats in both sites. Although tapir use of secondary forests within protected areas has been previously reported (Naranjo 1995, Muench 2001, Foerster and Vaughan 2002, Lira et al. 2004), human presence and activity was slight or absent on these forests when those surveys were conducted.

Red brocket deer used tropical evergreen forest habitat higher than expected in both sites according to Byers et al.'s method. However, the use of another habitat type according to their availability in Rio Azul (SV) and Ixcán (disturbed tropical evergreen forest) suggests that this species is using the habitat mosaic derived from fragmentation processes occurring in these sites. In addition, Johnson's method showed that the most used habitat in both sites was SV. Several authors (Leopold 1959, Álvarez del Toro 1991, Naranjo 2002, Gallina 2005) have previously reported the use of small openings and SV by this deer as feeding sites when mature forest is nearby. This is in agreement with our observations suggesting that habitat configuration favors the use of transformed areas by this ungulate either as refuges (mature forest fragments) or feeding sites (successional vegetation). An additional element supporting this supposition is current connectivity between rainforest fragments and the core area of Montes Azules, which *sensu* Naranjo and Bodmer (2007) may be functioning as the source of migrant deer towards surrounding transformed areas (sinks).

Confirming previous observations by Leopold (1959) and Naranjo et al. (2004), the white-tailed deer avoided mature rainforests in the Lacandon area. As we expected, Byer's method indicated that this deer used more frequently than expected disturbed rainforest and SV. The trend of this species to avoid using dense rainforest suggests that our study area is a frontier in its distribution range, where the species has benefited after human transformation of pristine forest.

Assuming that the collared peccary is a habitat generalist, a proportional use of each available habitat type was expected in the study area. In both sites, this peccary used FLs less than expected and used the other habitat types according to their availability, thus we rejected our null hypothesis. In addition, Johnson's method showed that the most frequently used habitat type was SV. Previous studies suggest that collared peccaries are tolerant to moderate habitat disturbance (Álvarez del Toro 1991, Sowls 1997, Naranjo 2002, March and Mandujano 2005), which is supported by our results. In fact, this species seems to have benefited from transformation of primary rainforest into the current heterogeneous landscape of the study area.

The following are among the most important findings in this work: (a) Baird's tapir appears in both study sites as a tropical evergreen forest specialist avoiding all the disturbed habitats; (b) the red brocket deer, usually considered a rainforest specialist, is present in moderately disturbed habitats, such as SV and logged forest in the study area; (c) the white-tailed deer avoids pristine rainforest, but is favored by human disturbance resulting in disturbed forest and SV; and (d) the collared peccary, frequently reported as a habitat generalist, avoided FLs and frequently used SV. These findings suggest that

fragmentation patterns have an effect on habitat use of ungulate species in the Lacandon Forest. Consequently, a better knowledge of landscape and habitat configuration effects on ungulate distribution and abundance is needed in the study area. Future research on these topics should take variables, such as forest fragment size, shape, and connectivity, edge effects, corridor traits, and matrix quality, into consideration (Forman 1995, Cuarón 2000, Turner et al. 2001). We also emphasize that hunting pressure is often synergic with habitat fragmentation in shaping habitat use of many wildlife species (Peres 2001, Reyna-Hurtado and Tanner 2005). Therefore, we recommend including hunting as an important variable in future surveys aiming at ungulate habitat use in the Lacandon Forest. Additionally, landscape fragmentation seems to allow coexistence of both deer species in the study area. Thus, niche partitioning between these species should be analyzed to verify competitive interactions among them (Desbiez et al. 2009). The results obtained through those studies will be helpful to improve our understanding of habitat selection, distribution and abundance of wildlife populations in an increasing scenario of forest frontier, fragmentation, and coexistence with human settlements.

Finally, at least four recommendations are made for habitat management of ungulates around Montes Azules Biosphere Reserve: (1) protection of mature rainforest should be enforced in Montes Azules core zone as the main habitat of Baird's tapir and white-lipped peccary in the study area; (2) agreements between managers of the protected area and residents are needed to conserve critical habitat elements, such as remaining rainforest patches within communities and functional natural corridors with connection to Montes Azules core zone; (3) collared peccaries, red brocket deer, and white-tailed deer can benefit by maintaining heterogeneous landscapes through traditional agricultural practices involving short periods of land use and long periods (>10 years) without it; and (4) extensive cattle ranching may shift to more diversified and sustainable systems combining livestock, agroforestry, and intensive pastureland management, in order to avoid further loss of forested areas and expansion of pasturelands.

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References

- Aebischer, N.J., P.A. Robertson and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74: 1313–1325.
- Allredge, J.R. and J.T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. *J. Wildl. Manage.* 50: 157–165.
- Allredge, J.R. and J.T. Ratti. 1992. Further comparison of some statistical techniques for analysis of resource selection. *J. Wildl. Manage.* 56: 1–9.
- Allredge, J.R. and J. Griswold. 2006. Design and analysis of resource selection studies for categorical resource variables. *J. Wildl. Manage.* 70: 337–346.
- Álvarez del Toro, M. 1991. Los mamíferos de Chiapas. Consejo Estatal de Fomento a la Investigación y Difusión de la Cultura, DIF Chiapas, Instituto Chiapaneco de Cultura, Tuxtla Gutiérrez, Chiapas, México. pp. 133.
- Aranda, M. 2000. Huellas y otros rastros de los mamíferos grandes y medianos de México. CONABIO, Instituto de Ecología, A.C., Xalapa, Veracruz, México. pp. 212.
- Arthur, S.M., B.F.J. Manly, L.L. MacDonald and G.W. Garner. 1996. Assessing habitat selection when availability changes. *Ecology* 77: 215–227.
- Bolaños, C.J.E. and E.J. Naranjo. 2001. Abundancia, densidad y distribución de las poblaciones de ungulados en la cuenca del río Lacantún, Chiapas, México. *Rev. Mexicana Mastozool.* 5: 45–57.
- Bodmer, R.E. 1990. Responses of ungulates to seasonal inundations in the Amazon floodplain. *J. Trop. Ecol.* 6: 191–201.
- Byers, C.R., R.K. Steinhorst and P.R. Krausman. 1984. Clarification of a technique for analysis of utilization-availability data. *J. Wildl. Manage.* 48: 1050–1053.
- Carmiña-Cardenal, A. 2003. Preferencias de hábitat en una comunidad de grandes mamíferos en la Rioja durante el otoño e invierno. *Zubía* 21: 51–62.
- Cascelli de Azevedo, F.C. and V. Amorim-Conforti. 2008. Declines of peccaries in a protected subtropical forest of Brazil: toward conservation issues. *Mammalia* 72: 82–88.
- CI, 2000. Mapa de Vegetación de la Selva Maya. Conservación Internacional, México.
- Cuarón, A.D. 2000. Effects of land-cover changes on mammals in a Neotropical region: a modeling approach. *Conserv. Biol.* 14: 1676–1692.
- Desbiez, A.L.J., S.A. Santos, A. Keuroghlian and R.E. Bodmer. 2009. Niche partitioning among white-lipped peccaries (*Tayassu pecari*), collared peccaries (*Pecari tajacu*), and feral pigs (*Sus scrofa*). *J. Mammal.* 90: 119–128.
- Escamilla, A., M. Sanvicente, M. Sosa and C. Galindo-Leal. 2000. Habitat mosaic, wildlife availability, and hunting in the tropical forest of Calakmul, México. *Conserv. Biol.* 14: 1592–1601.
- Foerster, C.R. and C. Vaughan. 2002. Home range, habitat use, and activity of Baird's tapir in Costa Rica. *Biotropica* 34: 423–437.
- Forman, R.T.T. 1995. Land mosaics. The ecology of landscapes and regions. Cambridge University Press, Cambridge, UK. pp. 632.
- Fragoso, J.M.V. 1998. Home range and movements patterns of white-lipped peccary (*Tayassu pecari*) herds in the northern Amazon. *Biotropica* 30: 458–469.
- Fragoso, J.M.V. 1999. Perception of scale and resource partitioning by peccaries: behavioral causes and ecological implications. *J. Mammal.* 80: 993–1003.
- Galindo-Leal, C. and M. Weber. 2005. Venado cola blanca. In: (G. Ceballos and G. Oliva, eds) Los mamíferos silvestres de México. CONABIO, Fondo de Cultura Económica, México. pp. 517–521.
- Gallina, S. 2005. Temazate. In: (G. Ceballos and G. Oliva, eds) Los mamíferos silvestres de México. CONABIO, Fondo de Cultura Económica, México. pp. 512–513.
- Grubb, P. 2005a. Order Perissodactyla. In: (D.E. Wilson and D.M. Reeder, eds) Mammal species of the World. A taxonomic and geographic reference. Vol. 1. Johns Hopkins University Press, Baltimore, MD, USA. pp. 629–636.
- Grubb, P. 2005b. Order Artiodactyla. In: (D.E. Wilson and D.M. Reeder, eds) Mammal species of the World. A taxonomic and geographic reference. Vol. 1. Johns Hopkins University Press, Baltimore, MD, USA. pp. 637–722.
- Guzmán-Lenis, A. and A. Camargo-Sanabria. 2004. Importancia de los rastros para la caracterización del uso del hábitat de mamíferos medianos y grandes en el Bosque Los Mangos (Puerto López, Meta, Colombia). *Acta Biol. Colomb.* 9: 11–22.
- Inda, E.A. 2005. Pesca de subsistencia en la Selva Lacandona, Chiapas, México. MSc thesis, El Colegio de la Frontera Sur, Chiapas, México. pp. 24.
- INE, 2000. Programa de Manejo de la Reserva de la Biosfera Montes Azules, México. Instituto Nacional de Ecología, SEMARNAP, México. pp. 255.
- INEGI, 2006. Principales resultados por localidad, 2005. II Conteo de Población y Vivienda 2005 (CD). Instituto Nacional de Estadística, Geografía e Informática, Aguas Calientes, México.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preferences. *Ecology* 61: 65–71.
- Koehler, K.J. and Larntz, K. 1980. An empirical investigation of goodness-of-fit statistics for sparse multinomials. *J. Am. Stat. Assoc.* 75: 336–344.
- Leopold, A.S. 1959. Wildlife of Mexico. The game birds and mammals. University of California Press, Berkeley, CA, USA. pp. 568.
- Lira, T.I., E.J. Naranjo, D.M. Güiris and E. Cruz. 2004. Ecología de *Tapirus bairdii* (Perissodactyla: Tapiridae) en la Reserva de la Biosfera El Triunfo (polígono I), Chiapas, México. *Acta Zool. Mex.* 20: 1–21.
- Lira, T.I., E.J. Naranjo and M.A. Reyes-Chargoy. 2005. Ampliación del área de distribución de *Tapirus bairdii*, Gill 1865 (Perissodactyla: Tapiridae) en Oaxaca, México. *Acta Zool. Mex.* 21: 107–110.
- March, I. 1993. The white-lipped peccary (*Tayassu pecari*). In: (W.L.R. Oliver, ed) Pigs, peccaries and hippos: status survey and conservation action plan. IUCN, SSC Pigs and peccaries Specialists Group, Gland, Switzerland. pp. 13–22.
- March, I. 2005. Pecarí de labios blancos. In: (G. Ceballos and G. Oliva, eds) Los mamíferos silvestres de México. CONABIO, Fondo de Cultura Económica, México. pp. 522–524.
- March, I. and S. Mandujano. 2005. Pecarí de collar. In: (G. Ceballos and G. Oliva, eds) Los mamíferos silvestres de México. CONABIO, Fondo de Cultura Económica, México. pp. 524–527.
- March, I. and E.J. Naranjo. 2005. Tapir. In: (G. Ceballos and G. Oliva, eds) Los mamíferos silvestres de México. CONABIO, Fondo de Cultura Económica, México. pp. 496–497.
- Mariaca, R. 2002. Marqués de Comillas, Chiapas: procesos de inmigración y adaptabilidad en el trópico cálido húmedo de México. PhD thesis, Universidad Iberoamericana, México. pp. 382.
- Matola, S., A.D. Cuarón and H. Rubio-Togler. 1997. Status and action plan of Baird's tapir (*Tapirus bairdii*). In: (D.M. Brooks, R.E. Bodmer and S. Matola, eds) Tapirs. IUCN, SSC Tapir Specialist Group, Gland, Switzerland. pp. 29–45.
- Mayer, J.J. and R.M. Wetzel. 1987. *Tayassu pecari*. *Mammal. Spec.* 293: 1–7.

- Morrison, M.L., B.G. Marcot and R.W. Mannan. 2006. Wildlife-habitat relationships, concepts and applications. Island Press, Washington, DC, USA. pp. 493.
- Muench, P. 1998. Conservación y Desarrollo en la Selva Lacandona, Chiapas. evaluación de un programa regional. Unpublished document, Universidad Autónoma Chapingo. Chiapas, México. pp. 124.
- Muench, C.E. 2001. Patrones de uso del hábitat del tapir (*Tapirus bairdii*) en dos localidades de la selva lacandona, Chiapas. B.S. thesis, Universidad Nacional Autónoma de México, México. pp. 67.
- Naranjo, E.J. 1995. Abundancia y uso de hábitat del tapir (*Tapirus bairdii*) en un bosque tropical húmedo de Costa Rica. *Vida Silv. Neotrop.* 4: 20–31.
- Naranjo, E.J. 2002. Population ecology and conservation of ungulates in the Lacandon Forest, México. PhD thesis, University of Florida, Gainesville, FL, USA. pp. 160.
- Naranjo, E.J. and E. Cruz. 1998. Ecología del tapir (*Tapirus bairdii*) en la Reserva de la Biosfera La Sepultura, Chiapas, México. *Acta Zool. Mex.* 73: 111–125.
- Naranjo, E.J. and R.E. Bodmer. 2002. Population ecology and conservation of Baird's tapir (*Tapirus bairdii*) in the Lacandon Forest, Mexico. *Tapir Conserv.* 11: 25–33.
- Naranjo, E.J. and J.E. Bolaños. 2003. Correlación entre índices de abundancia y densidades poblacionales de mamíferos en la Selva Lacandona, México. In: (R. Polanco-Ochoa, ed) *Manejo de fauna silvestre en Amazonía y Latinoamérica*. CITES, MacArthur Foundation, Fundación Natura, Colombia. pp. 181–184.
- Naranjo, E.J. and R.E. Bodmer. 2007. Source-sink systems and conservation of hunted ungulates in the Lacandon Forest, México. *Biol. Conserv.* 138: 412–420.
- Naranjo, E.J., M.M. Guerra, R.E. Bodmer and J.E. Bolaños. 2004. Subsistence hunting by three ethnic groups of the Lacandon Forest, Mexico. *J. Ethnobiol.* 24: 233–253.
- Neu, C.W., C.R. Byers and J.M. Peek. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* 38: 541–545.
- Norris, D., C.A. Peres, F. Michalski and K. Hinchcliffe. 2008. Terrestrial mammal responses to edges in Amazonian forest patches: a study based on track stations. *Mammalia* 72: 15–23.
- Ojasti, J. 2000. Manejo de fauna silvestre neotropical. In: (F. Dallmeier, ed) *SIMAB Series No. 5*. Smithsonian Institution/MAB Program, Washington, DC, USA. pp. 290.
- Pennington, T.D. and J. Sarukhán. 1998. Árboles tropicales de México. Universidad Nacional Autónoma de México, Fondo de Cultura Económica, México. pp. 523.
- Peres, C.A. 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conserv. Biol.* 15: 1490–1505.
- Reid, F.A. 1997. A field guide to the mammals of Central America and Southeast México. Oxford University Press, New York, USA. pp. 334.
- Reyna-Hurtado, R. and G.W. Tanner. 2005. Habitat preferences of ungulates in hunted and non-hunted areas in the Calakmul Forest, Campeche, México. *Biotropica* 37: 676–685.
- Reyna-Hurtado, R. and G.W. Tanner. 2007. Ungulate relative abundance in hunted and non-hunted sites in Calakmul Forest (Southern Mexico). *Biodiversity Conserv.* 16: 743–756.
- Ríos-Uzeda, B., H. Gómez and R.B. Wallace. 2006. Habitat preferences of the Andean Bear (*Tremarctus ornatus*) in the Bolivian Andes. *J. Zool.* 268: 271–278.
- Robinson, J.G. and E.L. Bennett (eds). 2000. Hunting for sustainability in tropical forests. Columbia University Press, New York, USA. pp. 582.
- Rodstrom, C., S. Olivieri and L. Tanglely. 1999. Un enfoque regional de la conservación en la Selva Maya. In: (R.B. Primack, D. Bray, H.A. Galleti and I. Ponciano, eds) *La Selva Maya, conservación y desarrollo. Siglo XXI*, México. pp. 23–42.
- Roscoe, J.T. and J.A. Byars. 1971. Sample size restraints commonly imposed on the use of the chi-square statistic. *J. Am. Stat. Assoc.* 66: 755–759.
- SEDUE. 1992. Diagnóstico socioeconómico de la Selva Lacandona (bases para la planeación regional). Secretaría de Desarrollo Urbano y Ecología, México. pp. 154.
- Sowls, L.K. 1997. Javelinas and other peccaries. Their biology, management and use. Texas A&M University Press, TX, USA. pp. 325.
- Teer, J. 1994. El venado cola blanca: historia natural y principios de manejo. In: (C. Vaughan and M.A. Rodríguez, eds) *Ecología y manejo del venado cola blanca en México y Costa Rica. Serie Conservación Biológica y Desarrollo Sostenible No. 2*. Universidad Nacional de Costa Rica, Heredia, Costa Rica. pp. 33–47.
- Tejeda-Cruz, C. and C. Márquez-Rosano. 2006. Apropiación territorial y aprovechamiento de recursos forestales en Frontera Corozal, Selva Lacandona, Chiapas, México. *Rev. Geog. Agr.* 37: 79–96.
- Tobler, M.W. 2002. Habitat use and diet of Baird's tapir (*Tapirus bairdii*) in a montane cloud forest of the Cordillera de Talamanca, Costa Rica. *Biotropica* 34: 468–474.
- Tobler, M.W., E.J. Naranjo and I. Lira-Torres. 2006. Habitat preference, feeding habits and conservation of Baird's tapir in Neotropical montane oak forests. In: (M. Kappelle, ed) *Ecology and conservation of Neotropical montane oak forests*. Springer-Verlag, Germany. pp. 347–361.
- Turner, M.G., R.H. Gardner and R.V. O'Neil. 2001. Landscape ecology in theory and practice. Pattern and process. Springer, New York, USA. pp. 401.
- Vasquez, M.A. and M.A. Ramos (eds). 1992. Reserva de la Biosfera Montes Azules, Selva Lacandona: investigación para su conservación. *Publ. Esp. Ecosfera*, Chiapas, México. pp. 436.
- Zar, J.H. 1999. Biostatistical analysis. Prentice Hall, New Jersey, USA. pp. 663.