

Research Article

Habitat and human factors associated with white-tailed deer density in the tropical dry forest of Tehuacán-Cuicatlán Biosphere Reserve, Mexico

Michelle Ramos-Robles¹, Sonia Gallina² and Salvador Mandujano^{2*}

¹ División de Posgrado, Instituto de Ecología A. C., Carretera Antigua a Coatepec No. 351, El Haya, Xalapa 91070, Ver., México.

² Red de Biología y Conservación de Vertebrados, Instituto de Ecología A. C., Carretera Antigua a Coatepec No. 351, El Haya, Xalapa 91070, Ver., México.

*Corresponding author: salvador.mandujano@inecol.edu.mx

Abstract

The main objective of this study was to analyze the relationship between population densities of the white-tailed deer *Odocoileus virginianus* and certain habitat and human characteristics in the tropical dry forest of the Tehuacan-Cuicatlan Biosphere Reserve (TCBR), Mexico. To estimate population density and characterize the habitat, we established 32 strip transects (500 x 2 m) at four different locations in the TCBR from May to June during the dry season of 2010. Principal component analyses were used to order the 32 transects using habitat/human impact variables and tree species composition. Estimated average density was 1.7 deer/km², ranging from 0.1 to 2.9 deer/km². The variables associated with white-tailed deer density were: basal area, distance to roads, distance to the area with largest human population, slope, aspect and presence of cattle; the principal plant species were Zapotillo (*Lantana camara*), Chintoborrego (*Vallesia glabra*), Nanche (*Bunchosia biocellata*), Cuachalalate (*Amphipterigyum adstringens*) and Cuajote Amarillo (*Bursera aptera*). Compared to other tropical dry forests, estimated white-tailed deer densities in the TCBR were lower. We discuss the possible effect of these variables on deer density and suggest management actions.

Key Word: *Odocoileus virginianus*, pellet-groups count, human influence, management.

Resumen

El objetivo principal de este estudio fue analizar la relación entre la densidad poblacional del venado cola blanca *Odocoileus virginianus* con algunas características del hábitat en el bosque tropical seco de la Reserva de la Biosfera de Tehuacán-Cuicatlán (TCBR), México. Para estimar la densidad y caracterizar el hábitat, se colocaron 32 transectos de franja (500 x 2 m) en cuatro diferentes localidades de la TCBR de mayo a junio de 2010. Se llevaron a cabo análisis de componentes principales para ordenar los 32 transectos conforme a las variables del hábitat, impacto humano y su composición vegetal. La densidad promedio fue de 1.7 venados/km², con una variación entre de 0.1 a 2.9 venados/km². Las variables relacionadas con la densidad del venado fueron el área basal, la distancia a caminos, la distancia a la localidad con mayor número de habitantes, la orientación y la presencia de ganado. En las localidades con mayor densidad de venados las plantas dominantes fueron Zapotillo (*Lantana camara*) Chintoborrego (*Vallesia glabra*), Nanche (*Bunchosia biocellata*), Cuachalalate (*Amphipterigyum adstringens*) y Cuajote Amarillo (*Bursera aptera*). Comparado con otros bosques tropicales, las densidades estimadas en la TCBR fueron menores. Se discute el posible efecto de estas variables sobre la densidad del venado y se sugieren algunas acciones de manejo.

Palabras clave: *Odocoileus virginianus*, conteo de grupos fecales, influencia humana, manejo.

Received: 15 August 2012; Accepted: 19 December 2012; Published: 18 March 2013.

Copyright: © Michelle Ramos-Robles, Sonia Gallina and Salvador Mandujano. This is an open access paper. We use the Creative Commons Attribution 3.0 license <http://creativecommons.org/licenses/by/3.0/> - 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 the 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 Ramos-Robles, M., Gallina, S. and Mandujano, S., C. 2013 Habitat and human factors associated with white-tailed deer density in the tropical dry forest of Tehuacan-Cuicatlan Biosphere Reserve, Mexico. *Tropical Conservation Science* Vol. 6(1):70-86. Available online: www.tropicalconservationscience.org

Introduction

The wide geographic distribution of the white-tailed deer *Odocoileus virginianus* is largely due to its ability to adapt to different environmental conditions [1]. This species is one of the most studied in Mexico [2-4]; it has the ability to modify vegetation structure [5, 6], is a main prey for larger carnivores [7] and is one of the most utilized animals for subsistence and game hunting [8, 9]. In the Neotropical region, white-tailed deer inhabit various ecosystem types, including tropical dry forest [3, 4]. The marked seasonality of this forest affects the availability of food, water and cover [10, 11]. Because cover and tree density provide protection against extreme temperatures and potential predators, transformation of these factors can have an effect on deer population density [12, 13]. In addition, anthropic pressure factors such as settlements, roads, agricultural activity and hunting, among others, are likely to have a negative effect on deer populations [14].

Studies that have evaluated the effect of environmental variables on deer densities in tropical ecosystems have focused on the structural attributes of vegetation and landscape [15-17]. In contrast, little information exists regarding the effects of human pressure on deer population densities [18-20]. This pressure occurs mainly in ecosystems that are undergoing serious fragmentation, such as the tropical dry forest [21]. The role played by protected areas, including the large Biosphere Reserves, in the generation of biological knowledge and conservation of white-tailed deer is of great importance [22-24]. The Tehuacan-Cuicatlan Biosphere Reserve (TCBR) is an area of high biodiversity and endemism of species in central Mexico [25]. Three species of native ungulates inhabit this site, all of which are important in subsistence hunting: white-tailed deer, red brocket deer (*Mazama temama*) and the collared peccary (*Pecari tajacu*). In the TCBR at present, there is great interest in the sustainable use of white-tailed deer in Management Units for the Conservation of Wildlife (UMAs by their Spanish acronym). The objective of this study was therefore to characterize habitat and human attributes in order to identify the most important variables associated with white-tailed population density, and to use these findings to suggest possible management actions.

Methods

Study area

The Tehuacan-Cuicatlan Biosphere Reserve, comprising an area of almost 5,000 km² (Fig.1), is located in the southern part of Puebla state and the northern part of Oaxaca state (17° 39' - 18° 53' N and 96° 55' - 97° 44' W) and is considered a biological province of the Mexican xerophytic

region [26]. It contains a complex physiographic mosaic with internal valleys separated by numerous mountains. Altitude ranges from 600 to 2,950 m asl, while annual mean temperature varies from 18 to 22 °C and annual precipitation from 250 to 500 mm [27, 28]. The vegetation types are tropical dry forest (33%), semi-arid shrub land (30%) and temperate pine-oak forest (20%). The most common species in tropical dry forest are: *Bursera* spp., *Acacia cochliacantha*, *Mimosa* spp., *Prosopis laevigata*, *Parkinsonia praecox*, *Marginatocereus marginatus*, *Opuntia pubescens* and *O. decumbens* which are associated with the columnar cacti *Pachycereus weberi*, *Neobuxbaumia tetezo* and *Cephalocereus columna-trajani* [29]. The incidence of deforestation and fragmentation in the TCBR is considerably lower than in other tropical dry forests in Mexico [21].

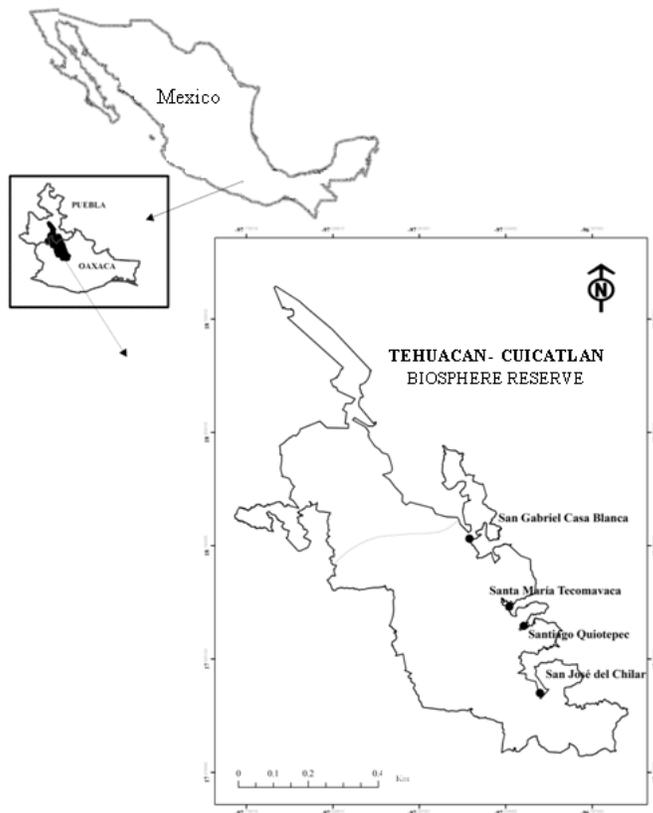


Fig. 1. Location of the four studied communities in the Tehuacan-Cuicatlan Biosphere Reserve, Mexico.

Density estimation

To estimate white-tailed deer density, four locations were chosen (San Gabriel Casa Blanca, San Juan Quiotepec, Santa Maria Tecomavaca and San Jose del Chilar) within the region known as La Cañada, which is dominated by tropical dry forest (Fig. 1). These locations were chosen because of the interest among the inhabitants in establishment of an UMA for developing the sustainable use of white-tailed deer [30]. To estimate population density, we used the indirect method of counting pellet-groups [31]. We established 32 transects (eight per location), which were surveyed from May to June 2010 during the dry season. Transects were 500 x 2 m wide, a width that was considered adequate to census complete pellet-groups in dense vegetation understory [32]. Fecal groups were collected following the Fecal Standing Crop (FSC) method [33, 34], which consists of visiting each sampling plot once and counting the total standing crop of feces accumulated during the dry season. According to a previous study in other tropical dry forests [17, 32, 35], fecal loss is

minimal during the dry season, while in the rainy season the fecal decay rate is almost 100% from June to December because of the action of rain and insects. Additionally, visibility is low in the rainy season because of dense understory plants and therefore the detection probability of feces is lower. Due to the fact that we sampled each location only once, our analysis does not take possible seasonal changes in habitat use into account.

To estimate population density (D , individuals/km²), we applied the equation proposed by Eberhardt and Van Etten [36] as: $D = (NP \times D_{pg}) / (T \times dR)$, where NP = number of strip transects per square kilometer, D_{pg} = mean pellet groups per transect; T = mean decay time; and dR = defecation rate. To estimate mean pellet-groups, we used the equation: $D_{pg} = n / 2Lw$, where n = number of fecal groups, w = transect width (1 m) and L = total transect length sampled. Variance of density was estimated according to Plumptre [37] as: $Var(D) = [(NP \times D_{pg}) / (T \times dR)]^2 \times [(CV(D_{pg}))^2 + (CV(dR))^2 + (CV(T))^2]$. Estimations of $CV(D_{pg})$ were calculated following a negative binomial distribution to estimate standard error (Se) as: $Se = \sqrt{(x + x^2 / k) / n}$, where k = parameter of the binomial negative and n = number of transects; in particular $k = D_{pg}^2 / (S^2 - D_{pg})$, and S^2 = variance. $CV(dR)$ was calculated according to an estimated defecation rate for tame deer, as a mean of 17 ± 4 (Se) fecal groups/deer/day [38]. Estimation of $CV(T)$ was considering a mean of 123 ± 2.4 days [32].

Habitat description

Habitat characterization was obtained by sampling every 50 m in the same transects used for the pellet-groups count. We chose this distance because of the heterogeneity conferred by the irregular topography in the studied region. We thus obtained data of 352 sampled points (88 per location). Data included vegetation variables (tree diversity, tree density, basal area, protection cover and understory richness), physical variables (altitude, slope, orientation and distance to the nearest permanent water body) and human-impact variables (distance to roads and locations, distance to the area with largest population and livestock presence) (Appendix 1). To obtain vegetation data, we applied the point-centered quarter method [39], which consists of sampling the four nearest trees in each quarter for each point along the transect. Each tree was identified and diameter at breast height (dbh) measured. With this information, we estimated Shannon diversity index using PAST software [40], as well as tree density and basal area. Vertical protection cover was measured using a rule of 200 x 5 cm divided into 10 sections of 20 cm alternately painted in black and white. The rule was placed vertically on a point and the number of sections visible at a distance of 25 m was counted. Difference in the total number of sections was expressed as a percentage of protection cover [41]. Understory plant richness was estimated using circular plots of radius 2 m. Terrain variables such as elevation, slope and aspect were generated from a digital elevation model of 90 m from INEGI [42]. Distance to permanent rivers was obtained from the average of three points away from each transect. The variables of human influence with a negative effect on deer populations (distance to roads, to locations and the area with largest population) were estimated using a Geographical Information System in Arc View 3.2 [43]. Finally, in order to test whether a relationship existed between the presence of deer and cattle, we also counted the cattle dung deposited in the transects. It should be noted that, while hunting is an important variable of anthropic pressure, it was not evaluated in this study, although we assume it to be similar across the whole study area. We recognize, however, the importance of quantifying hunting in future studies.

Statistical analysis

A nonparametric Kruskal-Wallis test was applied, along with a Mann-Whitney contrast, to test if deer density varied significantly between studied sites. To determine differences in habitat factors among locations, we used a one-way ANOVA test and an *a posteriori* multiple comparison Tukey test. Data were normalized using log-transformation [\log and $\log(x + 1)$]. Where variables were not transformed, a non-parametric Kruskal-Wallis test and multiple comparisons Mann-Whitney test were used. For this analysis, we used the statistical software JMP 3.2.1 [44]. To identify the relationships of each variable with deer density, we used simple linear regressions. To determine the relationships between white-tailed deer density and habitat variables, we used principal component analysis (PCA). In the first PCA, the density was ordered considering habitat and human pressure variables using the correlation matrix, while in the second PCA, ordination of density was conducted using tree species composition (presence/absence). The statistical software MVSP 3.2 [45] was used for this analysis.

Results

We counted a total of 174 pellet-groups in 24 out of the 32 transects in the four studied locations. Mean population density was 1.7 ind/km², but this value varied significantly among sites ($P < 0.05$). Highest densities, 2.9 and 2.6 ind/km², were estimated for Chilar and Casa Blanca, respectively; in Tecomavaca, density was 1.1 ind/km², while in Quiotepec it was 0.1 ind/km² (Appendix 1). Habitat structure varied among sites, but Tecomavaca and Casa Blanca were quite similar while Quiotepec showed the most contrasting result.

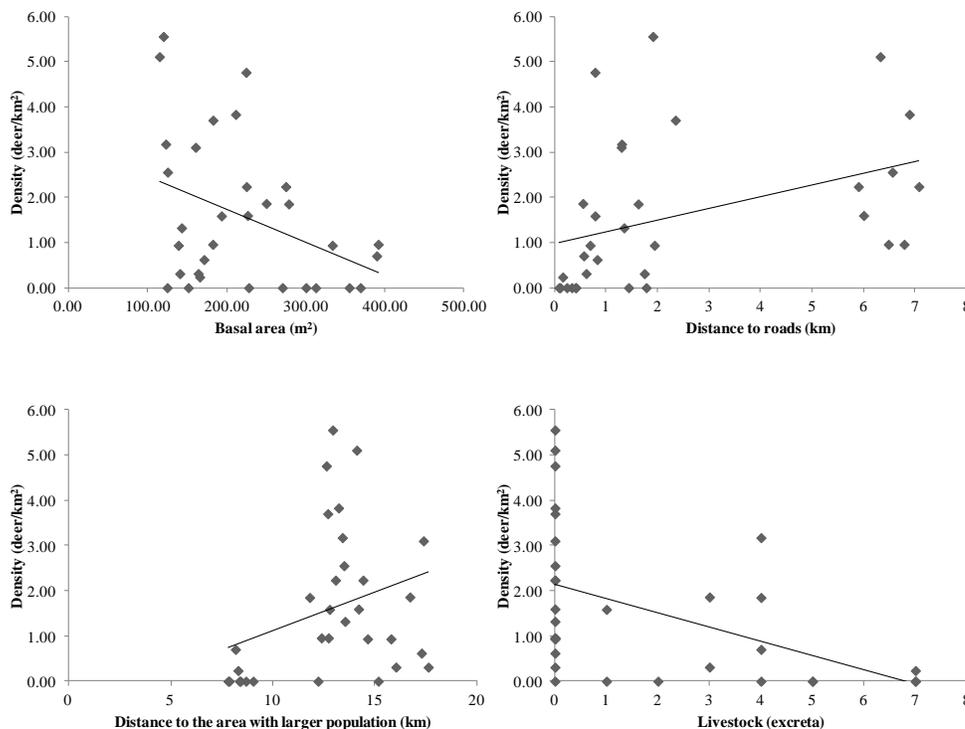


Fig. 2. Correlations of the deer density and habitat variables in different studied sites of the Tehuacan-Cuicatlan Biosphere Reserve, Mexico.

Regression analysis showed that the habitat variables that had a negative relationship with density were basal area ($r = -0.355$, $P = 0.045$) and cattle presence ($r = -0.563$, $P = <0.05$). On the other hand, distance from roads ($r = 0.613$, $P = 0.002$), and from the town with the highest population density ($r = 0.363$, $P = 0.04$), were both positively related to deer density (Fig. 2).

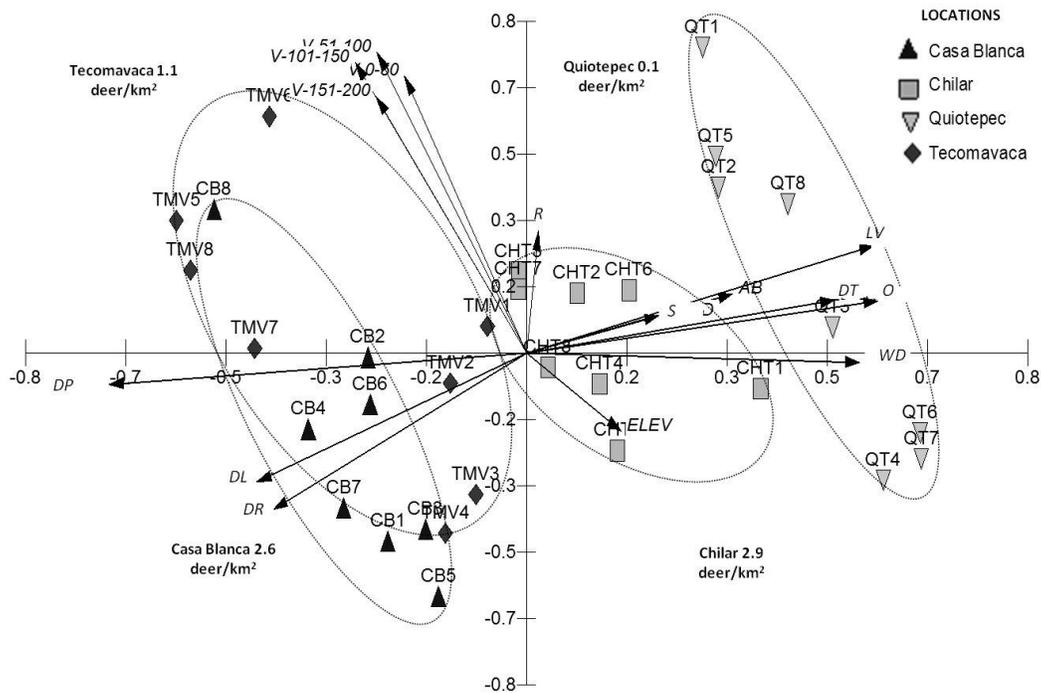


Fig. 3. Principal component analysis ordination of 32 transects based on 15 habitat variables: basal area (AB), tree density (DT), richness (R), protection cover 0-50 cm (V-0-50), protection cover 51-100 cm (V-51-100), protection cover 101-150 (V-101-150), protection cover of 151-200 (V-151-200), distance to roads (DR), distance to locations (DL), distance to water bodies (WD), distance to largest human community (DP), altitude (ELEV), slope (S), orientation (O) and presence of livestock (LV). Locations: CB = Casa Blanca, CH = Chilar, QT = Quiotepec, TCMV = Tecomavaca.

Ordination of transects based on habitat and human attributes defined three distinct groups: Casa Blanca-Tecomavaca, Chilar and Quiotepec (Fig. 3). The first component was positively associated with tree density, aspect, distance to rivers and presence of livestock, and negatively associated with the distance from the largest human community (Appendix 2). Meanwhile, the second component was associated positively with cover variables, and negatively with distance to the nearest road.

In the second ordination of transects according to tree composition, it was found that Quiotepec and Chilar had similar plant composition; in contrast, Tecomavaca and Casa Blanca showed different plant associations (Fig. 4, Appendix 3). In sites with higher white-tailed deer density, the main plant species were *Lantana camara*, *Vallesia glabra*, *Bunchosia biocellata*, *Amphipterygum*

adstringens and *Bursera aptera*, while sites with lower deer density were associated with *Neobuxbaumia* sp., *Bursera schlectendalii* and *Acacia* sp.

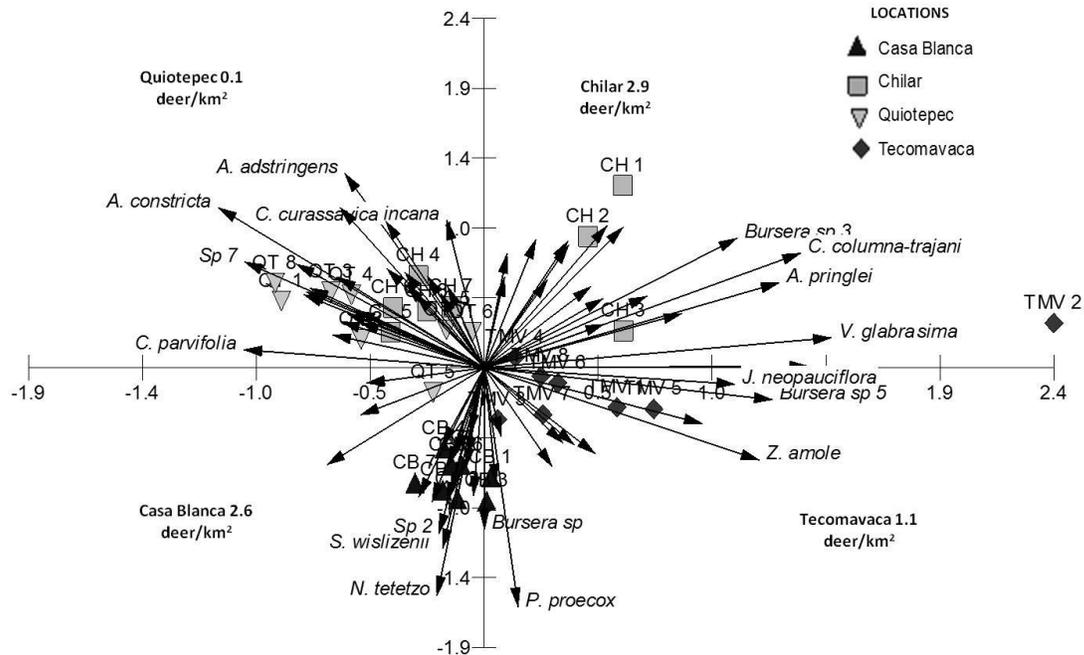


Fig. 4. Principal component analysis ordination of 32 transects based on tree species composition.

Discussion

Our results suggest that white-tailed deer population density was low in the study sites, at 0.1 to 2.9 deer/km². This finding is very similar to densities reported in other tropical dry forests in the Mixteca Poblana using the same indirect method of feces counts [46, 47]. However, higher densities have been reported in some other tropical dry forests (from 6 to 12 deer/km²) [35]. Density estimations were obtained in a systematic way at all four sites using the fecal standing crop method [33, 34], and for the estimation of population density we applied the equation proposed by Eberhardt and Van Etten [36] following the recommendations by Camargo-Sanabria and Mandujano [32]. We used this method because it was considered the most appropriate for the topography and vegetation characteristics of the region with its conditions similar to other sites, including the presence of tropical dry forest [16,17, 20, 48,49]. However, we recognized that pellet-group counts could produce biased estimates, especially where defecation rate is unknown [38]. We tried to diminish this bias using the mean and coefficient of variation of the defecation rate obtained from tame deer near the study site [38]. Previously, Mandujano and Gallina [35] showed that this method produced similar results, with respect to relative density estimated with both direct counts in transect lines and track counts, and it can be used as an index to detect population changes over time. Therefore, even if our population densities estimates are biased,

they were used as a density index with which to compare sites, and therefore we consider that they are valid in terms of their relationships with habitat and human variables.

Specific characteristics of the habitat can explain differences between densities. For example, rainfall season length is shorter and annual average rainfall is lower in our study site (553 mm), which could affect temporal food availability for the deer and the carrying capacity of the site [24, 47, 50]; however we did not evaluate this latter variable in our study. Another possible fact that could explain the relatively low densities in this study is that these wild populations are currently under anthropogenic pressures such as habitat loss, competition with cattle for food and space, and poaching, which is one of the most important causes of wild fauna decline [8, 48]. Despite the fact that hunting was not evaluated within the study area, we suppose that it was constant and uniform among the four sites. In a study by Reyna-Hurtado and Tanner [51] in southeastern Mexico, relative abundance of the white-tailed deer was found to be significantly higher in hunting areas than in those with lower hunting pressure and these authors therefore concluded that deer can tolerate a certain amount of hunting pressure. However, hunting could have a greater effect on the deer in different habitat types, and it is therefore necessary that this variable be quantified in a future study. Within the region, vigilance committees have been established because of the interest of these communities in this resource. The efforts of these committees will surely reduce the incidence of poaching. In addition, the four study sites are relatively close to a principal highway (Tehuacan to Oaxaca city), but recently Yañez-Arenas *et al.* [49] modeling abundance distribution of white-tailed deer with a niche modeling approach, showed that higher deer densities could be expected in sites with irregular topography and lower human activities, which in the TCBR are mainly in the eastern mountainous region. Thus, the distribution of abundance is heterogeneous among locations within the TCBR.

Our results suggest that the studied locations have different habitat conditions for white-tailed deer. In general, Casa Blanca and Tecomavaca were more similar, while Chilar and Quiotepec were the most contrasting locations. However, this ordination of locations was not consistent with deer densities. Significantly higher densities were found in sites with more suitable habitat conditions, while lower densities were found in sites with a higher incidence of human activity. In addition, the multivariate analysis showed that even if some habitat and human variables were associated with deer abundance, the explained variance was low, suggesting that other factors we did not measure could be affecting deer density. Similarly, some of the habitat characteristics, such as vegetation structure and land and human pressure, were significantly different among locations, which could influence the variance in density values among them.

It has been proved that there is a relationship between habitat structure characteristics, such as cover protection, and the presence of this species, owing to the protection offered against high temperatures and predators [52, 53]. Basal area related negatively to density, probably because Quiotepec, the location with the lowest deer density, had trees and columnar cacti with the largest basal area. On the other hand, the northern slopes had more deer presence, as has been reported in other dry forests [54]. This is a very important habitat attribute for the species [55], because northern slopes are less exposed to solar radiation, which reduces the likelihood of dehydration. Although the importance of water access for wild species is well known [13], it did not influence the presence of deer, as the communities where the highest density was found were those located at a longer distance from water sources, and there were no significant differences between this community and another with lower density. Studies of habitat quality for white-tailed deer define distances from water sources of 0.3 km as high quality and 1.4 km as low

quality. In fact, this was the average distance range in the locations we studied. It has also been reported that distances in excess of 1.6 km are considered inadequate for the species [19]. However, it is important to take water availability into account when evaluating whether habitat is appropriate for the species [13,18], particularly in places where the dry season is as marked as it is in the tropical dry forest of the TCBR. During periods of water shortage, it has been found that the white-tailed deer complements its water intake by ingesting certain wild plants and fruits [56,57]. In this regard, other studies [11,58] report that the most important species for the maintenance of deer populations are *Ceiba parvifolia*, *Pachisereus weberi*, *Ficus* spp., *Ficus contifolia*, *Acacia farnesiana* and *Opuntia* spp. In the communities we studied, these species were found to coincide with higher deer density.

Lower densities were related to the presence of livestock; however, with the adaptability of deer, they can also be associated with agricultural areas [3]. Nevertheless, higher deer densities are associated with temperate and tropical deciduous forests, and scrublands. Livestock production affects deer directly in terms of competition for food and space and indirectly by modifying habitat quality, and this is reflected in deer population densities [16, 59-61]. Other human pressure variables, such as proximity of settlements and roads, have an effect on the presence of white-tailed deer. It is known that noise and habitat fragmentation negatively affect populations of wild species, and also the easy access provided by roads increases poaching, which can affect distributions and deplete deer populations [14,18,62]. While poaching was not evaluated in this study, it has been reported as an important factor in the presence of this and other wild species [26,63,64].

Implications for conservation

Our results suggest complex relationships between the habitat and human activities affecting white-tailed deer populations in the studied locations in La Cañada region, where tropical dry forest is the dominant vegetation type. Long-term climatic trends, vegetation changes and human impact determine herbivore population dynamics [14,65]. Current deer population density is the result of these interactions, so that habitat-density relationships analysis, a common approach in studies with this deer species [17,20,48,66,67], does not necessarily explain the causal effects. From a management perspective, however, it was found that these relationships help to define habitat and population actions [68] and this could be useful for the protection and sustainable use of this game hunting species in the TCBR.

Temporal corn-crops, sugarcane production, logging in the mountain region that dominates the landscape, and extensive livestock production are the main economic activities in this region [69, 70]. Subsistence hunting of wildlife, mainly white-tailed deer, for local consumption is a common traditional practice in the Tehuacan-Cuicatlan Valley [71]. In common with other tropical dry forests [46,72,73], we propose that Management Units for the Conservation of Wildlife (UMAs by their Spanish acronym) could be adopted as an alternative management system in the localities of Chilar and Casa Blanca, where the highest densities of deer were found. This system of management will enable the sustainable use of the deer at that site. At Casa Blanca, there have been estimates of deer density carried out for the last three years, and the results are similar to those found in this study (S. Mandujano, pers. comm.). In the particular case of Tecomavaca and Quiotepec, the sites with lowest deer densities, it is necessary to leave the populations to recover so that a system of sustainable use can be put in place at a later date. It should be noted that an UMA already exists at the latter site for the military macaw (*Ara militaris*), and it has served to protect this species. Current management policy of the TCBR includes the sustainable use of

white-tailed deer as a game trophy within the extensive UMA model [74]. Factors such as population density and habitat quality/quantity must be considered in order to estimate carrying capacity and potential production of white-tailed deer for human use [75].

In places where cattle production is practiced, it is recommended to implement appropriate management, so that it has a reduced impact on wild species. For instance, switching from extensive to semi-extensive cattle production could reduce the impact of livestock on a particular site, and the negative impact on the white-tailed deer population. It is necessary to generate information regarding poaching, so that future studies can accurately evaluate the impact it has on this deer population. It is strongly recommended to increase vigilance in the studied communities in order to prevent illicit hunting, as well as enforce the established harvest rates. Besides fieldwork, it is also necessary to create habitat suitability index models that will allow us to extend our knowledge concerning the optimal habitat for this species, and to identify conservation and exploitation areas.

Acknowledgements

We thank the Consejo Nacional de Ciencia y Tecnología (CONACYT) for the scholarship (39795) awarded to the first author. Financial support for this study was obtained from the Red de Biología y Conservación de Vertebrados from Instituto de Ecología (INECOL) A.C., the PROCODES-RBTC and CONACYT (CB-2009-01 No. 130702). This work is also the result of the program Retiros Académicos del Instituto de Ecología, A.C. We thank J. C. Pizana, J. M. Torres Salazar, A. Vasquez, L. A. Perez Solano, C. Yañez-Arenas, A. Mendez, F. Contreras, L. A. Escobedo-Morales, A. I. Ortiz-García, T. Perez-Perez, A. Lopez-Carretero and R. Rodriguez for their help with different aspects of the study. Thanks also go to the commissioners of the towns involved in this study.

References

- [1] Smith W. P. 1991. *Odocoileus virginianus*. *Mammalian Species* 388: 1-13.
- [2] Villarreal, J. 1999. *Venado cola blanca: manejo y aprovechamiento cinegético*. Unión ganadera regional de Nuevo León, México.
- [3] Gallina, S., Mandujano, S., Bello, J., López-Arévalo, H. F. and Weber, M. 2010. White-tailed deer *Odocoileus virginianus* (Zimmermann 1780). In: *Neotropical Cervidology*. Duarte, J. M. B. and González, S. (Eds.), pp. 101-118. Jaboticabal, Brazil: Funep and Glnad, Switzerland, IUCN.
- [4] Ortega, A., Mandujano, S., Villarreal, J., Dimari, M.I., López-Arevalo, H., Correa, M and Molina, M. 2011. White-tailed deer in Latin America. In: *Biology and Management of White-tailed Deer*. Hewitt, D. (Ed.), pp. 565-597. Taylor and Francis Group, Boca Raton, Florida.
- [5] Webster, C.R., Jenkins, M. A. and Rock, J. H. 2005. Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA. *Biological Conservation* 125: 297–307.
- [6] Rooney, T. P. and Waller, D. M.. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181: 165–176.
- [7] De la Torre, A.J. and De la Riva, G. 2009. Food habits of pumas (*Puma concolor*) in a semiarid region of central Mexico. *Mastozoología Neotropical* 16: 211-216.
- [8] Naranjo, E. J., Guerra, M. M., Bodmer, R. E. and Bolaños, J. E. 2004. Subsistence hunting by three ethnic groups of the Lacandon forest, Mexico. *Journal of Ethnobiology* 24: 233-253.
- [9] Villarreal-Espino, O. 2002. El Grand-slam de venado cola blanca mexicano, una alternativa sostenible. *Archivos Zootécnicos* 51: 187-193.
- [10] Mandujano, S. and Gallina, S. 1995a. Disponibilidad de agua para el venado cola blanca en un

- bosque tropical caducifolio de México. *Vida Silvestre Neotropical* 4: 107-118.
- [11] Arceo, G., Mandujano, S., Gallina, S. and Pérez, I. A. 2005. Diet diversity of white-tailed deer (*Odocoileus virginianus*) in a tropical dry forest in Mexico. *Mammalia* 69: 1-10.
- [12] Bowyer, R.T., Kie, J. G. and Ballenberghe, V.V. 1998. Habitat selection by neonatal black tailed deer: climate, forage, or risk of predation?. *Journal of Mammalogy* 79: 415-425.
- [13] Bello, J., Gallina, S. and Equihua, M. 2001. Characterization and habitat preferences by white-tailed deer in Mexico. *Journal of Range Management* 54:537-545.
- [14] Cuarón, A.D. 2000. A global perspective on habitat disturbance and tropical rainforest mammals. *Conservation Biology* 14: 1574–1579.
- [15] Mandujano, S., Gallina, S., Arceo, G. and Pérez-Jiménez, L. A. 2004. Variación estacional del uso y preferencia de los tipos vegetacionales por el venado cola blanca en un bosque tropical de Jalisco. *Acta Zoológica Mexicana* 20: 45-67.
- [16] Corona, Z. P., Gallina, S. and Contreras, A. H. 2010. El aprovechamiento del venado cola blanca en una UMA de la Sierra de Huautla, Morelos. In: *Uso y manejo de fauna silvestre en el norte de Mesoamérica*. Guerra, M. M., Calmé, S., Gallina, S. and Naranjo, E.J. (Eds.), pp. 263-294. Secretaría de Educación de Veracruz, Xalapa, Veracruz, México.
- [17] López-Téllez, M. C., Mandujano, S. and Yánes, G. 2007. Evaluación poblacional del venado cola blanca en un bosque tropical seco de la Mixteca Poblana. *Acta Zoológica Mexicana* 23: 1-16.
- [18] Segura, W. 1998. Application of the HEP Methodology and Use of GIS to Identify Priority Sites for the Management of White-Tailed Deer. In: *GIS Methodologies for Developing Conservation Strategies*. Tropical Forest Recovery and Wildlife Management in Costa Rica. Savitsky, B. and Lache, T. (Eds.), pp. 127-137. Columbia University Press, New York.
- [19] Delfín-Alfonso, C., and Gallina, S. 2007. Modelo de evaluación de hábitat para el venado cola blanca en un bosque tropical caducifolio en México. In: *Escarabajos, Diversidad y Conservación Biológica: Ensayos en homenaje a Gonzalo Halffter*. Zunino, M. and Mellic, A. (Eds.), pp. 193-202. Zaragoza, España.
- [20] Yáñez-Arenas, C. 2009. Distribución y densidad poblacional del venado cola blanca (*Odocoileus virginianus*) en el Bajo Balsas, Michoacán, México Tesis Maestría. Instituto de Ecología A. C., Xalapa, Veracruz, México.
- [21] Trejo, I. and Dirzo, R. 2000. Deforestation of seasonally dry tropical forest: a national and local analysis in Mexico. *Biological Conservation* 94: 133-142.
- [22] Gallina, S., Mandujano, S., and Delfín-Alfonso, C. 2007. Importancia de las áreas naturales protegidas para conservar y generar conocimiento biológico de las especies de venados en México. In: Halffter, G., Guevara, S. and Melic, A. (Eds.), In: *Hacia una cultura de la conservación de la diversidad biológica*. Pp. 187.196. Monografías Tercer Milenio, Zaragoza, España.
- [23] Mandujano, S. and González-Zamora, A. 2009. Evaluation of natural conservation areas and wildlife management unit to support minimum viable populations of white-tailed deer in Mexico. *Tropical Conservation Science* 2:237-250.
- [24] Mandujano, S. and Naranjo, E. 2010. Ungulate biomass across a rainfall gradient: a comparison of data from Neotropical and Paleotropical forests and local analysis in Mexico. *Journal of Tropical Ecology* 26:13-23.
- [25] Ruedas, M., Valverde, T. and Zavala-Hurtado, J. A. 2006. Analysis of the factors that affect the distribution and abundance of three *Neobuxbaumia* species (Cactaceae) that differ in their degree of rarity. *Acta Oecológica* 29:155-164.
- [26] Davila, P., Arizmendi, M. C., Valiente-Banuet, A. J., Villaseñor, L., Casas, A. and Lira, R. 2002. Biological diversity in the Tehuacán-Cuicatlán Valley, Mexico. *Biodiversity and Conservation* 11: 421–442.

- [27] INEGI. 1981. Carta topográfica, 1:250,000. Oaxaca, E 14-9. Instituto Nacional de Estadística, Geografía e Informática (INEGI) México.
- [28] Enge, K. I. and Whiteford, S. 1989. The keepers of water and earth. In: *Mexican rural social organization and irrigation*. pp 222. Universidad of Texas Press, Austin.
- [29] Vázquez, L., Moya, H. and Arizmendi, M. C. 2009. Avifauna de la selva baja caducifolia en la cañada del río Sabino, Oaxaca, México. *Revista Mexicana de Biodiversidad* 80: 535-549.
- [30] Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT). 2011. Sistema de Unidades de Manejo para la Conservación de la Vida Silvestre (SUMA). <http://www.semarnat.gob.mx/temas/gestionambiental/vidasilvestre/Paginas/umas.aspx>
- [31] Ezcurra, E. and Gallina, S. 1981. Biology and population dynamics of white-tailed deer in northwestern Mexico. In: *Deer biology, habitat requirements, and management in western North America: a binational Mexico-United States Man and Biosphere (MAB) Program Investigation*. Ffolliot, P. F. and Gallina, S. (Eds.), pp. 77–108. Instituto de Ecología, A.C. México.
- [32] Camargo-Sanabria, A. A. and Mandujano, S. 2011. Comparison of pellet-group counting methods to estimate population density of white-tailed deer in a Mexican tropical dry forest. *Tropical Conservation Science* 4: 230-243.
- [33] Marques, F., Buckland, S.T., Goffin, D., Dixon, C.E., Borchers, D.L., Mayle, B.A. and Peace, A.J. 2001. Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. *Journal of Applied Ecology* 38: 34-363.
- [34] Campbell, D., Swanson, G.M. and Sales, J. 2004. Comparing the precision and cost-effectiveness of faecal pellet group count methods. *Journal of Applied Ecology* 41: 1185-1196.
- [35] Mandujano, S. and Gallina, S. 1995b. Comparison of deer censusing methods in a tropical dry forest. *Wildlife Society Bulletin* 23: 180-186.
- [36] Eberhardt, L. L. and Vanetten, R. C. 1956. Evaluation of the pellet group count as a deer census method. *Journal of Wildlife Management*. 20: 70-74.
- [37] Plumptre, A. 2000. Monitoring mammal populations with line transect techniques in African forest. *Journal of Applied Ecology* 37: 356-368.
- [38] Pérez-Mejía, S., Mandujano, S. and Martínez-Romero, L. E. 2004. Tasa de defecación del venado cola blanca, *Odocoileus virginianus mexicanus*, en cautividad en Puebla. *Acta Zoológica Mexicana* 20: 167-170.
- [39] Mueller-Dombois, D. and Ellenberg, H. 1974. Aims and methods of vegetation ecology. John Willey and Sons, Inc. New York.
- [40] Hammer, O., Harper, D.A.T. and Ryan, P. D. 2001. PAST: Paleontological statistics software package for education and data analysis (v. 2.16 for Windows).
- [41] Griffith, B. and Youtie, B. A. 1988. Two devices for estimating foliage density and deer hiding cover. *Wildlife Society Bulletin* 16: 206-210.
- [42] INEGI. Instituto Nacional de Estadística, Geografía e Informática (INEGI). 1995. Modelo de elevación digital raster de 1 dato cada 90 m.
- [43] ESRI. 1998. ArcView GIS Version 3.2. Environmental Systems Research Institute, New York.
- [44] SAS Institute. 1996. JMP IN Version 3.2.1 for Windows. Duxbury Press.
- [45] Kovach, W.L. 1998. MVSP - A Multivariate Statistical Package for Windows, v. 3.0. Kovach Computing Services, Pentraeth, Wales, U.K.
- [46] Villarreal-Espino, O. 2006. El Venado Cola Blanca en la Mixteca Poblana: Conceptos y Métodos para su Conservación y Manejo. Fundación Produce Puebla.
- [47] Mandujano, S. 2010. Potencial del bosque tropical seco para producción de venado cola blanca (*Odocoileus virginianus*) en México. pp. 101-130, In: *Conservación y manejo de fauna cinegética de México Vol. II*. O. A. Villarreal Espino Barros, J. E. Hernández, J. C. Camacho and F. J. Franco (coordinadores), Benemérita Universidad Autónoma de Puebla, Puebla, México. 302

- pp.
- [48] Ortiz-Martínez, T.S. 2005. Densidad poblacional y caracterización del hábitat del venado cola blanca (*Odocoileus virginianus oaxacensis*, Goldman y Kellog, 1940) en un bosque templado de la sierra norte de Oaxaca, México. *Acta Zoológica Mexicana* 21: 65-78.
- [49] Yáñez-Arenas, C. A., Martínez-Meyer, E., Mandujano, S., and Rojas-Soto, O. 2012. Estimating population density of the white-tailed deer in central Mexico via ecological niche modeling. *Oikos* 121: 2081-2089.
- [50] Mandujano, S. 2006. Preliminary Evidence of the Importance of ENSO in Modifying Food Availability for White-tailed Deer in a Mexican Tropical Dry Forest. *Biotropica* 38: 695–699.
- [51] Reyna-Hurtado, R. and Tanner, G.W. 2005. Habitat preferences of ungulates in hunted and nonhunted areas in the Calakmul Forest, Campeche, Mexico. *Biotropica* 37:676–685.
- [52] Gallina, S. 1994. Dinámica poblacional y manejo de la población del venado cola blanca en la Reserva de la Biosfera La Michilia, Durango, México. In: *Ecología y Manejo del venado cola blanca en México y Costa Rica*. Vaughan, C. and Rodríguez, M. (Eds.), pp. 207-234. Editorial de la Universidad Nacional de Costa Rica.
- [53] González-Pérez, G.E. 2003. Uso del hábitat y área y actividad del venado cola blanca (*Odocoileus virginianus sinaloae* J. Allen) en la Estación Científica Las Joyas, Reserva de la Biosfera de Manantlán, Jalisco. Tesis profesional. Facultad de Ciencias. Universidad Autónoma de México. México, D.F.
- [54] Sánchez-Rojas, G., Gallina, S. and Mandujano, S. 1997. Área de actividad y uso del hábitat de dos venados cola blanca (*Odocoileus virginianus*) en un bosque tropical de la costa de Jalisco, México. *Acta Zoológica Mexicana* 72: 39-54.
- [55] Nevo, E. 2001. Evolution of genome-phenome diversity under environmental stress. *Proceedings of the National Academy of Sciences* 98: 6233-6240.
- [56] Mandujano, S., Gallina, S. and Bullock S.H. 1994. Frugivory and dispersal of *Spondias purpurea* (Anacardiaceae) in a tropical dry forest of Mexico. *Revista de Biología Tropical* 42: 105-112.
- [57] Mandujano, S. and Martínez-Romero, L.E. 1997. Fruit fall caused by chachalacas (*Ortalis poliocephala*) on red mombim trees (*Spondias purpurea*): Impact on terrestrial fruit consumers, specially the white tailed deer (*Odocoileus virginianus*). *Studies on Neotropical Fauna and Environmental* 32: 1-3.
- [58] Villarreal Espino-Barros, O. A. and Marín-Fuentes, M.M. 2005. Agua de origen vegetal para el Venado Cola Blanca Mexicano. *Archivos de Zootecnia* 54: 191-196.
- [59] Hudson, R.J., Hebert, D. M. and Brink, V. C. 1976. Occupational patterns of wildlife on a major east Kootenay winter-spring range. *Journal of Range Management* 29: 38-43.
- [60] Kie, J. G., Evans, C. J., Loft, E. R. and Menke, J. W. 1991. Foraging behavior by mule deer: the influence of cattle grazing. *Journal of Wildlife Management* 55: 665–674.
- [61] Chaikina, N. A. and Ruckstuhl, K. E. 2006. The effect of cattle grazing on native ungulates: the good, the bad, and the ugly. *Rangelands* 28: 8-14.
- [62] Forman, R. T. T., and Alexander, L. E. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29: 207–231.
- [63] Alvard, M. S., Robinson, J.G., Redford, K. H. and Kaplan, H. 1996. The sustainability of subsistence hunting in the Neotropics. *Conservation Biology* 11: 977–982.
- [64] Kilgo, J. C., Labisky, R. F. and Fritzen, D. E. 1998. Influences of Hunting on the Behavior of White-Tailed Deer: Implications for Conservation of the Florida Panther. *Conservation Biology* 12:1359-1364.
- [65] Post, E. and Stenseth, N. C. 1999. Climatic variability, plant phenology and northern ungulates. *Ecology* 80: 1322–1339.
- [66] Sánchez-Rojas, G., Aguilar-Miguel, C. and Hernández-Cid E. 2009. Estudio poblacional y uso de

- hábitat por el Venado Cola Blanca (*Odocoileus virginianus*) en un bosque templado de la Sierra de Pachuca, Hidalgo, México. *Tropical Conservation Science* 2: 204-214.
- [67] Roseberry, J.L. and Woolf, V. 1998. Habitat population density relationships for white-tailed deer in Illinois. *Wildlife Society Bulletin* 26: 252–258.
- [68] Patton, D.R. 1997. Wildlife habitat relationships in forested ecosystem. Revised edition, Timber Press, Portland, Oregon.
- [69] Baraza, R. E. and Estrella, R. J. P. 2008. Manejo sustentable de los recursos naturales guiado por proyectos científicos en la mixteca poblana mexicana. *Ecosistemas* 2: 3-9.
- [70] Casas, A., Valiente-Banuet, A., Viveros, J.L., Caballero, J., Cortes, L., Dávila, P., Lira, R. and Rodríguez, I. 2001. Plant resources of the Tehuacan-Cuicatlan Valley, Mexico. *Economic Botany* 55: 129-166.
- [71] Flannery, K. V. 1967. Vertebrate fauna and hunting patterns. In: *The prehistory of the Tehuacan, Valley*. Byers, D.S. (Ed) pp. 132-167. University of Texas Press, Austin, Texas.
- [72] Montiel-Ortega, S., Arias, L.M. and Dickinson, F. 1999. La cacería tradicional en el norte de Yucatán: una práctica comunitaria. *Revista geografía agrícola* 29: 43-51.
- [73] González-Marín, R. M., Montes, E. and Santos, J. 2003. Caracterización de las unidades de manejo para la conservación, manejo y aprovechamiento sustentable de la fauna silvestre en Yucatán, México. *Tropical and Subtropical Agroecosystems* 2: 13-21.
- [74] Weber, M., García-Marmolejo G. and Reyna-Hurtado, R. 2006. The tragedy of the commons: wildlife management units (UMAs) in southeastern Mexico. *Wildlife Society Bulletin* 34: 1480-1488.
- [75] Mandujano, S. 2007. Carrying capacity and potential production of ungulates for human use in a Mexican tropical dry forest. *Biotropica* 39: 519-524.

Appendix 1. Habitat description of four sites in the study area. We report average values and standard deviation (\pm) for each locality. Values with different letters are statistically different by ANOVA (a) and Kruskal Wallis (k), $P < 0.05$. The most important plant species are presented with regard to their relative importance value for each location. * Lists of the plants that are eaten by deer in the dry season.

Variables	Chilar	Casa Blanca	Tecomavaca	Quiotepec	P
Deer density (deer/km ²)	2.9 ^a	2.6 ^a	1.1 ^b	0.1 ^c	<0.05 ^k
range (deer/km ²)	2.2 – 4.4	2.0 – 3.9	0.8 – 1.7	0.1 – 0.3	
Coefficient of variation	38.1	31.7	43.2	64.3	
<i>Vegetation structure</i>					
Basal area (m ²)	173.6 \pm 57.2 ^a	219 \pm 88.0 ^a	188.8 \pm 68.4 ^a	299 \pm 75.8 ^b	0.02 ^k
Density of trees (ind/100 m ²)	18.4 \pm 4.2 ^{ab}	14 \pm 5.9 ^a	3.8 \pm 6.0 ^c	21.8 \pm 7.2 ^b	<0.05 ^a
Understory richness	15.4 \pm 3.4 ^b	12 \pm 2.5 ^a	17.3 \pm 1.2 ^{bc}	14.9 \pm 4.2 ^{abc}	0.01 ^a
Protection cover 0-50 (%)	7.8 \pm 8.1	9.8 \pm 11.6	10.9 \pm 11.4	11.1 \pm 12.4	0.97 ^k
Protection cover 51-100 (%)	15.1 \pm 8.7	11.4 \pm 12.2	19.3 \pm 17.1	15.7 \pm 14.8	0.76 ^k
Protection cover 101-150 (%)	19.9 \pm 10.3	17.5 \pm 14.8	21.2 \pm 14.3	18.7 \pm 17.5	0.96 ^a
Protection cover 151-200 (%)	29.7 \pm 9.9	24 \pm 23.2	28.4 \pm 18.5	26.0 \pm 21.4	0.93 ^a
<i>Physionomic structure</i>					
Altitud (msl)	937.7 \pm 90.5 ^b	879.5 \pm 29.3 ^{ab}	825.7 \pm 84.5 ^a	849.9 \pm 75.3 ^a	0.03 ^a
Slope (°)	10.2 \pm 1.1 ^b	4.7 \pm 1.1 ^a	8.8 \pm 6.4 ^{ab}	8.6 \pm 4.0 ^b	0.04 ^a
Orientation (°)	98.8 \pm 32.4 ^a	68.5 \pm 18.9 ^a	124 \pm 113.6 ^a	271 \pm 27.9 ^b	<0.05 ^k
Distance to water bodies (km)	1.4 \pm 0.4	0.6 \pm 0.3	0.3 \pm 0.2	1.2 \pm 0.4	<0.05 ^a
<i>Human influence</i>					
Distance to roads (km)	1.5 \pm 0.5 ^b	6.5 \pm 0.4 ^a	1.1 \pm 0.5 ^b	0.3 \pm 0.2 ^c	<0.05 ^k
Distance to locations (km)	2.5 \pm 0.5 ^b	6.8 \pm 0.5 ^a	5.9 \pm 1.3 ^a	3.7 \pm 0.7 ^c	<0.05 ^k
Distance to the area with largest population (km)	51.3 \pm 0.6	13.5 \pm 0.7	24.4 \pm 1.6	31 \pm 0.6	<0.05 ^k
Livestock (feces per transect)	1.1 \pm 1.8 ^a	0 ^a	1 \pm 1.4 ^a	5 \pm 2.1 ^b	<0.05 ^k
<i>Plant communities</i>					
Number of plant Families	27	19	31	34	
Number of plant species	123	119	138	96	
<i>Relative importance value</i>					
<i>Lantana camara</i>		103.4			
<i>Bursera sp 2*</i>		57.7			
<i>Bursera linanoe*</i>		48.1			
<i>Agonandra sp</i>		47.8			
<i>Randia thurberi*</i>		40.3			
<i>Neobuxbaumia tetetzo</i>				554.0	
<i>Bursera schlectendalii*</i>				313.7	
<i>Mimosa sp</i>				311.1	
<i>Parkinsonia proecox</i>				207.4	
<i>Bursera sp*</i>				147.6	
<i>Vallesia glabra</i>			52.0		
<i>Acacia pringlei</i>			43.8		
<i>Bursera sp 3*</i>			39.7		
<i>Parkinsonia proecox</i>			31.8		
<i>Randia thurberi*</i>			28.8		
<i>Bunchosia biocellata</i>	40.1				
<i>Amphipterygium adstringens</i>	39.1				
<i>Bursera aptera*</i>	37.8				
<i>Lippia alba</i>	35.8				
<i>Bursera sp 3*</i>	32.4				
<i>Opuntia sp*</i>	32.4				
<i>Cyrtocarpa procera</i>	30.6				
<i>Asclepias curassavica</i>	30.3				
<i>Stenocereus stellatus</i>	30.2				

Appendix 2. Habitat variables in the first two principal component analyses and the percentage of variance explained for each axis and the cumulative percentage. Larger scores are shown in bold.

Variables	PC I	PC II
Eigenvalues	4.02	3.55
Variance explained	26.8	23.7
Cumulative variance	26.8	50.5
<i>Vegetation structure</i>		
Basal area (m ²)	0.215	0.093
Density of trees (ind/100 m ²)	0.321	0.083
Richness (num. ind)	0.012	0.193
Protection cover 0-50 (%)	-0.127	0.437
Protection cover 51-100 (%)	-0.156	0.474
Protection cover 101-150 (%)	-0.179	0.458
Protection cover 151-200 (%)	-0.157	0.405
<i>Physionomic structure</i>		
Altitud (msl)	0.099	-0.123
Slope (°)	0.138	0.059
Orientation (°)	0.366	0.082
Distance to water bodies (km)	0.347	-0.014
<i>Human pressure</i>		
Distance to roads (km)	-0.265	-0.246
Distance locations (km)	-0.281	-0.203
Distance to the largest human community (km)	-0.435	-0.049
Livestock presence	0.362	0.169

Appendix 3. Tree species that contributed with larger scores in the first two principal component analyses, with the percentage of variance explained for each axis and the cumulative percentage. Larger scores are shown in bold.

Variables	PC I	PC II
Eigenvalues	10.713	9.714
Variance explained	10.503	9.523
Cumulative variance	10.503	20.026
Plant Species		
<i>Acacia constricta</i>	-0.173	0.169
<i>Acacia pringlei</i>	0.192	0.09
<i>Amphipterigyum adstringens</i>	-0.091	0.206
<i>Bursera</i> sp	0	-0.171
<i>Bursera</i> sp 3	0.164	0.137
<i>Bursera</i> sp 5	0.187	-0.034
<i>Capparis incana</i>	-0.024	0.156
<i>Castela tortuosa</i>	0.225	0.032
<i>Ceiba parvifolia</i>	-0.156	0.019
<i>Ceiba</i> sp	0.225	0.032
<i>Cephalocereus columna-trajani</i>	0.206	0.121
<i>Cordia curassavica</i>	-0.064	0.155
<i>Ficus</i> sp	0.225	0.032
<i>Jatropha neopauciflora</i>	0.163	-0.017
<i>Montanoa mollissima</i>	0.225	0.032
<i>Neobuxbaumia tetetzo</i>	-0.031	-0.241
<i>Parkinsonia proecox</i>	0.022	-0.253
<i>Salix</i> sp	0.225	0.032
<i>Senna wislizenii</i>	-0.027	-0.191
Sp 13	0.225	0.032
Sp 2	-0.029	-0.175
Sp 7	-0.156	0.112
<i>Vallesia glabra</i>	0.225	0.032
<i>Ziziphus amole</i>	0.179	-0.098