

Native and no-native herbivorous relationships have mutual benefit: *Lepus flavigularis* case

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Lepus flavigularis is an endemic leporid from southeastern Oaxaca, México, listed as “endangered” under Mexican law and the IUCN Red List. The main threat to the species is severe habitat fragmentation due to human activities. The jackrabbit shares the grasslands with cattle (*Bos taurus*), but the trophic interaction between these herbivores is unknown. This study aimed to determine the seasonal diet of *Lepus flavigularis* and cattle, to identify the possible dietary overlap between these mammals. The study zone covers an area around the locality of Santa María del Mar in Oaxaca, southern México. Plant species were identified using linear transects, and vegetation cover was also estimated using circular plots. Throughout the study fresh *L. flavigularis* and *B. taurus* fecal samples were collected, which were processed using the microhistological technique to determine the seasonal botanical composition of diets from the two species. Twenty-three plant species were recorded in the diet of *L. flavigularis* and 29 species in the diet of *B. taurus*. Both herbivores fed primarily on Poaceae species throughout the year (*L. flavigularis*: dry season (ds) = 79.79 %, wet season (ws) = 91.54 %; *B. taurus*: ds = 78.02 %, ws = 84.63 %) despite the significant difference in the availability of plant species between seasons. No significant differences were found in the seasonal composition of the diet between the two species. Twelve plant species were consumed by both herbivores during the two seasons. The dietary overlap between the two species was high for both seasons (ds O_{jk} = 0.7311, ws O_{jk} = 0.8459). Trophic niche breadth was low for both species, with a high dietary overlap. We recorded low seasonal use values for *L. flavigularis* and *B. taurus* when compared to forage availability. Low trophic niche breadth and high dietary overlap between the two herbivores suggest forage resources competition. However, we expect that jackrabbits benefit from cattle presence, as long as the stocking rate does not increase. Furthermore, *B. taurus* grazing reduces height, cover, and density of vegetation, which could help *L. flavigularis* to avoid predators.

Lepus flavigularis es un lepórido del sureste de Oaxaca, México, categorizado como “en peligro de extinción” de acuerdo con la legislación mexicana y con la Lista Roja de la UICN. La principal amenaza para la especie es la severa fragmentación del hábitat a causa de las actividades humanas. La liebre comparte los pastizales con ganado vacuno (*Bos taurus*), pero la interacción trófica entre estos herbívoros se desconoce. Este estudio tuvo como objetivo determinar la dieta estacional de *L. flavigularis* y el ganado, así como identificar la posible superposición alimenticia entre estos mamíferos. La zona de estudio cubre un área alrededor de la localidad de Santa María del Mar en Oaxaca, al sur de México. Las especies de plantas se identificaron utilizando transectos lineales, y se estimó la cobertura vegetal utilizando parcelas circulares. A lo largo del estudio se colectaron muestras fecales frescas de ambas especies, las cuales fueron procesadas utilizando la técnica microhistológica para determinar la composición botánica estacional de la dieta de las dos especies. Se registraron 23 especies en la dieta de *L. flavigularis* y 29 para *B. taurus*. Ambos herbívoros se alimentaron principalmente de especies de Poaceae anualmente (*L. flavigularis*: temporada seca (ts) = 79.79 %, temporada húmeda (th) = 91.54 %; *B. taurus*: ts = 78.02 %, th = 84.63 %), a pesar de la significativa diferencia en la disponibilidad de especies vegetales entre temporadas. No se encontró una diferencia significativa en la composición estacional de la dieta entre ambas especies. Doce especies vegetales fueron consumidas por ambos herbívoros en las dos temporadas. La superposición alimenticia fue alta para ambas temporadas (ts O_{jk} = 0.7311, th O_{jk} = 0.8459). La amplitud del nicho trófico fue baja para ambas especies, con un traslape alimenticio alto entre éstas. Registramos un bajo uso estacional para *L. flavigularis* y *B. taurus* cuando se le compara con la disponibilidad de alimento. La baja amplitud de nicho trófico y la alta superposición alimenticia entre los dos herbívoros sugiere una competencia por recursos alimenticios en el corto plazo. Sin embargo, de acuerdo con estudios previos sobre uso de microhábitat, sugerimos que las liebres pueden beneficiarse de la presencia del ganado, siempre que la capacidad de carga no se incremente. Además, el ramoneo de *B. taurus* reduce la altura, cobertura y densidad de la vegetación, lo cual puede ayudar a *L. flavigularis* a evitar depredadores.

Keywords: Diet competition; diet overlap; grazing; México; Tehuantepec jackrabbit; livestock.

Introduction

For small and medium mammals like rodents and lagomorphs, food availability is one of the major limitations for population density (Prevedello *et al.* 2013). Studies exploring trophic interactions between leporids and other sympatric herbivores, such as livestock, are important to design conservation plans with an adequate livestock management program. It has been widely documented that, in some cases, heavy livestock grazing, and high stocking rates have an adverse impact on the density, distribution and population dynamics of leporids (Gahr 1993; Bock *et al.* 2006) and other mammals (Cortés-Marcial *et al.* 2014). Several studies have clearly shown that trophic competition occurs between leporids and other herbivores and ruminants such as cattle (Smith *et al.* 2004; Young *et al.* 2005), producing an adverse effect on leporid populations (Hulbert and Andersen 2001). However, certain leporids and livestock can coexist and obtain mutual benefits when stocking rates do not exceed the grazing capacity of their habitat (Karmiris *et al.* 2005; du Toit 2011). Furthermore, some evidence suggests that livestock grazing, whether by goats, sheep, or cattle, is beneficial to jackrabbits due to the reduction of standing biomass, which is a key factor in habitat suitability (Kuijper *et al.* 2008; Karmiris and Nastis 2010).

The Tehuantepec jackrabbit (*Lepus flavigularis*) lives in four disjunct populations within an area of 673 km² in the surroundings of Laguna Inferior and Laguna Superior in the Tehuantepec Isthmus, Oaxaca, México. This jackrabbit is an endangered species, endemic to Oaxaca, and is currently considered one of the most endangered leporids in the world (SEMARNAT 2010; Lorenzo *et al.* 2015, 2018; IUCN 2022). *L. flavigularis* inhabits open grasslands and xeric shrublands with the presence of isolated tree species (Carrillo-Reyes *et al.* 2012; Lorenzo *et al.* 2015). Land-use change due to the expansion of human settlements, overgrazing by cattle, and burning of pastures for seasonal agriculture, have reduced and fragmented its habitat. Existing populations are therefore almost entirely isolated and exhibit little genetic variability (Rioja *et al.* 2011; Lorenzo *et al.* 2015). A previous study described the diet of *L. flavigularis* in one locality (Montecillo Santa Cruz) and observed that it feeds mainly on grasses (66.7 % of diet). However, the diet of this species in localities that exhibit different ecological (vegetation associations) and anthropic scenario (production activities), remains unknown. At Santa María del Mar, the jackrabbit shares the grasslands with *Bos taurus* Zebu breed (treated here as synonym of *B. indicus* or *B. t. indicus*), but the trophic interaction between these herbivores is unknown. Because there is dietary overlap between cattle and other leporids like *L. californicus*, *Sylvilagus audubonii* (Peña-Neira 1980; Daniel *et al.* 1993), and *Oryctolagus cuniculus* (Bonino 2006, 2011), we hypothesize trophic competition between Tehuantepec jackrabbit (*L. flavigularis*) and cattle (*B. taurus*). The study aimed not only to determine the seasonal diet of an endangered leporid (*L. flavigularis*) and cattle, but also to identify possible dietary overlap between these herbivores to better understand this relationship.

Materials and methods

The study area covers an extension of 14 km² around the locality of Santa María del Mar (16° 14' 7", 16° 12' 46" N and - 94° 53' 9", - 94° 48' 15" W; Figure 1), in the municipality of Juchitán de Zaragoza, in the state of Oaxaca, southern México. It is located in the region of the Tehuantepec Isthmus between a coastal lake (Mar Tileme) and the Pacific Ocean. The town is inhabited by over 800 people whose main productive activities are fishing and cattle production, and occasionally, seasonal agriculture and subsistence hunting (Carrillo-Reyes *et al.* 2010). The local climate is warm sub-humid with a pronounced dry season, summer rains, and average annual precipitation of 800 mm (Aw₀, savanna like). The driest month has less than 60 mm of precipitation and the average annual temperature is 30 °C. The wet season occurs between May and October with a short dry period in August, while the long dry season begins in November and ends in April (García and Comisión Nacional para el Conocimiento y Uso de la Biodiversidad 1998; Rioja-Paradela *et al.* 2012).

This *L. flavigularis* population is the most abundant of the four existing; Vargas (2000) recorded 12 individuals/km² (0.12 individuals/ha) although this value has decreased to 8 individuals/km² (0.08 individuals/ha; Chacón-Trinidad *et al.* 2020). The habitat of *L. flavigularis* is characterized by extensive zones of grassland, dominated by *Eragrostis prolifera*, *Jouvea pilosa* and *Whalteria preslii* (Carrillo-Reyes *et al.* 2012). Also, isolated individuals of *Opuntia tehuantepecana* and *O. decumbens* are present; these areas are grazed by cattle (Carrillo-Reyes *et al.* 2010). *B. taurus* and *L. flavigularis* are the only large and medium herbivores present in this grassland. In the scrubland surrounding the pasture occurs the Eastern cottontail (*Sylvilagus floridanus*) but does not make use of the grassland; its habitat is limited to the bush, so it does not compete for food or territory with the jackrabbit or the livestock (Rioja-Paradela 2008). A recent study showed that in the grassland association the density of cattle was eight individuals/ha (800 individuals/km²; Chacón-Trinidad

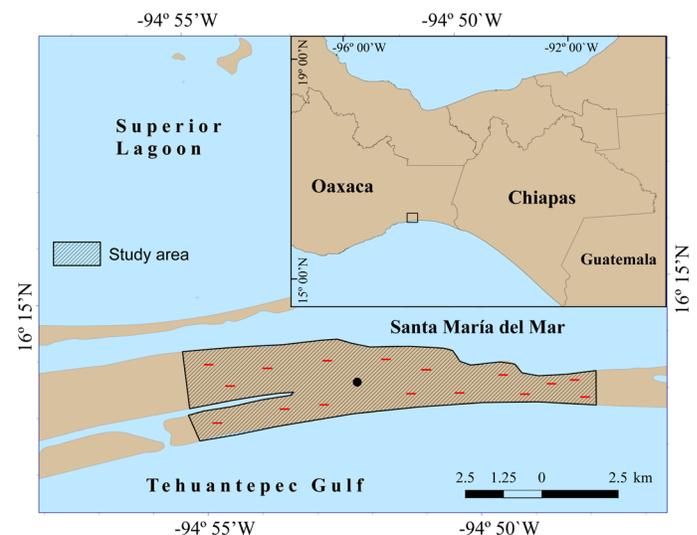


Figure 1. Study area, with vegetation transects shown in red lines.

[et al. 2020](#)), and those cattle grazed in paddocks from 8:00 to 20:00 hrs. There is no rotational grazing; cattle management depends on the availability of "paddocks to lease" and the ability of livestock owners to rent these paddocks.

We made two visits to the study area, one for dry and one for wet season, each lasting 15 days. For vegetation sampling in both seasons, 16 linear transects of 60 m were randomly established with a distance of at least 100 m between them ([Carrillo-Reyes et al. 2010](#)). Forage availability was estimated considering vegetation cover as an approximate measure of availability that is compatible with fecal samples at a spatial-temporal scale ([Norbury and San-son 1992](#); [Kufner et al. 2008](#); [Tirado et al. 2012](#)). To record the cover of grasses and herbaceous species along each transect, five circular plots of 1 m² were established at 10-m intervals along each linear transect, for a total of 80 circular plots. To estimate the shrub cover, one circular plot of 12.6 m² was established at the center of each linear transect, for a total of 16 circular plots. Calculation of absolute coverage was based on the methodology described by [Rio-Olague \(1999\)](#), and relative vegetation cover was calculated using the formula of [Franco-López et al. \(1989\)](#). Significant differences ($P < 0.05$) in the forage availability between dry and wet season were determined by U Mann-Whitney test ([Bauer 1972](#)). For all plant species, samples of leaves and fruits were collected and later processed by the microhistological technique to create a reference collection. This collection was later used to identify the species in the diet of the two herbivores.

During each visit to the study area, we collected *L. flavigularis* and *B. taurus* fecal samples. For each species, the freshest excreta were collected along the same transects used for vegetation (16 sampling sites, 1 per vegetation transect), to increase the probability of collecting samples from different individuals. At each transect, random *L. flavigularis* pellets and *B. taurus* dung pats were collected and placed in paper bags for transport at ambient temperature. From all fecal samples collected, a total of 20 *L. flavigularis* random pellets were chosen. Also, for *B. taurus* the sample was homogenized (the sample was dispersed and mixed homogeneously), and then a random sample of approximately 10 g of excreta was chosen. The samples were then dried at 75 °C for 24 h before subsequent analysis ([Bonino 2006](#); [Lorenzo et al. 2011](#)).

The seasonal and annual botanical composition of the diet was determined by microhistological analysis of plant epidermal fragments present in the feces ([Peña-Neira and Habib-de Peña 1980](#); [Kufner et al. 2008](#); [Lorenzo et al. 2011](#)). This technique was used because it does not imply disturbing wildlife and no extractions are needed, which is particularly important for a critically endangered species. For each transect and every species, five temporary slides were prepared, for a total of 80 slides per species. To prepare fecal samples for analysis, the material was cleared using a commercial solution of sodium hypochlorite; samples were immersed approximately five minutes in this solution

and washed in water for 20 minutes ([Kufner et al. 2008](#)). A plastic template with 7 mm diameter and 5 mm thick holes was used to mount the samples. The template was placed on the slides (so that each slide had the same amount of sample), and the holes were filled with the wet material after being washed. A commercial formula of corn syrup was used as mounting medium for temporary slides. After preparation, slides were sealed using transparent glaze and stored to dry for five days. Microphotographs were taken of all slides. On each slide, 20 fields were examined with an optical microscope (objective x40); five separate slides were examined for each sample, with a total of 100 fields per sampling site and a total of 1,600 per species. Slides were examined using randomly generated non-overlapping coordinates. Microscopic identification of species was performed by comparison with the reference collection of microscope slides of plants. Items whose tissue showed at least three diagnostic microhistological elements were identified to species level. Items that did not meet this criterion were not considered. Unidentified fragments were recorded as unidentified monocotyledons or dicotyledons. We recorded the plant species and accumulated frequency (number of fields in which each identified species was recorded). Botanical composition was obtained by transforming frequency to density using the [Fracker and Brischle \(1944\)](#) table ([Lorenzo et al. 2011](#)).

Species richness for each season was determined by the number of registered species ([Lorenzo et al. 2011](#)). Differences ($P < 0.05$) in the diet of both species between the dry and wet seasons were determined by U Mann-Whitney test ([Bertolino et al. 2009](#); [Desbiez et al. 2009](#)) and corroborated with a Sorensen quantitative test (QS; [Morgia and Bassano 2009](#)). The comparison was made by contrasting the density of each plant species in the diet. Niche breadth was assessed using Levins' measure, $B_j = 1/\sum p_{ij}^2$, where p_{ij} is the proportion of diet contributed by plant species i on a given mammal species (Levins 1968). This was standardized to a scale of 0 - 1 following $B_j = (B - 1)/(N - 1)$ where N is the total number of plant species. The total number of species eaten at least once by at least one herbivore in each season was used to calculate the index ([Mishra et al. 2004](#); [Bertolino et al. 2009](#)).

Interspecific trophic relationship was analyzed based on seasonal diet composition. Diet similarity was evaluated with U Mann-Whitney test ([Bertolino et al. 2009](#)) and corroborated with a Sorensen test ([Morgia and Bassano 2009](#)), contrasting the density of each plant species. Dietary overlap was estimated with the [Pianka \(1975\)](#) index, performing 5,000 Monte Carlo randomizations to determine the difference between the simulated data and the result of overlap ([Desbiez et al. 2009](#)).

To determine the relationship between the seasonal diet of each species and the forage availability in the same season the [Pianka \(1975\)](#) index ([Kufner et al. 2008](#)) was used. We use vegetation cover as an indicator of forage availability ([Kufner et al. 2008](#)). This analysis can indicate the degree of resource selection at a specific time and can

corroborate the role of the species as generalist or specialist. All analyses were performed with the software R and RStudio (R Core Team 2020; RStudio Team 2020) and packages "EcoSimR" (Gotelli et al. 2015), "spaa" (Zhang 2013) and "fossil" (Vavrek 2011).

Results

During the dry season, 33 species of non-woody plants (16 grasses and 17 forbs, *i. e.*, non-grass herbaceous plants) and 16 species of woody plants were recorded. In the wet season, 68 species of non-woody plants (18 grasses and 50 forbs) and 22 species of woody plants were recorded. We found a highly significant difference in forage availability

between the dry season and the wet season (U Mann-Whitney test, $W = 357$, $P = 0.001$; Figure 2).

Twenty-tree plant species were recorded in the diet of *L. flavigularis* and 29 species were in the diet of *B. taurus* (Table 1). Both herbivores fed primarily on Poaceae species throughout the year (*L. flavigularis*, dry = 79.79 %, wet = 91.54 %; *B. taurus*, dry = 78.02 %, wet = 84.63 %, Figure 3). Less consumed species were forbs (*L. flavigularis*, dry = 20.21 %, wet = 8.46 %; *B. taurus*, dry = 14.09 %, wet = 13.90 %) and shrubs (*L. flavigularis*, dry = 0.00 %, wet = 0.00 %; *B. taurus*, dry = 1.32 %, wet = 0.83 %).

The most important items in the diet of *L. flavigularis* were grasses and forbs, *Bouteloua repens* (27 %), *Stipa emi-*

Table 1. Botanical composition (%) of the diet of *L. flavigularis* and *B. taurus* by season. The percentages are presented in parentheses.

Family	Species	Life form	<i>L. flavigularis</i>		<i>B. taurus</i>	
			Dry	Wet	Dry	Wet
Amaranthaceae (7.69 %)	<i>Amaranthus scariosus</i>	Forb	0.56	0.00	0.00	0.00
	<i>Gomphrena globosa</i>	Forb	0.00	4.04	0.00	0.00
	<i>Gomphrena decumbens</i>	Forb	0.00	0.00	0.00	0.44
Asteraceae (5.12 %)	<i>Erigeron oxacanus</i>	Forb	6.62	2.01	1.85	2.63
	<i>Lactuca intybacea</i>	Forb	0.79	1.34	0.12	2.28
Cactaceae (2.56 %)	<i>Opuntia tehuantepecana</i>	Shrub	0.00	0.00	0.49	0.00
Commelinaceae (2.56 %)	<i>Commelina erecta</i>	Forb	7.13	0.00	0.00	0.00
Convolvulaceae (2.56 %)	<i>Ipomoea minutiflora</i>	Forb	0.00	0.00	0.59	0.77
Cyperaceae (2.56 %)	<i>Cyperus articulatus</i>	Forb	4.79	0.14	0.16	0.07
Euphorbiaceae (5.12 %)	<i>Chamaesyce lasiocarpa</i>	Forb	0.00	0.00	0.40	0.12
	<i>Dalechampia scandens</i>	Forb	0.00	0.00	2.39	0.00
Fabaceae (15.38 %)	<i>Acacia sp.</i>	Shrub	0.00	0.00	4.79	0.00
	<i>Centrosema pascuorum</i>	Forb	0.00	0.00	0.00	3.56
	<i>Chamaecrista hispidula</i>	Forb	0.00	0.00	0.00	0.28
	<i>Desmodium barbatum</i>	Forb	0.00	0.57	0.00	0.00
	<i>Desmanthus virgatus</i>	Shrub	0.00	0.00	2.61	1.48
	<i>Galactia argentea</i>	Forb	0.08	0.35	0.00	0.00
Gentianaceae (5.12 %)	<i>Eustoma exaltatum</i>	Forb	0.23	0.00	0.00	0.00
Malvaceae (5.12 %)	<i>Melochia pyramidata</i>	Forb	0.00	0.00	1.95	0.55
	.	Forb	0.00	0.00	4.32	0.00
Poaceae (41.02 %)	<i>Sorghum halepense</i>	Grass	0.00	10.64	0.00	0.00
	<i>Bouteloua aristidoides</i>	Grass	10.11	11.38	1.81	8.42
	<i>Bouteloua hirsuta</i>	Grass	0.00	0.00	0.00	0.04
	<i>Bouteloua repens</i>	Grass	27.00	18.55	22.13	22.94
	<i>Bouteloua sp.</i>	Grass	0.00	0.00	0.26	0.00
	<i>Cenchrus echinatus</i>	Grass	2.45	4.47	1.29	4.63
	<i>Digitaria ciliaris</i>	Grass	10.28	6.72	8.31	5.77
	<i>Digitaria filiformis</i>	Grass	0.29	1.37	2.43	2.66
	<i>Eragrostis glomerata</i>	Grass	0.48	0.00	0.00	0.00
	<i>Eragrostis prolifera</i>	Grass	2.24	5.01	20.47	10.18
	Grass - Unidentified sp1	Grass	3.07	0.97	0.31	2.19
	<i>Hilaria belangeri</i>	Grass	1.63	1.06	1.62	2.85
	<i>Jouvea pilosa</i>	Grass	0.54	0.80	4.48	1.87
	<i>Muhlenbergia sp.</i>	Grass	2.47	0.00	0.00	0.00
<i>Paspalum prostratum</i>	Grass	0.00	0.00	0.00	3.68	
<i>Stipa eminens</i>	Grass	16.87	29.32	14.88	19.43	
<i>Stipa sp.</i>	Grass	2.37	1.24	0.00	0.00	
Solanaceae (5.12 %)	<i>Hydrolea spinosa</i>	Forb	0.00	0.00	2.11	3.17
Verbenaceae (5.12 %)	<i>Phyla nodiflora</i>	Forb	0.00	0.00	0.19	0.02

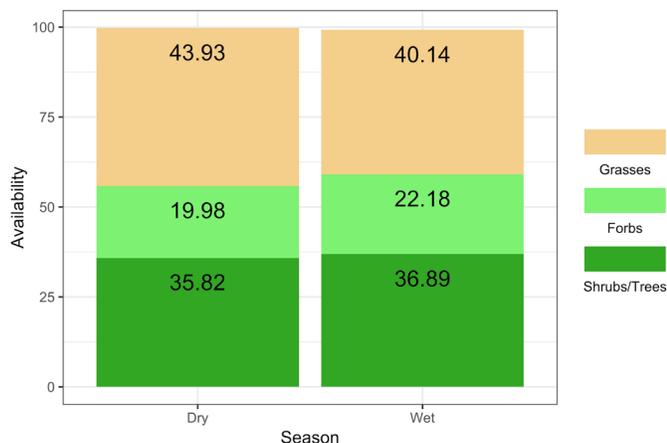


Figure 2. Availability (%) of plant species by growth form and by season in Santa María del Mar, Oaxaca, México.

nens (16.87 %) and *Digitaria ciliaris* (10.28 %), during the dry season, and *S. eminens* (29.32 %), *B. repens* (18.55 %) and *B. aridoides* (11.38 %) during the wet season. For *B. taurus*, the most important items were grasses and forbs, *B. repens* (22.13 %), *Eragrostis prolifera* (20.43 %) and *S. eminens* (14.88 %) during the dry season, and *B. repens* (22.94 %), *S. eminens* (19.43 %) and *E. prolifera* (10.18 %) during the wet season.

No significant differences were found in the seasonal composition of the diet of *L. flavigularis* ($W = 911.5$, $P = 0.78$) or *B. taurus* ($W = 893.5$, $P = 0.91$). These results were corroborated by the Sorensen quantitative test, which showed a high similarity between the seasonal diet of *L. flavigularis* ($QS = 0.8540$) and that of *B. taurus* ($QS = 0.8957$). The trophic niche breadth was low for both species (*L. flavigularis*, dry = 0.1439, wet = 0.1250; *B. taurus*, dry = 0.1663, wet = 0.1674).

From 39 species, 12 were consumed by both species during the two seasons. Seasonally, *L. flavigularis* and *B. taurus* shared 13 species on both dry and wet seasons (Table 1). This was coincident with dietary overlap analysis; according to the Pianka (1975) index, the dietary overlap between the two species was high for both seasons (dry $O_{jk} = 0.7311$, wet $O_{jk} = 0.8459$). We recorded low seasonal use of available plant species for *L. flavigularis* (dry season $O_{jk} = 0.1788$; wet season $O_{jk} = 0.3102$) and for *B. taurus* (dry $O_{jk} = 0.3378$; wet $O_{jk} = 0.4022$).

Discussion

Results indicate that *L. flavigularis* and *B. taurus* exploited a relatively narrow variety of available species of plants, suggesting that both herbivores are selective, showing a preference for Poaceae species throughout the year despite the significant difference in the availability of plant species between the dry and wet season. The Poaceae preference of *L. flavigularis* is consistent with the findings of Lorenzo et al. (2011) in another isolated *L. flavigularis* population and with other leporid diet studies (López-Cortés et al. 2007; Karmiris and Nastis 2010; Kontsiotis et al. 2011; Ge et al. 2013; Freschi et al. 2014, 2015; Luna-Casanova et al. 2016). However, we found that some species of plants consumed by *L. flavigularis* in Santa María represent new records for

this leporid. The Poaceae preference of *B. taurus* is also consistent with previous studies in other localities (Quinteros et al. 2013).

These results are also related to the plant species availability. The study area is located in a low precipitation region from the Tehuantepec Isthmus, with severe drought from November to April. Despite the fact that grasses have low protein content in comparison to other species (Codron et al. 2007), and contain abrasive silica (Sanson et al. 2007), these species are more resistant to drought than ephemeral or annual forbs (Tilman and Downing 1994) which may cause that grass availability is high year-round. Also, Poaceae species distribute in open areas (Gordon and Prins 2008), which is one of the main characteristics of grassland habitat in the Tehuantepec Isthmus (Farias and Fuller 2009; Rioja et al. 2011). In agreement with these findings, it has been reported that *L. flavigularis* prefer grassland over other available habitats because, besides providing food, it represents a suitable place to carry out its activities of resting, socialization and reproduction (Farias and Fuller 2009; Rioja et al. 2011; Carrillo-Reyes et al. 2012; Lorenzo et al. 2015; Luna-Casanova et al. 2016).

Studies show the clear occurrence of trophic competition between leporids and other herbivores and ruminants such as cattle (Smith et al. 2004, Young et al. 2005), producing an adverse effect on leporid populations (Hulbert and Andersen 2001). In our study, *Lepus flavigularis* and *B. taurus* had a low trophic niche breadth and high dietary overlap, which indicates a high level of resource (trophic) competition that could adversely affect the *L. flavigularis* population. Other studies state that *L. flavigularis* prefers to establish feeding, resting, and breeding sites in pastures with the presence of *B. taurus* (Carrillo-Reyes et al. 2010, 2012; Rioja et al. 2011; Luna-Casanova et al. 2016). It is likely that the presence of *B. taurus* influence the existence of certain plant species that could serve as a forage resource for *L. flavigularis*, through the establishment of seedlings from *B. taurus* feces (Kuijper et al. 2008). Furthermore, *B. taurus* grazing reduce height, cover, and density of vegetation (Smith et al. 2005; Karmiris

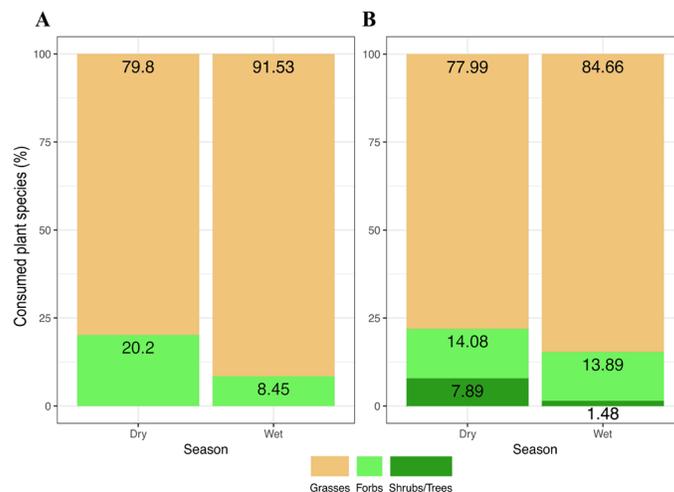


Figure 3. Percentage of consumed plant species (%) by growth form and by season in Santa María del Mar, Oaxaca, México. A: *L. flavigularis*, B: Cattle.

and Nastis 2010; Rioja *et al.* 2011). As Farías and Fuller (2009) stated, open grasslands with scattered trees and shrubs can help *L. flavigularis* to avoid predators like *Canis latrans*. Therefore, selection of areas with low vegetation cover may reduce the energy spent in monitoring its habitat, which favors the investment of more time in foraging (Karmiris and Nastis 2010; Rioja *et al.* 2011; Luna-Casanova *et al.* 2016). According to previous literature, we expect that jackrabbits benefit from cattle presence, as long as the stocking rate does not increase current levels. Research suggests that dietary partition between grazing herbivores is a common phenomenon and that leporids and cattle can coexist and obtain mutual benefits while not exceeding grazing capacity (Karmiris *et al.* 2005; Karmiris and Nastis 2010). Over long periods, livestock can even improve forage quality and foraging efficiency, facilitating food availability for leporids (Kuijper *et al.* 2008; du Toit 2011).

Low trophic niche breadth and high dietary overlap between *L. flavigularis* and *B. taurus*, combined with a low seasonal relationship between food availability and diet, suggest that forage resources competition is occurring in this system. Exotic species such as *S. eminens* and *D. ciliaris*, and a native species such as *B. repens*, were highly consumed by both species throughout the year. It is likely that these plant species remain permanently available to both herbivores, either as fresh or dry forage, due to its high silica content and their ability to survive in areas with low water content. On the other hand, certain species were consumed in a certain season by some species. For example, *C. articulatus* and *C. erecta* were consumed by *L. flavigularis* mainly during the dry season, while species *S. halepense* was consumed during the wet season. We believe that the mobility capacity of the species partly determined these differences. Cattle are restricted to using the resources available in the pastures and roads in which they are kept, while the hare can use almost the entire available area. Hence, it also has permanent or temporal access to all available plant species.

In conclusion, our results show trophic competition between native and no-native herbivorous species. However, we suggest that both species can coexist as long as the site's carrying capacity is not exceeded. On the one hand, although both species feed mainly on grasses, these plant species are the ones that persist throughout the year, even in drought conditions. Additionally, cattle have limited movement to pastures, while *L. flavigularis* can move freely throughout its range. Also, cattle grazing reduces vegetation's height, cover, and density, facilitating *L. flavigularis* to avoid potential predators. Overall, cattle management at moderate stocking densities, can be compatible with the subsistence of *L. flavigularis* populations.

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Literature cited

- BAUER, D. F. 1972. Constructing Confidence Sets Using Rank Statistics. *Journal of the American Statistical Association* 67:687–690.
- BERTOLINO, S., N. C. DI MONTEZEMOLO, AND B. BASSANO. 2009. Food–niche relationships within a guild of alpine ungulates including an introduced species. *Journal of Zoology* 277:63–69.
- BOCK, C. E., Z. F. JONES, AND J. H. BOCK. 2006. Abundance of Cottontails (*Sylvilagus*) in an Exurbanizing Southwestern Savanna. *The Southwestern Naturalist* 51:352–357.
- BONINO, N. 2006. Interacción trófica entre el conejo silvestre europeo y el ganado doméstico en el noroeste de la Patagonia Argentina. *Ecología Austral* 16:135–142.
- BONINO, N. A. 2011. Financial impact of exotic wild rabbits on livestock production in northwestern Patagonia, Argentina. 2nd World Conference on Biological Invasions and Ecosystem Functioning. Buenos Aires, Argentina.
- CARRILLO-REYES, A., *ET AL.* 2010. Home range dynamics of the Tehuantepec Jackrabbit in Oaxaca, Mexico. *Revista Mexicana de Biodiversidad* 81:143–151.
- CARRILLO-REYES, A., *ET AL.* 2012. Uso de hábitat de la liebre en peligro de extinción, *Lepus flavigularis*: implicaciones para su conservación. *Therya* 3:113–125.
- CHACÓN-TRINIDAD, F., *ET AL.* 2020. Ganado bovino en el hábitat de *Lepus flavigularis* (Wagner, 1844): ¿una relación de competencia? *Árido-Ciencia* 5:3–13.
- CODRON, D., *ET AL.* 2007. Nutritional content of savanna plant foods: implications for browser/grazer models of ungulate diversification. *European Journal of Wildlife Research* 53:100–111.
- CORTÉS-MARCIAL, M., Y. M. M. AYÓN, AND M. BRIONES-SALAS. 2014. Diversity of large and medium mammals in Juchitan, Isthmus of Tehuantepec, Oaxaca, Mexico. *Animal Biodiversity and Conservation* 37:1–12.
- DANIEL, A., *ET AL.* 1993. Range condition influences on Chihuahuan desert cattle and jackrabbit diets. *Journal of Range Management* 46:296–301.
- DESBIEZ, A. L. J., *ET AL.* 2009. Niche Partitioning Among White-Lipped Peccaries (*Tayassu pecari*), Collared Peccaries (*Pecari tajacu*), and Feral Pigs (*Sus scrofa*). *Journal of Mammalogy* 90:119–128.
- DU TOIT, J. T. 2011. Coexisting with cattle. *Science* 333:1710–1711.
- FARIAS, V., AND T. FULLER. 2009. Native vegetation structure and persistence of endangered Tehuantepec jackrabbits in a neotropical savanna in Oaxaca, México. *Biodiversity and Conservation* 18:1963–1978.
- FRACKER, S. B., AND H. A. BRISCHLE. 1944. Measuring the local distribution of ribes. *Ecology* 25:283–303.
- FRANCO-LÓPEZ, J., G. *ET AL.* 1989. Manual de ecología. Trillas. Ciudad de México, México.
- FRESCHI, P., *ET AL.* 2014. Diet of the Apennine hare in a southern Italy Regional Park. *European Journal of Wildlife Research* 60:423–430.
- FRESCHI, P., *ET AL.* 2015. Diet of the Italian hare (*Lepus corsicanus*) in a semi-natural landscape of southern Italy. *Mammalia* 79:51–59.

- GAHR, M. L. 1993. Natural history, burrow habitat and use, and home range of the pygmy rabbit (*Brachylagus idahoensis*) of Sagebrush Flat, Washington. M. Sc thesis. University of Washington. Washington, U. S. A.
- GARCÍA, E., AND COMISIÓN NACIONAL PARA EL CONOCIMIENTO Y USO DE LA BIODIVERSIDAD. 1998. Climas (Clasificación de Köppen, modificado por García). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. Ciudad de México, México.
- GE, D., ET AL. 2013. Evolutionary History of Lagomorphs in Response to Global Environmental Change. *Plos One* 8:e59668.
- GORDON, I. J., AND H. H. T. PRINS (EDS.). 2008. *The Ecology of Browsing and Grazing*. Springer Berlin Heidelberg. Berlin, Germany.
- GOTELLI, N. J., E. M. HART, AND A. M. ELLISON. 2015. EcoSimR: Null model analysis for ecological data R package v.0.1.0.
- HULBERT, I. A., AND R. ANDERSEN. 2001. Food competition between a large ruminant and a small hindgut fermentor: the case of the roe deer and mountain hare. *Oecologia* 128:499–508.
- IUCN. 2022. The IUCN Red List of Threatened Species. Version 2021.3. www.iucnredlist.org. Accessed May 2, 2022.
- KARMIRIS, I. E., Z. KOUKOURA, AND G. CHRISTODOULOU. 2005. Use of alpine ranges by brown hare (*Lepus europaeus*) and livestock in central Greece. Competition or facilitation? Proceedings of the XXVIIIth congress of the International Union of Game Biologists. Hannover, Germany.
- KARMIRIS, I. E., AND A. S. NASTIS. 2010. Diet overlap between small ruminants and the European hare in a Mediterranean shrubland. *Central European Journal of Biology* 5:729–737.
- KONTSIOTIS, V. J., A. CH. TSIOMPANOU, AND D. E. BAKALOU, D. E. 2011. The influence of habitat structure on the European brown hare *Lepus europaeus* food habits in mountainous areas of northern Greece. *Mammalia* 75:389–394.
- KUFNER, M. B., ET AL. 2008. Is the native deer *Mazama gouazoubira* threatened by competition for food with the exotic hare *Lepus europaeus* in the degraded Chaco in Córdoba, Argentina? *Journal of Arid Environments* 72:2159–2167.
- KUIJPER, D. P. J., ET AL. 2008. Time-scale effects in the interaction between a large and a small herbivore. *Basic and Applied Ecology* 9:126–134.
- LEVINS, R. 1968. *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton University Press. Princeton, U.S.A.
- LÓPEZ-CORTÉS, F., ET AL. 2007. Dietas de *Abrothrix andinus*, *Phyllotis xanthopygus* (Rodentia) y *Lepus europaeus* (Lagomorpha) en un ambiente altoandino de Chile. *Revista chilena de historia natural* 80:3–12.
- LORENZO, C., ET AL. 2011. Diet of the endangered Tehuantepec jackrabbit, *Lepus flavigularis*. *Therya* 2:67–76.
- LORENZO, C. M., T. M. RIOJA-PARADELA, AND A. CARRILLO-REYES. 2015. State of knowledge and conservation of endangered and critically endangered lagomorphs worldwide. *Therya* 6:11–30.
- LORENZO, C., ET AL. 2018. *Lepus flavigularis* Wagner, 1844. Pp. 191–193, in *Lagomorphs: Pikas, Rabbits, and Hares of the World* (Smith, A. T., C. H. Johnston, P. C. Alves, and K. Hackländer, eds.). Johns Hopkins University Press. Baltimore, U.S.A.
- LUNA-CASANOVA, A., ET AL. 2016. Endangered jackrabbit *Lepus flavigularis* prefers to establish its feeding and resting sites on pasture with cattle presence. *Therya* 7:277–284.
- MISHRA, C., ET AL. 2004. Competition between domestic livestock and wild bharal *Pseudois nayaur* in the Indian Trans-Himalaya. *Journal of Applied Ecology* 41:344–354.
- MORGIA, V. L., AND B. BASSANO. 2009. Feeding habits, forage selection, and diet overlap in Alpine chamois (*Rupicapra rupicapra* L.) and domestic sheep. *Ecology Research* 24:1043–1050.
- NORBURY, G. L., AND G. D. SANSON. 1992. Problems with measuring diet selection of terrestrial, mammalian herbivores. *Australian Journal of Ecology* 17:1–7.
- PEÑA-NEIRA, J. M. 1980. Similaridad de la dieta del ganado vacuno con las dietas de la liebre y el conejo de la zona central de Chihuahua. INIP-SARH. Chihuahua, México.
- PEÑA-NEIRA, J. M., AND R. HABIB-DE PEÑA. 1980. La técnica microhistológica. Un método para determinar la composición botánica de la dieta de herbívoros. Instituto Nacional de Investigaciones Pecuarias - Departamento de Manejo de Pastizales. Ciudad de México, México.
- PIANKA, E. R. 1975. Niche relations of desert lizards. Pp. 292–314, in *Ecology and Evolution of Communities* (M. Cody, and J. Diamond, eds.). Harvard University Press. Cambridge, U.S.A.
- PREVEDELLO, J. A., ET AL. 2013. Population responses of small mammals to food supply and predators: a global meta-analysis. *Journal of Animal Ecology* 82:927–936.
- QUINTEROS, C. P., ET AL. 2013. Dieta de verano de bovinos pastoreando en bosques de lenga (*Nothofagus pumilio*) y mallines de Chubut, Argentina. *Revista de la Facultad de Ciencias Agrarias* 45:285–292.
- R CORE TEAM. 2020. R: A Language and Environment for Statistical Computing v.3.6.3. R Foundation for Statistical Computing. Vienna, Austria.
- RIOJA, T., ET AL. 2011. Breeding and parental care in the endangered Tehuantepec jackrabbit (*Lepus flavigularis*). *Western North American Naturalist* 71:56–66.
- RIOJA-PARADELA, T., A. CARRILLO-REYES, AND C. LORENZO. 2012. Análisis de población viable para determinar el riesgo de extinción de la liebre de Tehuantepec (*Lepus flavigularis*) en Santa María del Mar, Oaxaca. *Therya* 3:137–150.
- RIOJA-PARADELA, T. M. 2008. Comportamiento reproductivo de la liebre de Tehuantepec (*Lepus flavigularis*) en su hábitat. Ph. D. thesis. El Colegio de la Frontera Sur, San Cristóbal de las Casas, México.
- RIO-OLAGUE, F. 1999. *Fundamentos y técnicas para medir vegetación*. Universidad Juárez del Estado de Durango. Gómez Palacio, México.
- RSTUDIO TEAM. 2020. RStudio: Integrated Development Environment for R v.1.3.1073.
- SANSON, G. D., S. A. KERR, AND K. A. GROSS. 2007. Do silica phytoliths really wear mammalian teeth? *Journal of Archaeological Science* 34:526–531.
- SEMARNAT. 2010. Norma Oficial Mexicana NOM-059-SEMARNAT-2010. Protección ambiental-especies nativas de México de flora y fauna silvestres-categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo. México. December 30, 2010.
- SMITH, R. K., ET AL. 2004. Conservation of European hares (*Lepus europaeus*) in Britain: Is increasing habitat heterogeneity in farmland the answer? *Journal of Applied Ecology* 41:1092–1102.
- SMITH, R. K., ET AL. 2005. Vegetation quality and habitat selection by European hares *Lepus europaeus* in a pastoral landscape. *Acta Theriologica* 50:391–404.
- TILMAN, D., AND J. A. DOWNING. 1994. Biodiversity and Stability in Grasslands. *Nature* 367:363–365.

- TIRADO, C., ET AL. 2012. Trophic preferences in an assemblage of mammal herbivores from Andean Puna (Northern Chile). *Journal of Arid Environments* 79:8–12.
- VARGAS, J. 2000. Distribución, abundancia y hábitat de la liebre endémica *Lepus flavigularis* (Mammalia: Lagomorpha). M. Sc thesis. Universidad Nacional Autónoma de México. Ciudad de México, México.
- VAVREK, M. J. 2011. Fossil: palaeoecological and palaeogeographical analysis tools. *Palaeontologia Electronica* 14:1T.
- YOUNG, T. P., T. M. PALMER, AND M. E. GADD. 2005. Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. *Biological Conservation* 122:351–359.
- ZHANG, J. 2013. spaa: SPecies Association Analysis R package v.0.2.1.

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