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Diet diversity of four herbivores in Coahuila, Mexico

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Understanding the annual and seasonal composition of herbivore diets is essential for effective population management and habitat conservation. This study aimed to evaluate the annual and seasonal dietary composition and diversity of four wild herbivores in a desert scrubland of Coahuila, Mexico, during the dry season (October 2018 and February 2019) and the wet season (May and August 2019). The research was conducted at the Rancho San Juan Wildlife Management Unit (UMA) using captive populations of desert bighorn sheep (*Ovis canadensis mexicana*), aoudad (*Ammotragus lervia*), white-tailed deer (*Odocoileus virginianus texanus*), and mule deer (*O. hemionus*). A total of 280 fecal group samples per species (140 per season) were collected and analyzed using microhistological techniques. Dietary diversity was estimated using Hill numbers by season. Differences in dietary composition were assessed with the Kruskal–Wallis test and principal component analysis. Aoudad exhibited the highest dietary diversity (64 species), followed by desert bighorn sheep (50), white-tailed deer (49), and mule deer (43). Shrub species predominated in all diets. No significant differences were detected between seasons, although grouping patterns were observed in plant occurrence frequencies. Principal component analysis indicated that 55% of the consumed plant species constituted the common dietary base of the four herbivores. White-tailed deer and mule deer, as browsing ruminants, showed greater selectivity for shrubs, while mule deer stood out for including lechuguilla (*Agave lechuguilla*), a dominant species in the rosetophyllous desert scrub. These findings underscore the importance of incorporating dietary diversity into wildlife management strategies and highlight the need for long-term studies to better understand patterns of plant resource use in arid ecosystems.

Key words: *Acacia rigidula,* agaves, management, microphyllous desert scrub, rosetophyllous desert scrub, *Opuntia engelmannii.*

Comprender la composición anual y estacional de las dietas de los herbívoros es esencial para una gestión efectiva de las poblaciones y la conservación del hábitat. El objetivo de este estudio fue evaluar la composición y diversidad dietaria anual y estacional de cuatro herbívoros silvestres en un matorral desértico de Coahuila, México, durante la estación seca (octubre de 2018 y febrero de 2019) y la estación húmeda (mayo y agosto de 2019). La investigación se llevó a cabo en la Unidad de Manejo para la Conservación de la Vida Silvestre (UMA) Rancho San Juan, utilizando poblaciones en cautiverio de borrego cimarrón del desierto (*Ovis canadensis mexicana*), arruí (*Ammotragus lervia*), venado cola blanca (*Odocoileus virginianus texanus*) y venado bura (*O. hemionus*). Se recolectaron y analizaron un total de 280 muestras de grupos fecales por especie (140 por estación) mediante técnicas microhistológicas. La diversidad dietaria se estimó por estación utilizando los números de Hill. Las diferencias en la composición de la dieta se evaluaron mediante la prueba de Kruskal–Wallis y un análisis de componentes principales. El arruí presentó la mayor diversidad dietaria (64 especies), seguido por el borrego cimarrón del desierto (50), el venado cola blanca (49) y el venado bura (43). Las especies arbustivas predominaron en todas las dietas. No se detectaron diferencias significativas entre estaciones, aunque se observaron patrones de agrupamiento en las frecuencias de ocurrencia de las plantas. El análisis de componentes principales indicó que el 55 % de las especies vegetales consumidas constituyeron la base alimentaria común de los cuatro herbívoros. El venado cola blanca y el venado bura, como rumiantes ramoneadores, mostraron una mayor selectividad por los arbustos, mientras que el venado bura destacó por incluir la lechuguilla (*Agave lechuguilla*), una especie dominante en el matorral desértico rosetófilo. Estos hallazgos subrayan la importancia de incorporar la diversidad dietaria en las estrategias de manejo de vida silvestre y resaltan la necesidad de realizar estudios a largo plazo para comprender mejor los patrones de uso de los recursos vegetales en los ecosistemas áridos.

Palabras clave: *Acacia rigidula,* agaves, manejo, matorral desértico micrófilo, matorral desértico rosetófilo, *Opuntia engelmannii.*

Coahuila, Mexico, is home to native species of large herbivores, which play a central role in the nutrient dynamics of ecosystems by participating in plant phenology through herbivory, contributing to soil compaction and nutrient supply (Gastelum-Mendoza *et al.* 2019), and constituting a source of food for natural predators (Rosas-Rosas *et al.* 2003). The white-tailed deer (*Odocoileus virginianus texanus*) is one of the 14 subspecies recorded in Mexico, distributed throughout the country, except for the Baja California peninsula (Mandujano *et al.* 2010; De la Rosa-Reyna *et al.* 2012). This species is mainly associated with the desert shrublands of northeastern Mexico and the southern United States of America; it represents an alternative for the development of the rural economy and livestock production through sustainable hunting (Valdez *et al.* 2006; Lozano-Cavazos *et al.* 2020).

Similarly, the mule deer (*Odocoileus hemionus eremicus*), whose distribution area in Mexico mainly includes the Sonoran Desert, is a species adapted to arid environments in northern Mexico, thriving in desert shrublands and mountain ranges (Weber and Gonzalez 2003). This subspecies plays an important ecological role as a browser, influencing the structure and composition of vegetation (Krausman *et al.* 1999). In addition, its hunting value has supported its inclusion in intensive management programs in Coahuila (Velázquez *et al.* 2010), and its adaptation to desert shrublands in northeast Mexico is considered viable due to the similarity in habitat conditions (Olivas-Sánchez *et al.* 2018b).

Additionally, some mountain ranges in Coahuila were part of the natural distribution of bighorn sheep (*Ovis canadensis*) until the mid-nineteenth century, when their populations were extirpated from northeastern Mexico by poaching and disease transmission from domestic livestock (O'Farrill *et al.* 2019). In this regard, the Mexican Official Standard NOM-059-SEMARNAT-2010 has listed *O. canadensis* as Special Protection (Pr; DOF 2019), and reintroduction programs have been promoted in regions such as the Sierra Maderas del Carmen and private land in the state of Coahuila (Espinosa and Contreras-Balderas 2010). However, the presence and rapid expansion of Barbary sheep (*Ammotragus lervia*), an exotic bovine native to North Africa, represents a threat to wildlife diversity in northern Mexico, as it competes directly for food and space with the species mentioned above, in addition to being a carrier and vector of parasites and diseases (Ben Mimoun and Nouira 2013; 2015; Gastelum-Mendoza *et al.* 2023).

Managing these herbivores requires knowledge about the plant species that are consumed as food (Gastelum-Mendoza *et al.* 2019), as it provides key information on herbivory pressure, which can adversely affect the dispersal and diversity of plant species, in addition to being useful for estimating carrying capacity (Serna-Lagunes *et al.* 2024), assessing the nutritional status of populations, and establishing priority areas for conservation (Saucedo-Uuh *et al.* 2024). In this regard, several studies in Mexico and the United States indicate that the white-tailed deer is a selective browser, feeding preferentially on twigs of shrubs and some herbaceous plants (Fulbright and Ortega-Santos 2007; Lozano-Cavazos *et al.* 2020). In contrast, mule deer show a greater capacity to adapt to changes in habitat conditions, modifying their diet according to seasonal forage availability (Olivas-Sánchez *et al.* 2018b). On the other hand, studies on bighorn sheep and Barbary sheep have documented that both species have opportunistic feeding habits (Ben Mimoun and Nouira 2015; Gastelum-Mendoza *et al.* 2021). In addition, habitat factors, such as topography and escape vegetation cover, are key drivers of their distribution and population development. Information available on the diet of exotic species of herbivores in Mexico is currently scarce (Olguín-Hernández *et al.* 2017).

Therefore, the objective of this study was to identify and compare the composition and diversity of the seasonal diet of bighorn sheep, Barbary sheep, white-tailed deer, and mule deer in north Coahuila. The results obtained are relevant to identifying potential areas for the reintroduction and management of these species in desert scrub ecosystems in northeastern Mexico.

Materials and methods

Description of the study area. The study was carried out at the *Rancho San Juan* Unit for Wildlife Conservation, Management, and Sustainable Use (*Unidad para la Conservación, Manejo y Aprovechamiento Sustentable de la Vida Silvestre*; UMA, in Spanish) (26°49'31.11" N, 101°01'57.77" W), located in the municipality of Monclova, state of Coahuila de Zaragoza, Mexico (Figure 1). Rancho San Juan includes four areas dedicated to intensive wildlife management. The first, with an area of 450 ha, is home to 70 bighorn sheep from Tiburón Island, Sonora. The second area, comprising 1020 ha, is dedicated to the management of 550 Texas white-tailed deer; the third, with an extension of 200 ha, is intended for the conservation of 20 mule deer from the state of Sonora. Additionally, Sierra Las Hormigas, a mountainous area of 1200 ha, is used to manage approximately 120 Barbary sheep in confinement. These four populations are isolated from each other. In addition, in the intensive management units for white-tailed deer, mule deer, and bighorn sheep, alfalfa food supplementation is carried out during the driest months of the year (July and August) to mitigate the effects of natural forage shortages.

In the areas of intensive management of the two deer species, microphyllous desert shrubland predominates, characterized by shrubs of the genus *Acacia* and cacti of the genus *Opuntia*, as well as extensive areas of open grasslands. In these areas, 46 species of plants have been reported, some of which have high forage value, such as *Acacia berlandieri* and *A. rigidula*, as well as others that provide thermal protection for cervids, such as *Cenchrus ciliaris* and *Yucca filifera* (Gastelum-Mendoza *et al.* 2020). On the other hand, the management areas of the two species of bovids show the dominance of rosetophyllous desert shrublands,

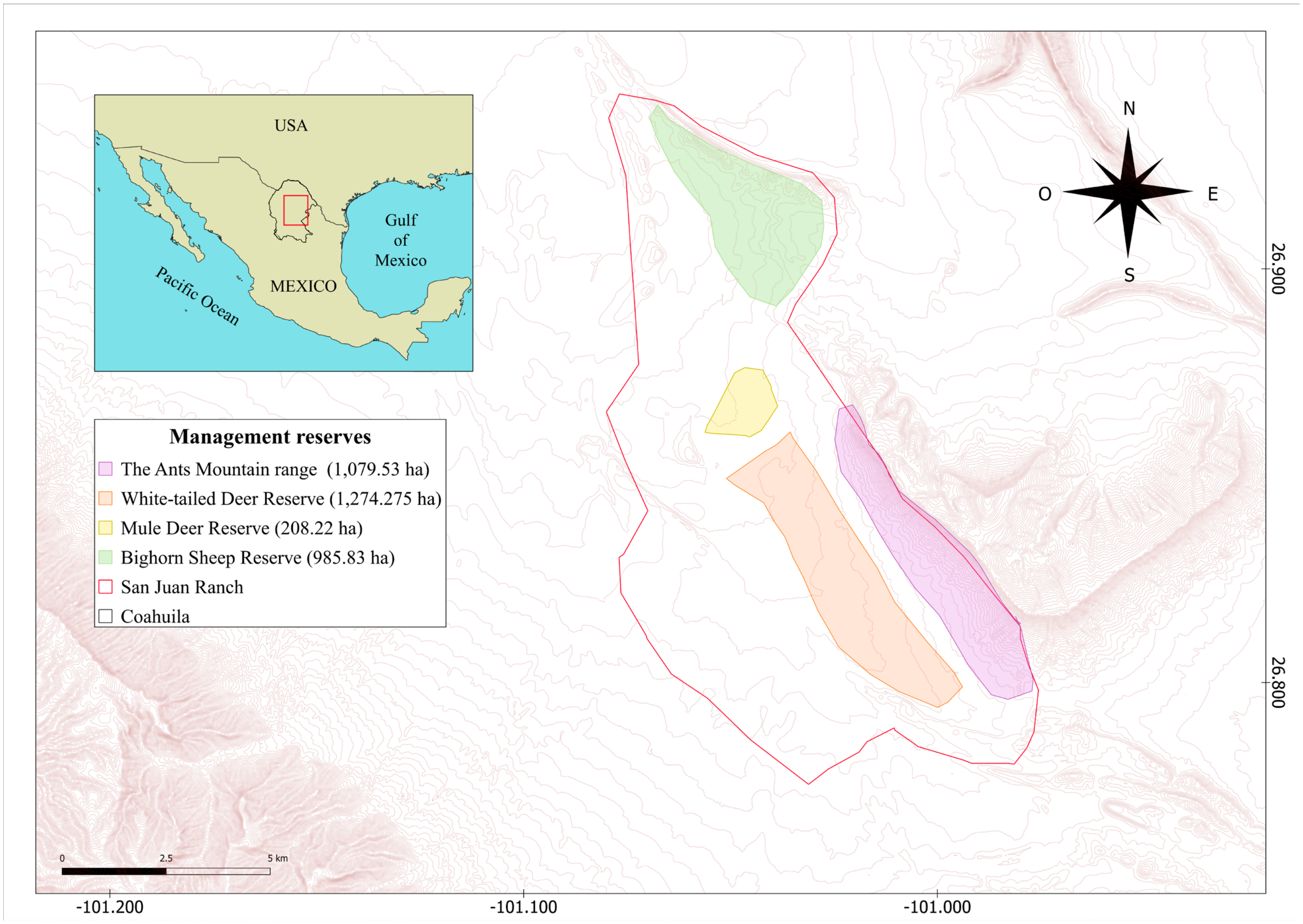


Figure 1. Location and delimitation of reserves for the management of wild herbivores in Rancho San Juan UMA, Coahuila, Mexico.

with low shrubs and abundant succulent species such as *lechuguilla* (*Agave lechuguilla*), *guapilla* (*Hechtia glomerata*), and *candelilla* (*Euphorbia antisyphilitica*; Miranda and Hernández 1963; Gastelum-Mendoza *et al.* 2019).

The local climate is semi-arid (BS), with a mean annual temperature of 21 °C, which can exceed 40 °C in summer and drop below 0 °C in winter. Annual precipitation ranges between 200 mm and 900 mm (García 1988).

Analysis of the composition and diversity of diets. The plant species that make up the annual and seasonal diet of bighorn sheep, Barbary sheep, white-tailed deer, and mule deer were identified using the microhistological technique. This methodology allows the identification and quantification of plant epidermal structures in fresh feces through microscopic analysis (Peña and Habib 1980). To this end, fresh feces from the four herbivore species studied were collected during the dry season (October 2018 and February 2019) and the wet season (May and August 2019). The samples were placed in paper bags, labeled, and transferred to the Wildlife Laboratory of the Faculty of Forestry Sciences of the Autonomous University of Nuevo León, Nuevo León, Mexico. These samples were dried in a 120 VAC, 60 Hz stainless steel oven at 75 °C for 48 hours. Once dried, the samples were sorted by time of year and ground in a Wiley mill using a No. 10 sieve (1.70 mm mesh opening). A composite sample was obtained from each seasonal group, clarified with sodium hypochlorite, and fixed on slides following the protocol described by Peña and Habib (1980). A total of 80 slides were mounted (10 per season for each species), and 800 microscope fields (10 per slide) were analyzed using an OMAX M82ES 40X–2000X® microscope with a 10X objective and a 10X ocular lens.

To identify and quantify plant cell fragments in fecal samples, a reference catalog was prepared consisting of photomicrographs of characteristic epidermal structures — trichomes, stomata, silica cells, and crystals, among others — corresponding to 141 plant species present in the study area. These were classified according to their biological form (shrub, herbaceous, grass, and succulent) and by family and species. The plant samples underwent the same drying, rinsing, and grinding procedures as fecal samples to ensure a comparison of the cell structures.

Numerical analysis. The diet composition of each herbivore species was determined by the frequency of each plant species in fecal samples, following the methodology of Fracker and Brischle (1944). The diversity of the diet for the four herbivore species was compared by estimating the true diversity profile based on Hill numbers (Hill 1973). This

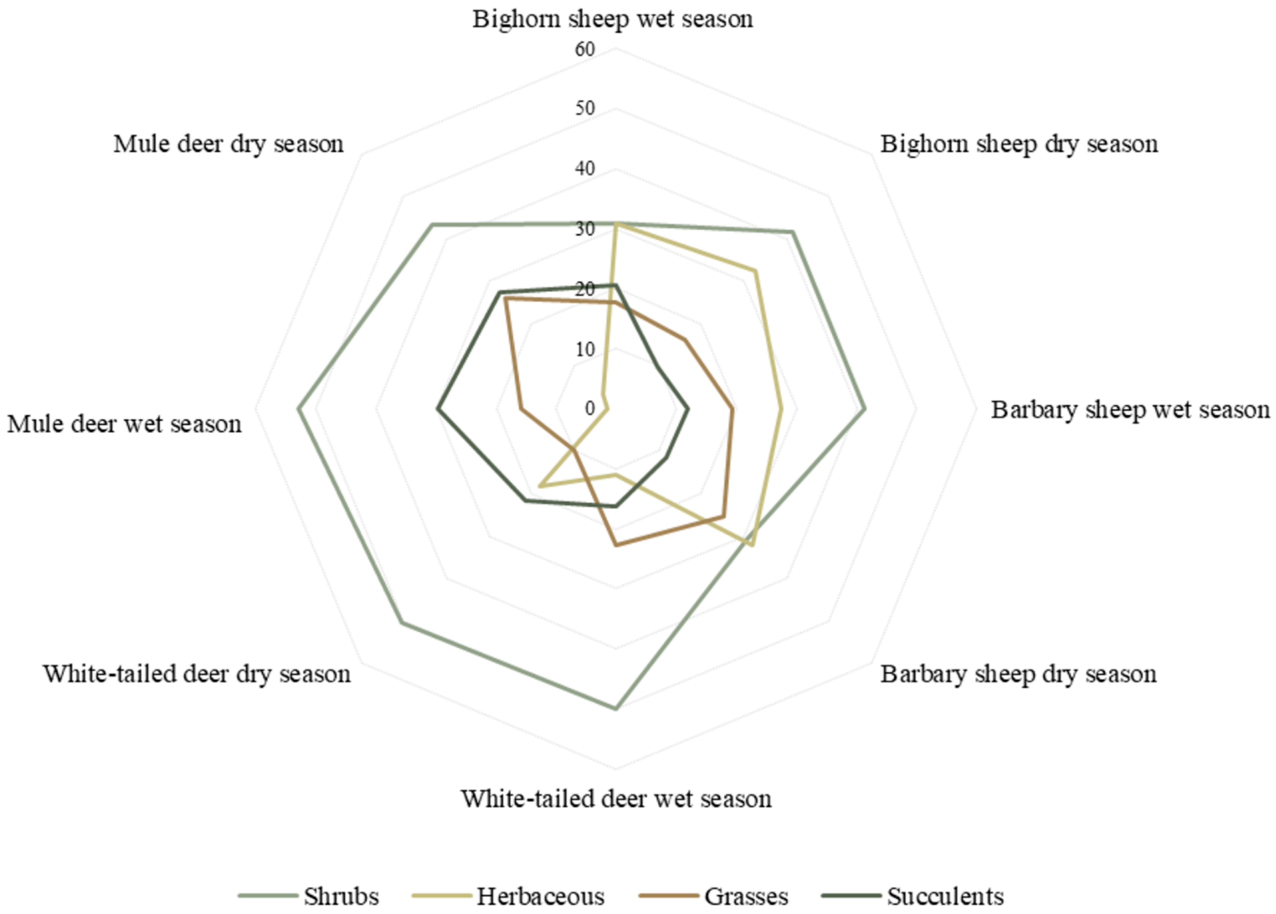


Figure 2. Variation in diet composition according to season, biological form of the forage consumed, and species of herbivores in Rancho San Juan UMA, Coahuila, Mexico (values expressed in relative frequency).

approach allows for the construction of diversity curves based on species richness and the presence/absence of the species recorded in the samplings. This analysis also yields sample coverage and sample size through inter- and extrapolations (along with 95% confidence intervals) calculated from 1000 bootstrap replicates, using the online platform of the iNEXT software (Chao *et al.* 2016). The comparison between species was performed considering the effective number of species for the orders q0 (species richness), q1 (exponential of the Shannon index), and q2 (inverse of the Simpson index) (Chao *et al.* 2014). Differences (α ≤ 0.05) between dietary diversity profiles were assumed when the confidence intervals did not overlap (Cumming *et al.* 2007).

Food similarity between the four species was evaluated by calculating the Jaccard and Sorensen indices (based on the presence or absence of plant the species consumed), as well as the Horn, Morisita-Horn, and Bray-Curtis indices (based on the relative abundance of the species consumed) (Chao *et al.* 2000; Pan *et al.* 2009) using the SpadeR software available online (Chao *et al.* 2015). In addition, the completeness of the sampling between species was compared using the sample coverage estimator, which indicates the degree of completeness of the dietary inventory. Coverage close to 100 % suggests that the sampling effort and technique were sufficient to adequately characterize the diet (Chao and Jost 2012), supporting valid comparisons between assemblages with a similar completeness level (Magurran and Henderson 2010).

Diets of the herbivore species were compared using an analysis based on frequency density (α ≤ 0.05). The similarity between diets was assessed using a cluster analysis, with Euclidean distance as a measure of similarity. Additionally,

Table 1. Diversity indicators according to Hill numbers for four species of herbivores living in Rancho San Juan UMA, Coahuila, Mexico.

Indicators	Bighorn sheep	Barbary sheep	White-tailed deer	Mule deer
Sample size	394	409	399	400
q0	50	64	49	43
q1	24	28	27	26
q2	14	17	19	20
Sample coverage	0.97	0.94	0.97	0.97
Percentage of sample coverage	97 %	94 %	97 %	97 %

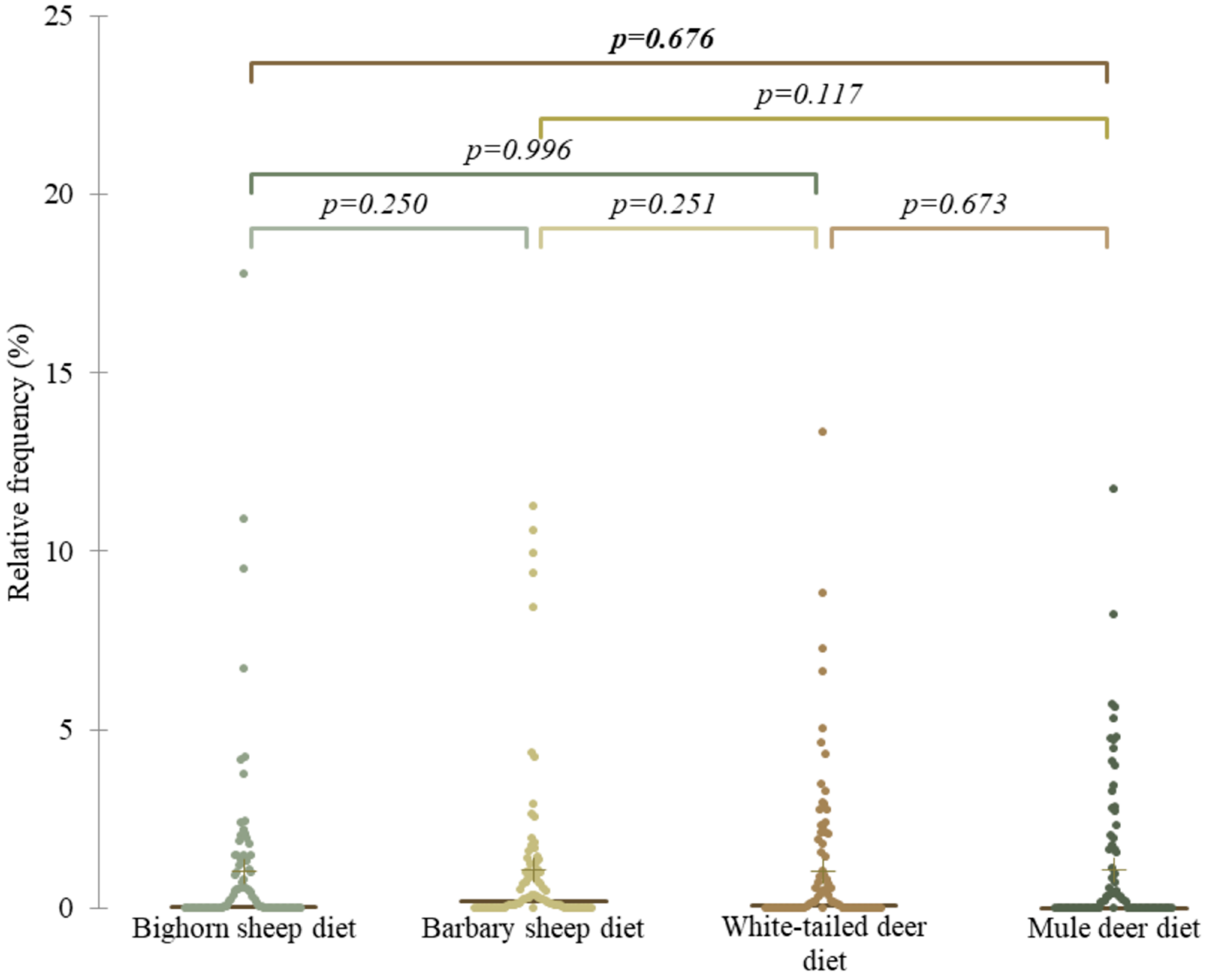


Figure 3. Comparison of the relative frequency of plant species in the diet of four wild herbivores living in Rancho San Juan UMA, Coahuila, Mexico, using the nonparametric Kruskal-Wallis test.

the proportion of consumed plant species shared by the four herbivore species was analyzed by applying the Whittaker index (α ≤ 0.05).

Likewise, nonparametric statistical tests were applied to evaluate differences in diet composition between species and times of the year. These included the Kruskal-Wallis test (α ≤ 0.05) and the paired Mann-Whitney test (α ≤ 0.05). A principal component analysis (PCA) was performed using the frequencies of consumption of plant species as independent variables and the diversity of plants consumed as dependent variables. This analysis allowed for the identification of correlations between variables through principal components, which were represented in a three-dimensional space (factorial planes). The percentages of variance explained by each principal component were calculated. The statistical analyses were performed in Past 3.0 and XLSTAT.

Results

Composition and diversity of diets. A total of 280 fecal samples were collected per species, evenly distributed between the two seasons of the year (140 per season). The sample coverage was greater than 90% for the four species of herbivores, which indicates a representative sample (Table 1). The richness of plant species varied between herbivore species, ranging from 43 to 64. The diet of the bighorn sheep included 50 plant species (q0): 28 shrubs, seven herbs, 11 grasses, and four succulents. Annually, the most consumed species were woody crinklemat (*Tiquilia canescens*; 17.75 %), Torrey's croton (*Croton torreyanus;* 10.89 %), and rabbit cactus (*Opuntia microdasys*; 9.51 %; Table 2). Regarding the seasonal contribution of biological forms in the diet of bighorn sheep, shrub species predominated throughout the year (Figure 2). No differences were found between the consumption of the different biological forms and the time of year (Figure 3). However, a higher consumption of shrubs and herbaceous plants was observed during the dry season (41.54 % and 32.59 %, respectively), while the consumption of grasses and succulents was higher in the wet season (17.74 % and 20.57 %, respectively; Figure 2).

Barbary sheep consumed 64 species (q0), including 34 shrubs, 12 herbs, 15 grasses, and three succulents. *Tiquilia canescens* (11.28 %), *chaparro prieto (Acacia rigidula*; 10.6 %), and desert prickly pear (*Opuntia engelmannii*; 9.96 %),

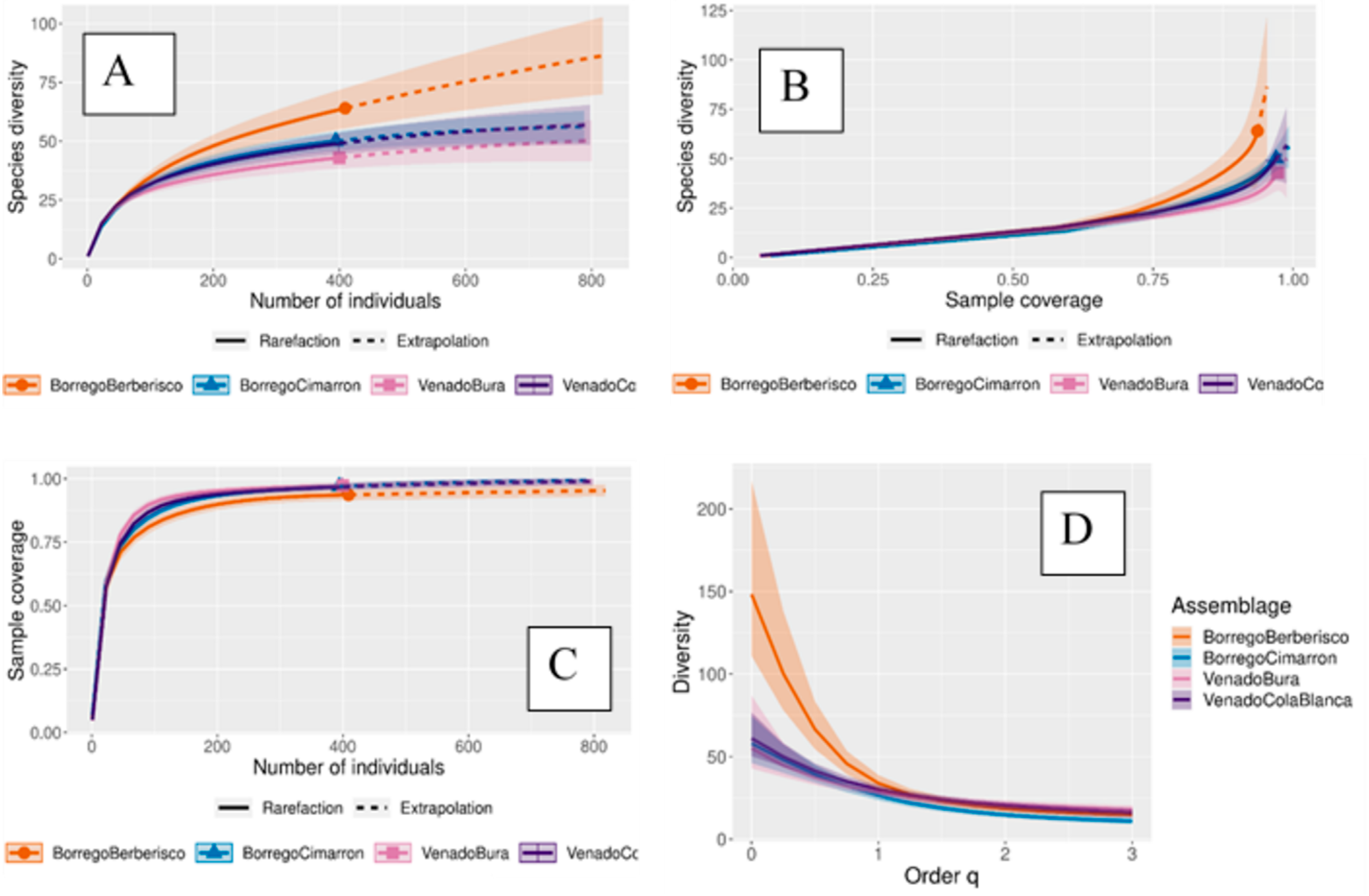
Table 2. Seasonal composition of the diet of bighorn sheep, Barbary sheep, white-tailed deer, and mule deer living in Rancho San Juan UMA, Coahuila, Mexico, expressed in percentage of the consumption values.

	Ovis canadensis mexicana		***Ammotrgus lervia***		***Odocoileus virginianus texanus***		***Odocoileus hemionus eremicus***	
Species	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**
Abutilon wrightii		4.16	1.03	1.47	1.96	1.64		
Acacia berlandieri		0.98	2.58		0.29		2.88	1.04
Acacia farnesiana	2.35	5.12	0.26	1.14	0.43	0.33		
Acacia rigidula	1.00		9.59	11.60	11.93	5.73	7.24	2.26
Acourtia runcinata			0.25		0.14			
Agave lechuguilla	0.62	0.44					12.65	10.81
Agave sp.							2.54	2.89
Allionia incarnata	1.86	0.53		0.22	0.99	4.85		
Aloysia macrostachya	0.13	2.80	2.96	0.37	1.41	0.44	2.16	1.35
Aloysia wrightii		1.06		0.15				
Ambrosia dumosa	0.66	1.33	0.13	2.01	0.14	4.11		
Aristida adscensionis	0.26	0.65	0.39	0.37	0.57	0.77		
Aristida adscensionis			1.35					0.63
Aristida purpurea	0.78	1.90	0.65	3.04	0.83	2.07		
Astrolepis integrifolia	2.71	0.88	4.87	0.22				
Baccharis glutinosa								0.81
Baccharis texana					1.11	0.65		
Bothriochloa laguroides								0.95
Bothriochloa saccharoides			0.62					
Bouteloua curtipendula			2.25	1.29		0.98	0.74	2.50
Bouteloua eriopoda	0.25	2.68	0.13	0.37				
Bouteloua gracilis			0.13				4.97	3.28
Bouteloua hirsuta	0.13	0.11	0.13	1.98	0.28	1.77		
Bouteloua sp.	0.74	1.41						
Calliandra sp.							3.26	
Casimiroa edulis			0.99					
Castela texana		0.33	0.13	0.44				0.91
Celtis pallida							0.73	0.72
Cenchrus ciliaris	3.60	4.88	2.58	6.12	3.80	2.10	2.93	8.48
Chamaecrista greggii		0.11	0.74					
Chilopsis linearis					0.42			
Cordia parvifolia	0.26	0.19	2.19	1.73				
Croton dioicus			3.07	2.23				
Croton pottsii				0.30				
Croton punctatus		0.10	0.65	1.10		4.66		
Croton sp.				0.15				
Croton torreyanus	9.22	12.57	0.90	4.94	0.99	7.60		
Cynodon dactylon	1.93	1.05						
Cynodon dactylon					0.42	0.34		
Dalea aurea	0.90	0.52	0.78	1.02				
Dalea bicolor	1.15	0.84		0.44	2.42	1.44		
Dalea greggii							1.11	
Diospyros texana					0.29		0.37	
Ephedra pedunculata					0.55	0.12	4.05	
Ephedra trifurca	0.99			0.59				
Erioneuron pulchellum	7.55	0.78	10.55	6.34	12.69	0.56		
Euphorbia antisyphilitica	0.50	1.31		1.10	2.22	4.71	4.33	1.35
Evolvulus alsinoides			5.22	3.22	0.57	0.44		
Eysenhardtia texana	3.47	0.95	0.65	0.77	7.99	6.55		

Ferocactus sp.							1.79	0.41
Flourensia cernua							4.85	4.07
Forestiera angustifolia	0.26	0.11	1.60	0.15	0.83	2.29	2.93	2.69
Gochnatia hypoleuca	0.50	1.06	3.20				0.35	0.32
Guaiacum angustifolium	1.18		1.39		5.15	0.33	4.00	3.99
Gymnosperma glutinosum	0.13			0.15		0.11		
Hechtia glomerata							1.08	0.63
Heteropogon contortus	0.89	1.94	0.52	2.39	3.84	0.34		
Hilaria mutica	0.63			0.30	0.29		4.26	5.35
Hymenoxys odorata			0.13	0.15	0.15	0.22		
Jatropha dioica					0.15		4.35	6.27
Karwinskia humboldtiana		1.09		0.11	0.15	0.12	3.63	1.04
Koeberlinia spinosa								0.50
Krameria erecta	0.13	0.95	0.13	0.15	1.00	0.11		
Lantana camara			0.13					0.32
Larrea tridentata	0.37	0.33	1.39	0.26	0.43	0.68		
Lesquerella fendleri			0.37					
Leucophyllum frutescens	1.85	1.93	2.59	0.15	1.25	3.52	1.82	1.28
Lippia graveolens	0.50			0.15	0.29		2.84	6.62
Medicago sativa	6.52	6.86	6.94	11.79	3.52	3.02		
Mimosa zygophylla	1.40	3.41	0.49	0.55	2.66	2.86		
Opuntia engelmannii	4.45	0.42	10.29	9.63	11.51	15.15	7.95	8.52
Opuntia leptocaulis	2.23	1.66	1.11	0.88	4.86	5.20	2.93	3.59
Opuntia microdasys	12.28	6.75	0.52	1.10		0.23	0.73	
Panicum hallii			0.13	2.68				
Parthenium argentatum			1.03	0.85	0.15		0.37	
Parthenium hysterophorus	0.89	2.08						1.89
Parthenium incanum	0.00		1.97					
Parthenium sp.					0.28	1.15		
Paspalum notatum							2.48	4.36
Phaulothamnus spinescens								0.63
Physaria fendleri				0.55		1.58		
Prosopis glandulosa	0.50	2.10			6.33	2.91	5.42	5.86
Salvia coccinea							0.36	
Setaria leucopila		0.11		0.44				
Sidneya tenuifolia	1.85	2.22						
Solanum elaeagnifolium		0.10		0.15	0.42	0.45		
Solanum nigrum			0.37	0.11				
Telosiphonia macrosiphon								0.81
Tiquilia canescens	18.45	17.05	9.93	12.63	1.15	3.11		
Tridens muticus				0.11				
Viguiera stenoloba			0.13					
Wedelia texana								0.63
Yucca filifera								0.32
Ziziphus obtusifolia					3.43	1.09		

were the most consumed species. In addition, Barbary sheep consumed mostly shrubs throughout the year (Table 2), although with a higher consumption in the wet season (41.2 %). Herbaceous plants and grasses were more common in the diet during the dry season (32.17 % and 25.39 %, respectively). Succulents were equally consumed in both seasons (Figure 2).

The diet of white-tailed deer consisted of 49 plant species (q0), including 27 shrubs, ten herbs, nine grasses, and three succulents. *Opuntia engelmanni* (13.33 %), *A. rigidula* (8.83 %), and Texas kidneywood (*Eysenhardtia texana*; 7.27 %) were the dominant plant species in the diet throughout the year (Table 2). Shrub species represented more than one-half of food consumption during the dry season (50.47 %). Also, herbs (18.16 %) and succulents (21.53 %) were consumed more commonly in the dry



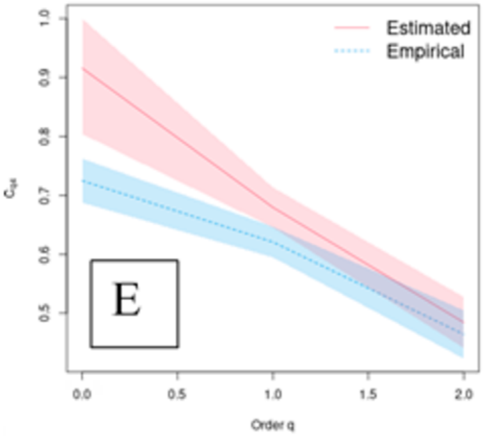


Figure 4. Analysis of the diversity of consumed species; A, Rarefaction curve and extrapolation for the comparison of dietary diversity; B, Rarefaction curve and extrapolation of the diversity of consumed species as a function of the sampling coverage; C, Rarefaction curve and extrapolation of the number of consumed species according to the sampling coverage; D, Comparison of the effective number of species of order q0 (analog of species richness), q1 (exponential of the Shannon index), and q2 (inverse of the Simpson index); E, group comparison of the diversity of plants consumed by four ungulates.

season, while grasses were consumed mainly during the wet season (22.7 %; Figure 2).

The diet of mule deer consisted of 43 plant species (q0), of which 25 were shrubs, four herbs, seven grasses, and seven succulents. The most representative plant species consumed all year round were *Agave lechuguilla* (11.73 %), *O. engelmannii* (8.23 %), and *Cenchrus ciliaris* (5.7 %; Table 2). The consumption of shrub species was predominant throughout the year, with a higher incidence during the wet season (52.83 %). Succulents also contributed significantly at this time of the year, accounting for 30 % of the diet. In contrast, grasses were consumed mainly during the dry season (26 %), while herbs made a low proportion of the diet throughout the year (Figure 2).

According to the true diversity profile based on Hill numbers, Barbary sheep showed a higher diversity of species consumed compared to the other three herbivore species, which exhibited a relatively similar dietary composition (Table 1). Extrapolations suggest that, given the increased availability of plant species in the ecosystem, herbivores would be able to incorporate a diversity of plants proportional to that of the habitat (Figure 4). When comparing the diversity of the diet between the four species, we observed that the observed diversity exceeded the expected one (Figure 4E), with significant differences ($P \leq 0.05$) in the composition of the plants consumed. In particular, Barbary sheep showed the highest species richness in their diet (q0). However, in terms of the number of common species (q1) and the number of dominant species (q2) in the diet, no significant differences were observed between the species analyzed (Figure 4D).

Similarity of diet composition and diversity. According to the results of the Kruskal-Wallis test ($X^2 = 2.48$, $df = 3$, $P = 0.68$), no statistically significant differences were observed in the

Table 3. Significance values of the paired Mann-Whitney test (α ≤ 0.05) according to the diet composition of the herbivorous species and the seasons of the year.

Species – season of the year	Bighorn sheep – wet season	Bighorn sheep – dry season	Barbary sheep – wet season	Barbary sheep – dry season	White-tailed deer – wet season	White-tailed deer – dry season	Mule deer – wet season
Bighorn sheep – dry season	0.63						
Barbary sheep – wet season	0.36	0.61					
Barbary sheep – dry season	0.37	0.63	0.97				
White-tailed deer – wet season	0.73	0.89	0.61	0.55			
White-tailed deer – dry season	0.89	0.82	0.43	0.45	0.87		
Mule deer – wet season	0.6	0.36	0.15	0.14	0.36	0.48	
Mule deer – dry season	0.84	0.47	0.27	0.27	0.62	0.69	0.77

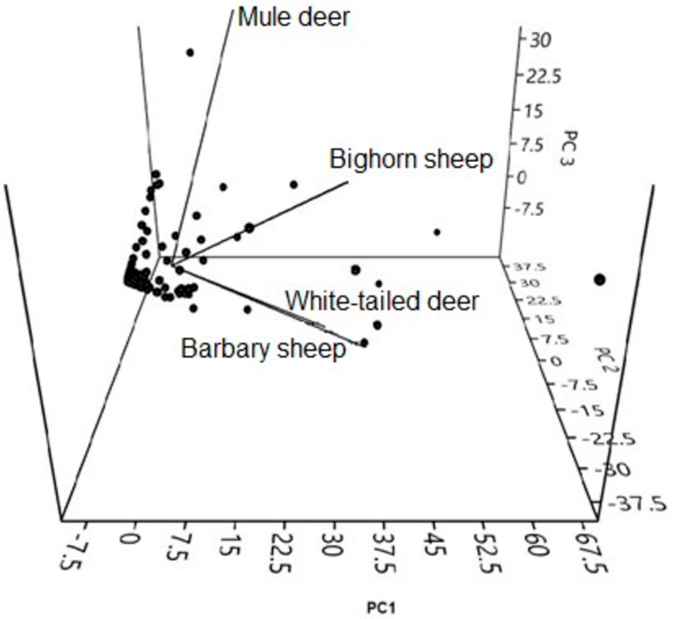


Figure 5. Dendrogram of dissimilarity in the seasonal diet composition of four wild herbivores at the Rancho San Juan UMA, Coahuila, Mexico.

annual diet composition between the herbivore species studied (Figure 3). Similarly, no significant differences were found in the consumption of the different biological forms of forage between seasons ($X^2 = 3.04$, $df = 7$, $P = 0.82$). Furthermore, the results of the Mann-Whitney paired test indicated that there are no differences in diet composition between herbivore species or between seasons of the year (Table 3). The cluster analysis indicated two groups based on the similarity of the diets (Figure 5). The first group included the seasonal diet composition of white-tailed deer, bighorn sheep, and Barbary sheep; the second included the diet of mule deer in both periods (Figure 6).

In the PCA (Figure 5), PC1 and PC2 explained 55.20 % and 25.5 % of the variance, respectively; together, the first two components accounted for 80 % of the variance. This variation is explained by the correlation between the diversity of plant species consumed by bighorn sheep and mule deer, which are associated with PC3. This position in the two-dimensional plane highlights the difference with the white-tailed deer and Barbary sheep, which correlate in PC2, suggesting the similarity in the diet of these two species.

The Whittaker comparison analysis (Table 4) indicated the proportion of plant species consumed by the four ungulates, with a greater similarity of species consumed between Barbary sheep and mule deer (61 %), mule deer and bighorn sheep (59 %), white-tailed deer and mule deer (57 %), and white-tailed deer, bighorn sheep, and Barbary sheep (29 %).

Table 4. Whittaker's comparison analysis to determine the plant species consumed by ungulates (proportion of species shared).

	Bighorn sheep	Barbary sheep	White-tailed deer	Mule deer
Bighorn sheep				
Barbary sheep	0.23			
White-tailed deer	0.29	0.29		
Mule deer	0.59	0.61	0.57	

Discussion

Smaller herbivores select a higher-quality diet due to their relatively high nutritional requirements (Ramírez *et al.* 1997). This preference is related to a distinctive characteristic of small ruminants classified as browsers, such as white-tailed deer and mule deer, which have morphological adaptations in the digestive tract that allow them to be more selective regarding the species and parts of plants they consume (Ramírez-Lozano 2004). In contrast, ruminants classified as grazers, such as bighorn sheep and Barbary sheep, have larger molars and digestive tracts, allowing them to digest a greater diversity of plant species more efficiently, especially grasses with a high fiber content and lower nutritional quality (Guerrero-Cárdenas *et al.* 2018). This explains why shrub browsing was the most important food component for white-tailed deer and mule deer, while the percentages of shrubs in the diet of the two bovid species were lower (Figure 2).

Each of the four herbivore species exhibits evolutionary adaptations that influence their patterns of food use and selection. For example, the habitat requirements of bighorn sheep are strongly conditioned by topography; this species depends on areas with canyons, steep slopes, and vegetation cover that facilitates the detection of predators (Tarango *et al.* 2002). This habitat component is even more relevant than food availability, as bighorn sheep are considered opportunistic foragers that can feed on a wide variety of plants (Gastelum-Mendoza *et al.* 2021; Méndez-Rosas *et al.* 2025). For its part, Barbary sheep, an exotic species in Mexico, shows a high plasticity in habitat

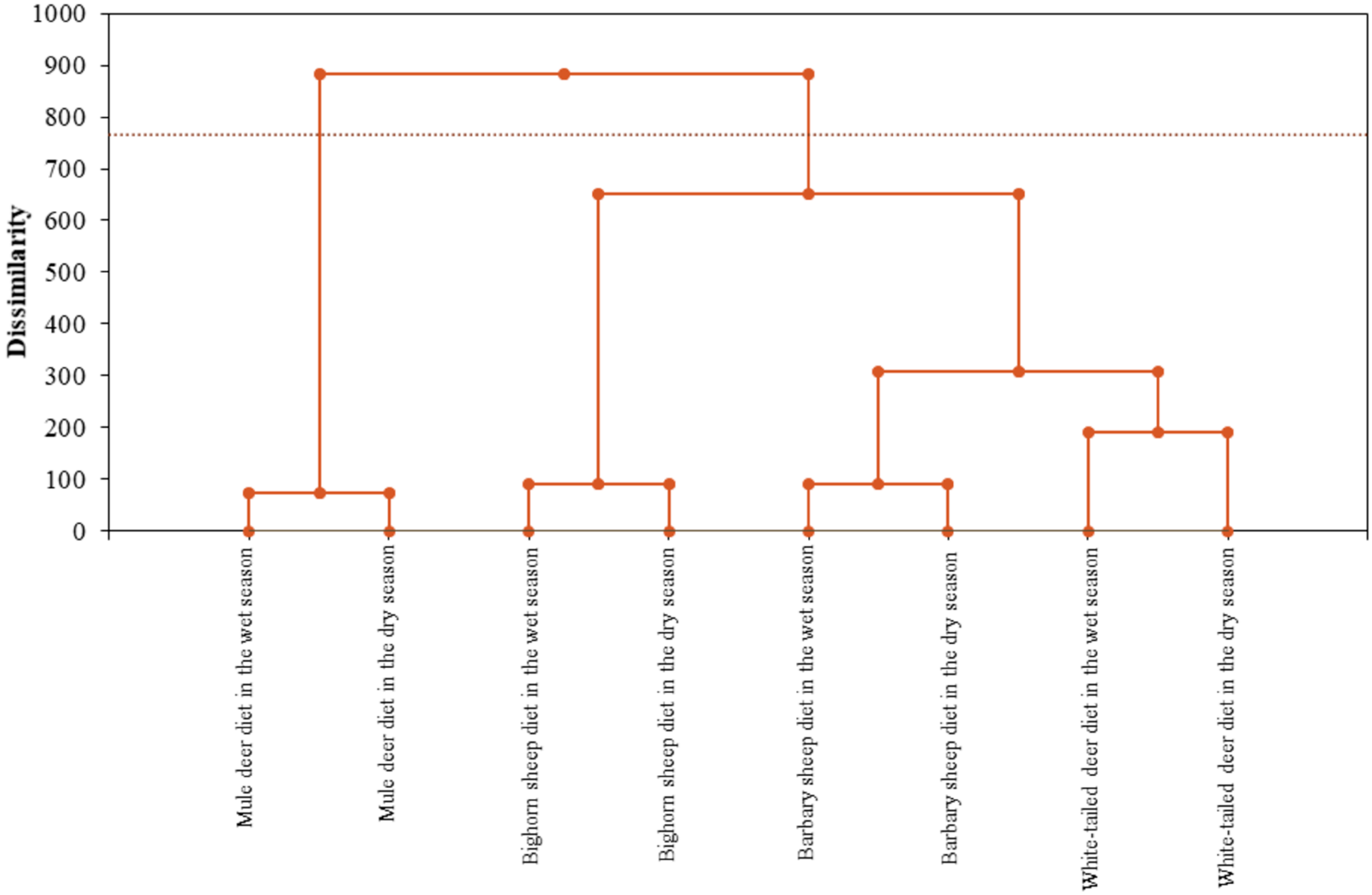


Figure 6. Principal Component Analysis (PCA) of the seasonal composition of the diet of four wild herbivores at Rancho San Juan UMA, Coahuila, Mexico.

use and food selection (Ben Mimoun and Nouira 2013). In Texas, USA, one of the few studies on this topic reveals that in the presence of white-tailed deer, Barbary sheep avoid browsing shrubs to prevent competition (Ramsey and Andereg 1972). This strategy suggests that, despite the high dietary similarity between white-tailed deer, bighorn sheep, and Barbary sheep (Figure 3), the habitat resources available for these species to compete for are different. In particular, competition could be expressed in the use and selection of escape terrain or water sources. Although common plant species were identified in the diet of the four herbivore species studied, they were not consumed in the same proportions. In particular, *A. rigidula* accounted for a significant percentage of the annual diet of Barbary sheep, but only contributed 0.5 % of the diet of bighorn sheep (Table 2), and few species accounted for high consumption percentages (Figure 3).

From a habitat management perspective, forage species for wild herbivores are classified as declining when their availability decreases in response to herbivory pressure (Fulbright and Ortega-Santos 2007). In the case of bovids, *T. canescens*, an annual herbaceous species, was classified as a declining species because it was the most representative in the annual diet of bighorn and Barbary sheep, with 17.75 % and 11.27 %, respectively. However, specific differences in diet composition were observed between the two species. A high percentage of occurrence of *C. torreyanus* was found in the annual diet of bighorn sheep (10.9 %), but not in the diet of Barbary sheep (2.9 %; $P \leq 0.05$). In contrast, *A. rigidula* was consumed in a higher proportion by Barbary sheep (10.6 %) compared to bighorn sheep (0.5 %; $P \leq 0.05$). As for cervids, both species showed a high consumption of *O. engelmannii* (Table 2). However, *A. lechuguilla*, a dominant succulent plant in the desert shrublands of northeastern Mexico (Alanís-Rodríguez *et al.* 2015), was consumed in a high proportion (11.7 %) only by mule deer. On the other hand, low woollygrass (*Erioneuron pulchellum*) was recorded exclusively in the diet of white-tailed deer (6.6 %).

Studies on forage competition are complex, since this ecological phenomenon occurs when multiple species or individuals simultaneously use a resource whose availability is insufficient to meet the minimum survival and development requirements of the individuals or populations involved (Olguín-Hernández *et al.* 2017). Under this definition, similarity in diet composition is considered a primary indicator of interspecific competition for food. In Mexico, studies on food competition between wild herbivores are scarce. In La Michilía Biosphere Reserve, Durango, studies on the long-term feeding habits of white-tailed deer and mule deer concluded that there is no significant competition in forage use between the two species (Gallina and Ezcurra 1981; Gallina 1993). For their part, Olguín-Hernández et al.

(2017), in a study carried out in Tamaulipas, identified that the most intense food competition between white-tailed deer and exotic species occurred in spring. During this season, a high similarity was observed between the diet of white-tailed deer and sika deer (*Cervus nippon*, 49 %), red deer (*Cervus elaphus*, 54 %), and eland antelope (*Taurotragus oryx*, 47 %). However, no studies have been carried out in Mexico on the competition between bighorn sheep and Barbary sheep. The cluster analysis (Figure 4) suggests that competition for forage use might be more likely among bighorn sheep, Barbary sheep, and white-tailed deer. Likewise, the consumption of herbs and grasses was more common in the diet of bovids, while shrubs and succulents were consumed more frequently by deer.

Shrub species constitute the food base of wild herbivores in arid ecosystems (Guerrero-Cárdenas *et al.* 2018; Bautista De Luna *et al.* 2022). During their development, shrubs that thrive in arid zones allocate nutrient reserves to building new tissues, which results in a relatively high crude protein content compared to some herbaceous and grass species (Mazaika *et al.* 1992; Memmott *et al.* 2011). In desert shrublands in northern Mexico, succulent plants represent an alternative source of water for herbivores during drought periods (Tarango *et al.* 2002; Gastelum-Mendoza *et al.* 2020). Within this group, *O. engelmannii* was recorded in high proportions in the diet of all species studied, except for bighorn sheep, whose consumption frequency was 2 %. This species showed a greater preference for *O. microdasys* (Table 2). In this regard, Gastelum-Mendoza *et al.* (2020) state that *O. engelmannii* is one of the dominant species in the study area, with a mean annual IVI of 77.09 ± 6.05 %. However, *O. microdasys* was one of the least available species in shrublands. Considering that bighorn sheep and Barbary sheep require particular topographic elements for their development and survival (Tarango *et al.* 2002), competition between the two species could be intense when they share the same habitat. In this sense, and due to the limited information available on the simultaneous use of the topographic space by these two species, it is not recommended that they share the same management area.

Studies on the diet of mule deer in northern Mexico and the southern U.S. have reported that it adapts to the consumption of a wide variety of plant species (Olivas-Sánchez *et al.* 2018b). In the Chihuahuan Desert, its diet mainly consists of browsing leaves, the regrowth of shrubs and succulents, and herbs as a key emerging resource during the period after rain. In the Mapimí Biosphere Reserve (state of Durango), *ocotillo* (*Fouquieria splendens*) inflorescences, which emerge in March, are an important nutritional contribution during the dry season. These resources, which are highly digestible (≈ 85 %), are consumed intensively during critical periods (Gallina *et al.* 2017). Likewise, studies carried out in Texas (Trans-Pecos and Panhandle) reveal that the annual diet of mule deer is composed on average of 70 % of shrub browsing, 25 % of grasses, and 5 % of grasses (Anderson 1949). The consumption of herbs increases markedly after summer rains, while it may include wheat and other crops growing in agricultural landscapes in winter (Short 1977). In general, mule deer require diverse shrubs and patches of herbaceous plants to maintain their body condition and promote reproduction.

The results of this study are consistent with Olivas-Sánchez *et al.* (2018a), who found that mule deer consume mainly shrubs and succulents throughout the year, with herb and grass consumption being less frequent (Figure 2). Unlike the white-tailed deer, which is a selective browser (Ramírez-Lozano 2004), the mule deer is considered an opportunistic forager, meaning its diet depends on the local availability of resources (Hanley 1997). This explains why *A. lechuguilla* was found in high percentages only in the mule deer diet (Table 2). Similarly, Geist (1981) points out that this species changes its diet from one based on herbs and grasses to one dominated by shrubs in response to extrinsic factors. The results of the present study suggest that the low availability and nutritional quality of herbaceous plants in the region are insufficient to meet the requirements of mule deer adequately. To better understand the trophic interactions between these four herbivore species, we recommend expanding these results with studies of simultaneous habitat use and analyses of the nutritional profile and availability of the main plant species consumed.

Conclusions

Barbary sheep showed a higher species richness in their diet compared to the three herbivores that share the same habitat. This high richness of species consumed by Barbary sheep may be related to its nature as a generalist herbivore capable of incorporating a wide variety of plants without showing a marked preference for any of them. In this sense, the creation of forage banks could contribute to reducing overgrazing in desert shrubland ecosystems. In general, shrub species formed the basis of the diet of the four species analyzed. Herbaceous plants were consumed in a greater proportion by sheep, while deer preferred succulents. No differences were recorded in the consumption of biological forms between seasons of the year or between herbivore species.

The principal component analysis revealed that the mule deer has the most distinct diet compared to the other herbivores. In contrast, the evidence collected in the present study suggests a low risk of trophic overlap between cervid populations, which could facilitate their management in shared areas without major adverse implications. Finally, the most consumed species can be a useful criterion for identifying new sites for repopulation, by delimiting key foraging areas in the desert shrublands of northeastern Mexico.

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