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Trophic resource partitioning and coexistence between bighorn sheep and burro feral in a mountainous area of Southern Baja California Sur, Mexico

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Abstract. Species coexistence largely depends on their sharing of resources to ensure survival and reproduction. Little is known about the mechanisms that favour coexistence between wild ungulates. However, it is expected that these are related to their habitat, food, and space requirements. This study aimed to find out which forage species are consumed by both ungulates and to determine whether there is any overlap in their use. The hypothesis to be tested was that, although both species have a low level of specialization, they can adapt to a wide variety of available forages with minimal overlap in the use of food resources, which favors their coexistence. We calculated the Pianka, Levins, and Ivlev indices to assess the degree of dietary overlap between bighorn sheep and feral donkeys. We found that bighorn sheep preferred shrubs and trees, while burros mainly preferred grasses and herbs and therefore consumed different plant species. Both mammal species were selective even when food was abundant. The feeding sites of burros and sheep were different, given the heterogeneity of habitat and vegetation. Spatial segregation in the activity of each species, together with differences in their diet, are factors that may favour their coexistence.

Keywords: coexistence, Ivlev index, Levins index, Pianka index, trophic resources, dietary overlap.

Introduction

The sharing of trophic resources between animals of different species (e.g., polygastric ruminants and monogastric herbivores or native and feral animals) varies according to changes in the distribution and abundance of food and the habitats they share (Schoener 1986, Minson 1990, Fritz et al. 1996, Behmer & Joern 2008). Therefore, understanding how available resources are shared among different species (e.g., food, water, and space) is a fundamental interest to specialists in animal population ecology (Schoener 1986, Chase & Leibold 2003, Luiselli 2008). In this regard, Gómez & Núñez (2016) argue that when two species occupy similar ecological niches, interspecific competition can lead to the displacement of one of them to less productive and more degraded areas. In arid regions where food abundance is low or unpredictable, the coexistence of ungulate species with similar ecological requirements, including native and exotic species, is particularly favored by the separation of resource use (Marshal et al. 2008, Gómez & Núñez 2016).

Coexistence between native ungulate species such as bighorn sheep (*Ovis canadensis*) and mule deer (*Odocoileus hemionus*) involves evolutionary processes that allow for spatial or trophic partitioning of resource use. The introduction of domestic ungulates (e.g., burros and feral horses, as well as cattle and goats) into natural areas where they interact with wild species results in high interspecific competition due to the lack of development of evolutionary mechanisms of resource partitioning (Connell 1980, Baldi et al. 2004). The study of interactions between native and alien species in natural environments is a key and relevant topic to understand how these coexistence mechanisms work (Jashon et al. 2008, National Invasive Species Advisory Committee 2010, Gómez & Núñez 2016).

The feral burro (*Equus asinus*) inhabits many parts of the world, including low-rainfall desert areas (Álvarez-Romero & Medellín 2005). As an exotic species, it has managed to adapt to virtually all vegetation types, with the highest incidence in xerophytic scrub (Nowak 1997, McDonnell 1998). The burro is a monogastric, herbivorous mammal that primarily feeds on forage, such as grasses and herbs (Janis 1976). Bighorn sheep are herbivorous bovids distributed exclusively in North America, where their populations have evolved and diversified based on biogeographic regions that delineate the phytogeographic and genetic aspects of their populations. Over time, they have also managed to disperse into different desert environments, where they have adapted their ways of life (Gastelum-Mendoza et al. 2024). It is also considered an opportunistic ruminant, morphologically and physiologically adapted to grazing, which is why it consumes a wide variety of forages, including grass and herbaceous plants (Cunningham 1989, DeYoung et al. 2000). Guerrero-Cárdenas et al. (2016) found that bighorn sheep in Sierra El Mechudo, Baja California Sur, fed mainly on shrub species throughout the year, and the same results were found for bighorn sheep in Coahuila, Mexico (Gastelum-Mendoza et al. 2024).

Bighorn sheep and burro feral have long coexisted in various regions of North America, including the Baja California Peninsula (Seegmiller & Ohmart 1981, Perryman & Muchlinski 1987), where food and water are often limited. Some studies have indicated limited overlap in resource use by these two species. However, such sympatric associations provide opportunities to investigate potential behavioral interactions and competition for resources between bighorn sheep and burros (Seegmiller & Ohmart 1981, Ginnett & Douglas 1982, Schoener 1986).

Due to the occurrence of rainfall and the resulting proliferation of diverse food resources, it is expected that both species will behave as specialists in their feeding, with bighorn sheep primarily selecting shrub species and burros consuming grasses and herbaceous plants. This behavior is anticipated to result in a low degree of dietary overlap between the two species. This study aimed to identify the forage species consumed by both ungulates and to assess whether there was any overlap in their use of forages. The hypothesis to be tested in this study was that, despite exhibiting a low level of specialisation, both species can adapt to consuming a wide variety of available forages, with minimal overlap in the use of food resources, thus favouring their coexistence.

Materials and methods

The study area is located at the southern end of the Sierra El Mechudo Mountain range, northwest of the Bay of La Paz, Baja California Sur, Mexico. The Sierra is located 50 km north of the city of La Paz, Baja California Sur, Mexico. According to the National Commission for the Knowledge and Use of Biodiversity (CONABIO), this area represents the last natural range of bighorn sheep in North America.

Sampling was conducted in an area of approximately 117,578 ha, spanning from the localities of El Califin in the southernmost part to Carrizalito (Mechudo) in the northern part of the Sierra, at extreme geographical coordinates: 24°24'44.17"N, 110°45'9.10"W (Fig. 1).

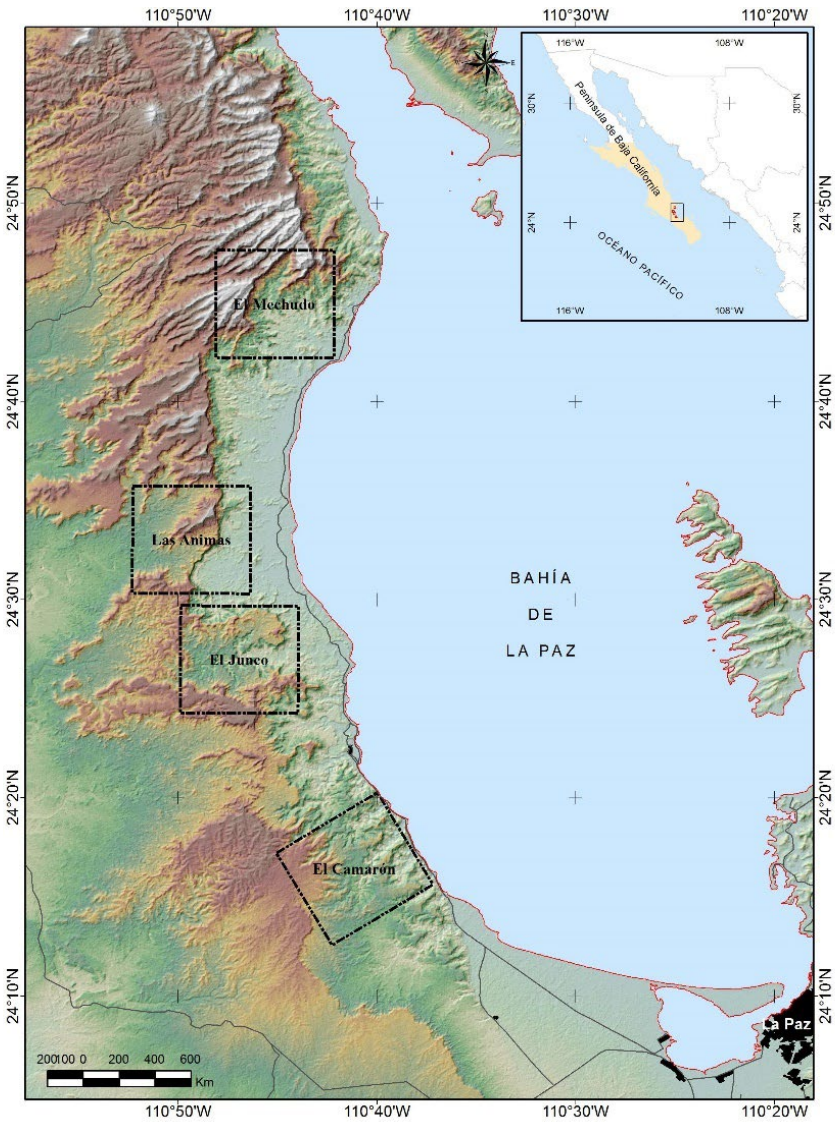

Figure 1. Location of Sierra El Mechudo, in the state of Baja California Sur, Mexico. Boxes represent the sites and areas where vegetation sampling and collection of bighorn sheep and burro feral excreta occurred.

There are three main vegetation types in the study area: 1) thorny scrub (deciduous shrub and tree species with prominent thorns) in the higher elevations, represented by *Pachycormus discolor*, *Stenocereus thurberi* and *Opuntia* sp. 2) scrubland (thornless and small-leaved species) on slopes and canyons, dominated by *Lysiloma candida*, *Ruellia californica* and *Fouquieria diguetii* and 3) scrubland-cardonal (association of different thornless species and succulent species with thorns) in the lower parts, dominated by *Pachycereus pringlei*, *Bursera epinnata* and *Prosopis glandulosa* (Álvarez-Cárdenas et al. 2001, Guerrero-Cárdenas et al. 2016).

The predominant climate is a hot and dry desert, with an average monthly temperature ranging between 17.9 and 35.3 °C between January and August, and an annual average that varies between 22 and 35 °C (García 1988). The average annual precipitation is 140 mm and occurs in two periods: the most intense in August-September (when hurricanes are most prevalent), followed by December and January (accounting for 5 to 10.2% of the total annual precipitation), which corresponds to winter rainfall (SARH 1983). During this study, climatic conditions were characterized by low rainfall and high temperatures, which exceeded 47 °C (Guerrero-Cárdenas et al. 2016). In the second half of the year, when this study was conducted (July-December), a period of rainfall occurred, with 88 mm recorded in August, and maximum temperatures reached up to 38°C (Fig. 2).

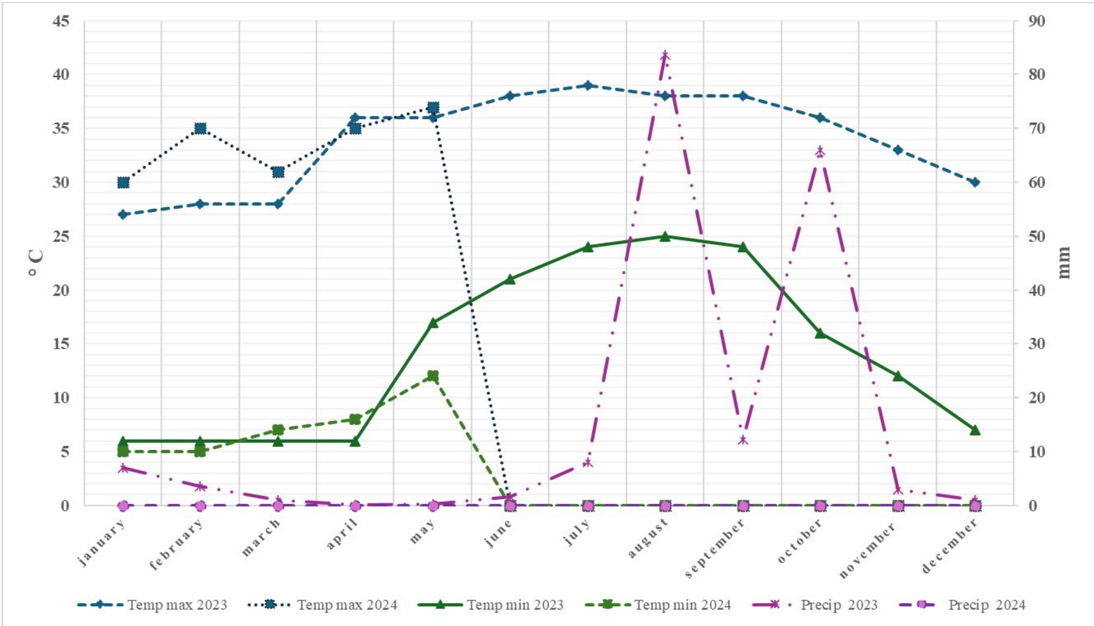

Figure 2. Climogram showing 2023 and 2024 values of maximum temperatures (dark blue), minimum temperatures (green), and rainfall (light pink) for the study area (Comisión Nacional del Agua, Alfredo V. Bonfil climate station, La Paz, BCS, Mexico).

Vegetation assessment

Eight field trips were conducted in two seasons: four during the rainy season, corresponding to July, August, September, and October 2023, and four during the dry season, starting in November and December 2023 and continuing through January and February 2024, to evaluate the availability of forage. To determine the floristic composition and vegetation structure and according to the procedures proposed by Mueller-Dombois & Ellenberg (1974) and Bonham (1989), 16 transects (eight in each season) of 50 m long by 5 m wide (250 m^2) were carried out by random sampling and random walks in different areas of the study area. The plant species were identified, the number of individuals was recorded (abundance per species), and the cover was measured (diameters and height of each individual). Specimens of all plant species present in the sampling sites were also collected to create a reference catalogue for microhistological analysis (Peña & Habib 1980, Gallina 2012). Branches and leaves of each of the species present in the study area were collected and taken to the Animal Nutrition and Morphophysiology Laboratory, Autonomous University of Baja California Sur, in La Paz, B.C.S., Mexico, for processing, which consisted of grinding and pulverizing each plant species using a Willey type mill with a 2 mm sieve.

Diet identification and analysis

The botanical composition of the diet of bighorn sheep and burro feral was determined seasonally (dry and wet between 2023 and 2024), using the microhistological technique, which identifies the epidermal fragments of plants found in the animals' excreta based on reference material (plant species of the habitat; Sparks & Malechec 1968, Peña & Habib 1980). In each season, 40 bighorn sheep (Anthony & Smith 1974) and 20 burro (Ginnett & Douglas 1982) excreta were collected randomly at the sites of greatest activity of the two animals. Excreta collection was conducted simultaneously with the forage availability assessment.

From each group of excreta collected per season for both species, five samples were randomly selected, and five slides of mixed samples were prepared per season. A metal slide with holes of approximately 7 mm in diameter was used to ensure uniform sample size. The epidermal structures (size, shape, and arrangement of cells, stomata, trichomes, glands, silicon crystals, and cell walls) of the consumed plants were compared with those in the reference catalogue. The identified species were then classified based on their importance in the diets (frequency of occurrence), temporal variation, and growth form (shrubby, arboreal, herbaceous, grassy, or succulent). For each slide, 20 microscopic fields were observed at 100x magnification (using a 10x objective and a 10x eyepiece) to identify and quantify plant fragments. The cumulative frequency was calculated ($F = 1 - e^{-x}$; where F is the frequency, e is the base of natural logarithms, and x is the mean density) and transformed into relative density for each study period (Peña & Habib 1980, Gallina 2012).

Data analysis

For each season, the richness and diversity of plant species sampled at the study sites and found in the diets of both animals were calculated using the Shannon-Wiener index (H'; Magurran 1983, Moreno 2001).

Using Pianka's (1973) index, dietary overlap between the two species was calculated and assessed with the formula $O = \Sigma(Pij \times Pik) / \sqrt{\Sigma Pij2 \times \Sigma Pij2}$, where Pij and Pik are the proportions of resource i used by species j and k, respectively. This test can range from 0, representing different diets, to 1, finding identical diets. To quantify how specialized the diet of sheep and burros is during the two seasons of this study, we used the standardized Levins index: $Best = (B - 1)/(n - 1)$, which expresses the breadth of trophic niche (understood as the sum total of the variety of food resources used by the two animals at the site), on a scale ranging from 0 (narrow niche) to 1 (broad niche). When the values of this index are less than 0.60, the species is considered a specialist (Levin 1970, Krebs 1999). We also assessed whether sheep and burros select the plant species they consume, based on their abundance with the Ivlev Selection Index (ISI; Strauss 1979). Since the index relates the proportions used of each food resource to its relative abundance in the habitat, $ISI = (ri-ni)/(ri + ni)$, where: ri is the percentage of species i in the diet, and ni is the percentage of species i in the available vegetation. According to Stuth (1991), plant species were classified into three categories of selectivity: preferred (> 0.35), proportional (-0.35 to 0.35) and avoided (< -1.0).

For data processing, the hypotheses of normality (Shapiro-Wilk test) and homogeneity of variance (Levene test) were tested. Once these hypotheses were discarded and because the data did not follow a normal distribution, the non-parametric Mann-Whitney (*U*) test for independent samples was applied to compare the means of each sample and determine if there are differences in the dependent variable, i.e. in the abundance or proportion of forage species in the habitat and those consumed by both ungulates, for two independent groups that are represented by the two climatic periods. Data with a p-value < 0.05 were considered significant.

Statistical analyses were performed using XLSTAT-ecology (version 2023.2.1414) and Microsoft® Excel®.

Results

<u>Structure and composition of vegetation cover</u>

A total of 7,311 individuals from 89 tree and shrub species, with an average height of 4.50 m and an average canopy cover of 6.50 m, were recorded in the vegetation transects throughout the year. Diversity was H'= 4.1. The species with the highest number of individuals were the shrubs: *Cordia brevispicata*, *F. diguetii*, *Jatropha cinerea*, and *R. californica*. The trees with the highest number of individuals were: *Cyrtocarpa edulis*, *L. candida*, *Olneya tesota*, and *P. glandulosa*. The herbaceous and grass species with the highest number of individuals were: *Antigonon leptopus*, *Bouteloua aristidoides*, *Cenchrus palmeri*, *Chamaesyce leucophylla*, and *Chloris virgata*. The species with the highest abundance (n = 485) in the entire study area was *C. brevispicata*.

Regarding the time of year, no significant differences were found in the abundance of individual plant species in the study area ($U = 3453$, $p < 0.215$). During the rainy season, 2,155 individuals and a richness of 72 species were recorded, with a diversity value of H' = 3.8. The most abundant species recorded was *R. californica* (Fig. 3). During the dry season, 5,143 individuals were recorded, with 88 species and a diversity of H'=4.0. The most abundant species during this season was the shrub *C. brevispicata*.

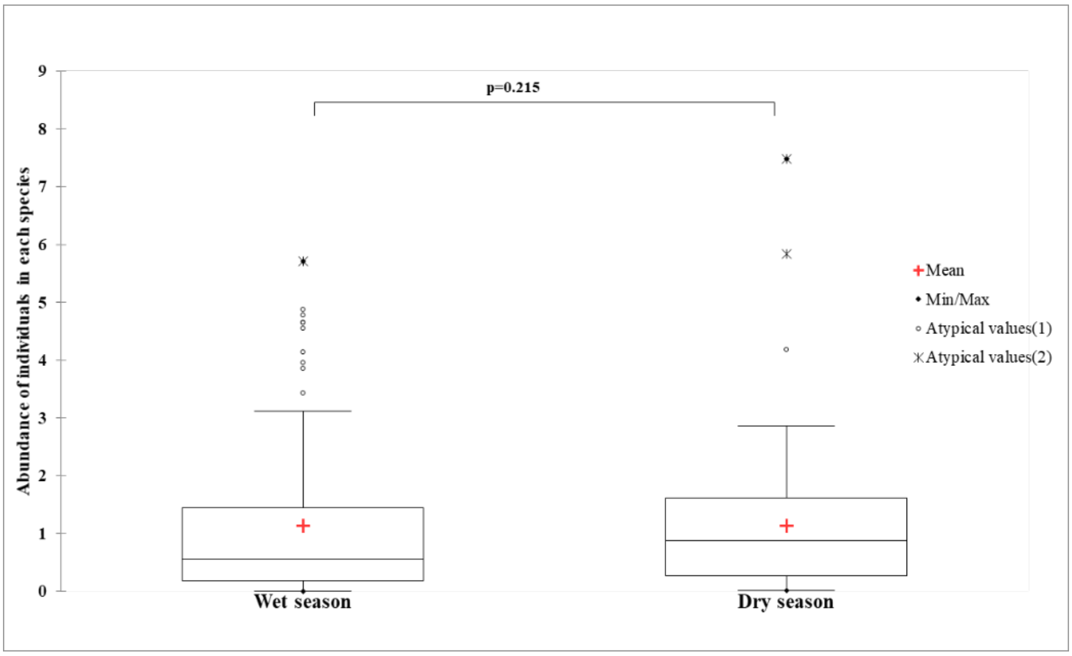

Figure 3. The box-and-whisker plot shows the sample mean values for the abundances of each species that were counted in the two seasons. No significant differences were found. * indicate the presence of outliers due to the presence of species with a higher number of individuals.

<u>Diet of bighorn sheep and burro feral</u>

Microhistological analysis identified 18 families in the diet of bighorn sheep across the two seasons, representing a richness of 46 species, mainly composed of 20 shrubs (22.3%), ten trees (10.5%), seven grasses (7.3%), six herbaceous plants (6.2%), and three succulents (3.1%). Diet diversity was H' = 3.4. The most consumed forage species were four shrubs (*A. leptopus*, *C. brevispicata*, *F. diguetii*, and *Mimosa xanti*), four trees (*C. edulis*, *J. cinerea*, *O. tesota*, and *Parkinsonia florida*), two succulents (*O. cholla* and *P. pringlei*), and one herbaceous plant (*Chamaesyce leucophylla*). During the rainy season, 20 species were found, with a diversity of H′ = 2.5. During the dry season, an increase in richness was observed with 38 species, and a diversity of H′ = 3.2.

For the diet of the feral burros, 12 families were found representing a richness of 28 species, with nine shrubs (9.9%), nine trees (9.9%), eight grasses (8.3%), one herbaceous plant, and one succulent, each with 1.0%. The corresponding diversity value was H′ = 2.9. The most consumed species were *C. edulis* (5.5%), *P. florida* (2.5%), *P. glandulosa* (7.0%) from the tree group; *A. leptopus* (33.5%) and *Eragrostis mexicana* (4.9%) from the grasses; *O. cholla* (6.0%) from the succulents; and *R. californica* (4.2%) from the shrubs. In the rainy season, the feral burros consumed 16 plant species with a diversity value of H′ = 2.5. For the dry season, there was a slight increase in richness with 19 species; however, the diversity remained similar to that of the rainy season (H′ = 2.5).

Analysis of diet similarity

Regarding the life forms consumed by both ungulates, it was observed that they share 14 species during the rainy season, with grass being the most consumed. During the dry season, 16 species were identified, with shrubs and trees being the most consumed items. In both study periods, sheep and burros consumed 22 plant species in common (Figs. 4 and 5A, B). In the Mann-Whitney U test, significant differences were found, albeit marginal, indicating a small difference in the consumption of plant species by both animals: sheep (n = 46) and burros (n = 28), U = 0.016 ($p < 0.0001$). Particularly, during the rainy season, three species were found to contribute the highest abundance of individuals in the diet of both species: *A. leptopus*, *P. florida*, and *P. glandulosa*. No significant differences were found for the dry season (Fig. 6).

Table 1 shows the plant species consumed by both ungulates, as well as the Ivlev Selection Index value in the two seasons of the study. Both ungulates particularly selected one tree during the rains: *Parkinsonia florida*. The result of the Pianka index test indicated a reduced dietary overlap between the two species during both periods of this study. The standardized Levins index revealed that the two mammal species behaved as specialists throughout the year, with no significant differences between seasons (Table 2).

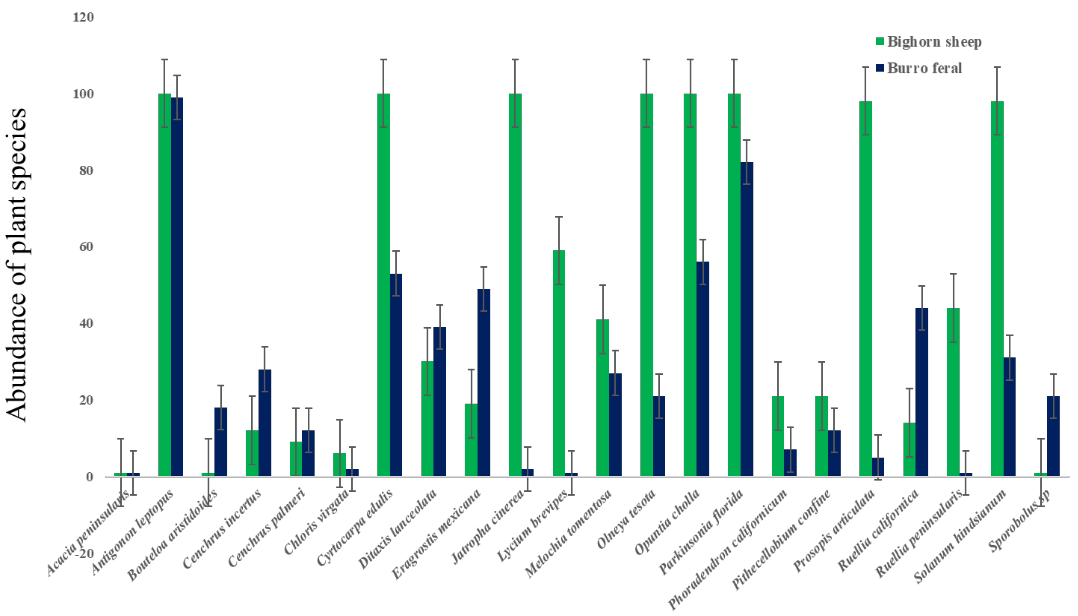

Figure 4. Similarity of forage species shared by bighorn sheep and feral burro throughout the year in the Sierra El Mechudo.

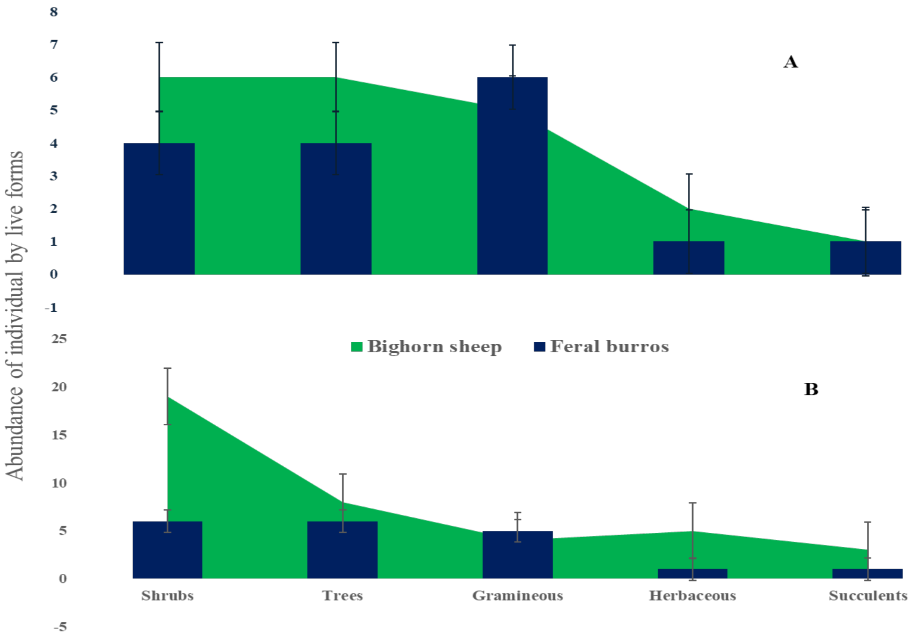

Figure 5. The life forms consumed by both ungulates are presented in a similar way, showing a dissimilarity in their consumption. The literals represent each of the seasons in this study. A= rainy season and B= dry season. The standard error bars (standard deviation) indicate the dispersion of values from the sample mean.

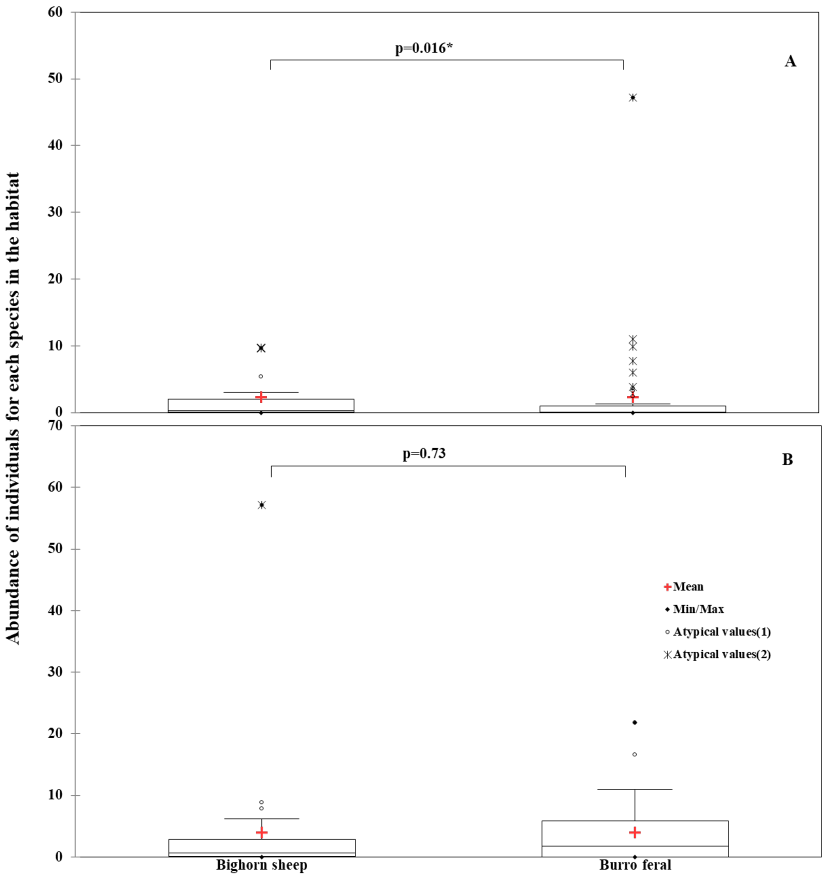

Figure 6. Box-and-whisker plot, showing that significant differences in diet composition are observed in the wet season (A; $p < 0.05$). The points above the boxes (representing the mean values) symbolize outliers, which are represented by the shrub *Antigono leptopus* with the highest number of individuals.

Table 1. Percentages of plant species fed and selected (Ivlev) by bighorn sheep and burro feral in the Sierra El Mechudo are presented.

Season	Live forms	Species	% Relative density in the diet Bighorn sheep	Burro feral	Ivlev´s (> 0.35)
Rainy season	**Grasses**	*Bouteloa aristidoides*	0.0	0.1	
		Cenchrus palmeri	0.1	1.3	
		Chloris virgata	0.0	0.2	
		Eragrostis mexicana	0.1	1.1	
		Sporobolus sp	0.1	0.1	
	Herbaceous	*Amaranthus palmeri*	0.0	0.0	
		Antigonon leptopus	9.7	47.2	
		Bahiopsis deltoidea	0.0	0.0	
		Bidens aurea	0.3	0.0	
		Cyperus perennis	0.0	0.0	
		Ditaxis lanceolata	0.0	3.7	
		Euphorbia leucophylla	9.7	0.0	
		Porophylum gracile	0.8	0.0	Prefe*
	Parasitic herbaceous	*Phoradendron californicum*	0.2	0.5	
	Trees	*Acacia farneciana*	0.0	0.0	
		Acacia peninsularis	0.0	0.1	
		Diospyros californica	0.2	0.0	
		Ebenopsis confinis	0.5	0.0	
		Jatropha cinerea	5.4	0.0	
		Jatropha cuneata	0.0	0.7	
		Lysiloma candida	0.1	0.0	
		Olneya tesota	9.7	2.4	
		Parkinsonia florida	9.7	11.0	**Prefe*** **
		Prosopis glandulosa	0.6	9.9	
	Shrubs	*Adelia virgata*	0.1	0.0	
		Ambrosia monogyra	1.1	0.0	
		Calliandra eriophylla	3.0	0.0	
		Cordia brevispicata	9.7	0.0	
		Croton magdalenae	1.2	0.0	
		Cyrtocarpa edulis	1.2	7.7	
		Encelia farinosa	0.4	0.0	
		Fouquiera diguetii	9.7	0.0	
		koeberlinia spinosa	0.0	0.0	
		Liipia palmeri	0.5	0.0	
		Lycium brevipes	1.2	0.1	
	Shrubs	*Melochia tomentosa*	0.3	3.2	
		Mimosa xanti	9.7	0.0	
		Ruellia californica	0.2	5.9	
		Sebastiana bilocularis	0.0	0.0	
		Solanum hindsianum	1.5	3.8	
	Succulents	*Opuntia cholla*	9.7	0.9	
		Pachycereus pringlei	2.4	0.0	
		Stenosereus sp.	1.6	0.0	

*** Selection by bighorn sheep, ** selection by feral burro, *** selection by two animals.**

Table 1 – continued next page

Table 1 - continuation

Season	Live forms	Species	% Relative density in the diet Bighorn sheep	Burro feral	Ivlev´s (> 0.35)
Dry season	**Grasses**	*Bouteloa aristidoides*	0.1	6.2	
		Cenchrus incertus	1.0	11.0	
		Chloris gayana	0.0	5.8	
		Chloris virgata	0.2	0.0	Prefe*
		Eragrostis mexicana	0.9	16.6	Prefe**
		Sporobolus sp	0.1	7.5	
	Herbaceous	*Antigonon leptopus*	57.2	0.0	
		Ditaxis lanceolata	2.9	3.3	
		Hibiscus denudatus	0.6	0.0	
	Parasitic herbaceous	*Phoradendron californicum*	0.4	0.7	Prefe*
	Trees	*Acacia peninsularis*	0.1	0.0	
		Cyrtocarpa edulis	6.2	0.0	
		Parkinsonia florida	8.8	5.8	
		Pithecellobium confine	1.9	4.3	
		Prosopis articulata	7.9	1.7	
	Shrubs	*Bourreria sonorae*	0.0	0.3	
		Capparis atamisquea	0.0	2.4	
		Jatropha cinerea	0.1	0.7	Prefe*
		Lycium sp.	0.4	0.0	
		Melochia tomentosa	2.0	0.0	
		Ruellia peninsularis	4.7	0.3	
		Solanum hindsianum	3.0	0.0	Prefe*
	Succulents	*Opuntia choya*	0.7	21.8	Prefe**

*** Selection by bighorn sheep, ** selection by feral burro.**

Table 2. Results of overlap and niche breadth in the diet of sheep and burros in the Sierra El Mechudo in the rainy and dry seasons are presented.

	Diet in the two periods	
Bighorn sheep vs Burro feral	Niche overlap of Pianka (1973) O = 0.27	
	Niche breadth Levins (1968), standardized by Krebs (1999)	
Bighorn sheep	BA = 0.51	Specialist
Burro feral	BA = 0.48	Specialist
	Rainfall diet	
Bighorn sheep vs Burro feral	Niche overlap	
	O = 0.31	
	Niche breadth	
Bighorn sheep	BA = 0.41	Specialist
Burro feral	BA = 0.54	Specialist
	Dry diet	
Bighorn sheep vs Burro feral	Niche overlap	
	O = 0.24	
	Niche breadth	
Bighorn sheep	BA = 0.55	Specialist
Burro feral	BA = 0.44	Specialist

Discussion

Food availability

It is fundamentally important to understand vegetation, a key component of the diets of herbivores. It is essential to understand how plant communities are constituted in the study sites, including richness and abundance variables, as well as phenological state, nutritional value, palatability, and diversity (Poppi & McLennan 1995). These elements are key to understanding seasonal changes in the habitat and the possible use of the different animal species that feed on them. In line with our study, Hansen (1980) explains that plant composition and cover are two useful parameters for predicting important feeding and refuge areas for species like bighorn sheep.

During this study, a large proliferation of grasses and herbaceous perennials was recorded, along with an increase in plant species diversity and canopy cover, particularly of trees and shrubs, due to rainfall, which is uncommon in these arid zones, especially in this study area. In this regard, Guerrero-Cárdenas et al. (2016) observed in the Junco area, part of the natural distribution area of Sierra El Mechudo bighorn sheep, that during two years of no rainfall (2010 and 2011), the diversity was H′ = 3.1 with 70 species. In contrast, our study found 89 species (n = 19 sp) with a diversity of H′ = 3.2, and after rainfall, diversity increased from H′ = 3.8 to 4.0.

It is important to note that diversity during the dry season is higher because this season, occurring at the end of the year, marks the climax of vegetation after summer rains. This aligns with findings by Alcala-Galvan & Krausman (2012), who showed that rainfall, particularly in desert habitats like the one in our study, significantly improves vegetation quality, especially grasses and herbaceous life forms, which increased in abundance across the study area. Rainfall thus helps us understand how food supply and availability influence how bighorn sheep and feral burros use and select forage. Understanding forage availability helps analyze these animals' survival and adaptation strategies in inhospitable environments (Hobbs & Swift 1985, Guerrero-Cárdenas et al. 2018).

On the diet of bighorn sheep and burro feral

Regarding the diet of bighorn sheep and feral burros, their coexistence, similar to that between bighorn sheep and feral burros in Sierra El Mechudo, may be due to the evolutionary strategies of each species to obtain food and partition the forage they consume (Gordon & Illius 1989, Arsenault & Owen-Smith 2008). According to Jarman & Sinclair (1979) and Chesson (2000), the adaptation of these animals to share cohabitation sites is one of the main factors contributing to their survival. Over time, both sheep and burros have adapted and developed strategies to maximize their food intake, especially in desert areas like Sierra El Mechudo, where high-quality forage is generally scarce, particularly during droughts (Krausman et al. 1989). These strategies, according to Owen-Smith (1989), are physiological (e.g., development of a digestive system that optimises food processing) and behavioral (e.g., skill in selecting feeding sites and diet components). In this regard, Belovsky (1978) and Hofmann (1989) argue that only species that can maximise the benefits of food while minimising energy costs survive in desert areas, which is the most logical explanation for the coexistence of sheep and burros. This is because bighorn sheep consume a greater amount of forage than burros, mainly shrubs.

Another explanation for these feeding strategies is the animals' activity patterns, particularly in their feeding schedules. This study observed that donkeys feed and drink water mainly at night and dawn (11:00 p.m. to 02:00 a.m. and 04:00 a.m.), resting during the hottest part of the day (Gordon & Illius 1989, Taylor 1999, Chirgwin et al. 2000). Sheep, on the other hand, feed and drink in the morning and part of the afternoon, using some of those hours for rumination while resting at night (Krausman et al. 1989). This suggests minimal overlap in feeding schedules. Stephens & Krebs (1986) and Stephens et al. (2007) note that many wild animals make important decisions based on interdependence, such as the type of area they visit for feeding, the time spent feeding, the forage they consume, and the zones they use for feeding and drinking. The fidelity, or philopatry, of bighorn sheep and feral burros to their home ranges explains their coexistence and forage use, as both species utilize the sites differently. Goodson & Stevens (1988) and Festa-Bianchet (1986) explain that in bighorn sheep populations, both sexes exhibit strong site fidelity, with females typically having a higher return rate than males.

Another rationale for coexistence and trophic resource partitioning is explained by Belovsky (1978) and Holt (2001), who suggest trophic spatial segregation as a key factor in enabling species to optimize their food search, thereby ensuring coexistence. This was observed during field sampling, where sheep were seen using higher-altitude areas (greater than 100 m) with steep slopes (greater than 70%) and abundant vegetation, while burros were found in stream beds and lower areas (foothills, below 50 m) of Sierra El Mechudo, sites they also used for resting (Cunningham 1989, Gedir et al. 2021). This pattern is consistent with MacArthur & Levins (1967) and Schoener (1974), who argue that coexistence depends on variables such as habitat use, food availability, activity schedules, and spatial use. In large, open spaces like Sierra El Mechudo, spatial heterogeneity plays a crucial role in the partitioning of food resources and understanding the coexistence of these two species. Asada (2002) and Santibáñez-Andrade et al. (2009) mention that the distribution and abundance of plant species in habitats are heterogeneous, influenced by spatial and temporal variations. Furthermore, the potential competition between sheep and burros is modified by seasonal variations, as forage availability fluctuates, leading to temporal separation between the two species and avoiding interference competition. This explains how both sheep and burros shift from specialists to generalists throughout the year.

The similar food consumption between the two species provides another explanation for their coexistence, supported by Huston & Pinchak (1991), who note that different animals (cattle, goats, sheep, deer, etc.) have different digestive potentials and preferences for certain plant groups. In this study, sheep preferred woody species (trees and shrubs), which are the most abundant and widely distributed, while burros preferred grasses and herbs. This preference by burros is due to their efficient digestive system, which optimizes the consumption of these foods. Their long digestive tract allows a longer time for food processing (Smith & Krausman 1988, Guerrero-Cárdenas et al. 2018), and the large size of their molars improves their ability to extract nutrients from their food (McNaughton 1986, Poppi & Mclennan 1995, Guerrero-Cárdenas et al. 2016). While burros feed on plants rich in structural carbohydrates (cellulose and hemicellulose), which are abundant in grasses and some herbaceous plants, these nutrients support the survival and development of these feral animals (Seegmiller & Ohmart 1981, Taylor 1999, Chirgwin et al. 2000).

Throughout the study, both species behaved as specialists, rejecting the hypothesis that donkeys are generalists. We believe this is because they exhibited minimal trophic breadth, even when resources were abundant. According to Stephens & Krebs (1986), Owen-Smith (1989), and Lehmann et al. (2013), animals that consume fewer plant species tend to select those that are abundant and of high nutritional quality, as the energetic cost of finding them is low. However, in times of scarcity, they become more generalist, as finding high-quality forage becomes costlier.

Understanding resource partitioning and coexistence goes beyond speculating about competition between these animals. It involves understanding their spatial distribution, digestive functionality, feeding behavior, and nutritional requirements. Additionally, it requires knowing the spatial and temporal distribution and phenological state of the vegetation they feed on, which is linked to the palatability and nutritional value of plants (Hanley 1997). The partitioning of food resources between bighorn sheep and feral burros likely explains their coexistence in Sierra El Mechudo in the short term, as this resource sharing may be seasonal or transient rather than permanent (Holt 2001).

The study of the diets, food habits, and/or feeding behavior of bighorn sheep and burro feral populations will allow us to understand the mechanisms that promote their coexistence in the different areas of distribution and use within the Sierra El Mechudo, anticipating possible effects on the sites and resources they share. Similarly, understanding and studying the availability of forage or plant species is a key and relevant factor that influences multiple aspects of the behavior, ecology, and survival of the two ungulates, and is crucial to understanding the interactions between these animals and their environment. Thus, the study and understanding of the elements that allow the coexistence of both ungulates are of fundamental importance for the conservation of bighorn sheep, as well as the control and management of feral burro populations in the Sierra El Mechudo. According to Pianka (1974) and Seegmiller & Ohmart (1981), there is currently no quantitative information demonstrating forage competition between bighorn sheep and feral burros. Additionally, it is essential to note that demonstrating competence can be challenging in the field.

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