*Journal of Mammalogy*, XX(X):1–12, 2022
https://doi.org/10.1093/jmammal/gyab171

# Spatial and trophic niche of an assemblage of native and non-native herbivores of arid Argentina

S. Yasmin Bobadilla,[1,*] Maria A. Dacar,[1] Fabian M. Jaksic,[2] Ricardo A. Ojeda,[1] and Maria F. Cuevas[1]

[1]*Grupo de Investigaciones de la Biodiversidad, Instituto Argentino de Zonas Áridas, Centro de Ciencia y Técnica Mendoza, CONICET, Avenida Ruiz Leal s/n Parque General San Martín, Mendoza, CP 5500, CC507, Argentina*
[2]*Center of Applied Ecology and Sustainability (CAPES), Pontificia Universidad Católica de Chile, CP 8331150, Santiago, Chile*

**To whom correspondence should be addressed:* ybobadilla@mendoza-conicet.gob.ar

The coexistence of ecologically similar species is facilitated by differential use of resources along habitat, diet, and/or temporal niche axes. We used feces of non-native rabbit (*Oryctolagus cuniculus*), hare (*Lepus europaeus*), goat (*Capra hircus*), and the native plains viscacha (*Lagostomus maximus*) to compare the utilization of spatial and trophic resources in an arid ecosystem of Argentina. We expected herbivores to present differential responses in the use of at least one of the niche axes (habitat and/or trophic) associated with seasonal changes in resource availability and according to the origin of the species (native, non-native). We evaluated habitat use and selection through Chi-squared goodness-of-fit tests and Bonferroni confidence intervals, and factors shaping habitat selection (particular components of the habitat type) using generalized linear mixed-effects models. We analyzed the seasonal compositions of diets, breadth of trophic niches, and dietary overlaps. The assemblage of herbivores did not segregate markedly in spatial resource use, showing that hares and goats were more generalist than rabbits and plains viscacha in the utilization of different habitat types. Native and non-native herbivores overlapped markedly in the trophic niche dimension but segregated to some degree in the use of space during wet and dry seasons. The four herbivores shared a similar diet composition. Among dietary items, grasses contributed high percentages during the wet season. Under conditions of resource limitation (dry season), the native plains viscacha differed in feeding strategy from the non-native herbivores. These results deepen our understanding of likely underlying mechanisms that allow coexistence of native and non-native herbivores in an arid ecosystem.

Key words: diet, habitat, native, non-native, overlap, segregation

La coexistencia de especies ecológicamente similares es facilitada por el uso diferencial de recursos como el hábitat, la dieta y/o los gradientes temporales. Utilizamos heces de las especies no nativa conejo (*Oryctolagus cuniculus*), liebre (*Lepus europaeus*), cabra (*Capra hircus*), y de la especie vizcacha nativa de las llanuras (*Lagostomus maximus*), para comparar la utilización de recursos espaciales y tróficos en un ecosistema árido de Argentina. Esperábamos que los herbívoros presentaran diferentes respuestas en el uso de al menos uno de los dos ejes de nicho (hábitat y/o trófico) asociados con cambios estacionales en la disponibilidad de recursos y de acuerdo con el origen de la especie (nativa, no nativa). Evaluamos el uso y selección de hábitat con la prueba de bondad de ajuste Chi-cuadrado e intervalos de confianza de Bonferroni; y factores que influyen en la selección de habitat (components paticulares del tipo de habitat) utilizando modelos lineales generalizados mixtos. Analizamos la estacionalidad de la composición de las dietas, la amplitud de los nichos tróficos y el sobrelape de dietas. El ensamble de herbívoros no se segregó marcadamente en cuanto el uso de recursos especiales, mostrando que las liebres y las cabras fueron más generalistas que los conejos y las vizcachas de llanuras en el uso de diferentes tipos de hábitats. Los herbívoros nativos y no nativos se solaparon en la dimensión del nicho trófico, pero se segregaron en el uso de los componentes del hábitat durante estaciones de lluvia y sequia. Los cuatro herbívoros compartieron la composición de la dieta, consumiendo principalmente gramíneas durante la estación húmeda. En condiciones de limitación de recursos (estación seca), la vizcacha native de llanuras difirieron en la estrategia de alimentación en comparación con los hervíboros no nativos. Los resultados amplían nuestra comprensión de los mecanismos subyacentes que permiten la coexistencia de herbívoros nativos y no nativos en un ecosistema árido.

Palabras claves: dieta, hábitat, nativo, no nativo, segregación, solapamiento

---

Non-native mammalian herbivores have been reported as a global problem because they directly or indirectly affect different components of the environment, generating fundamental changes in the composition of species, habitat structure, and ecological and evolutionary processes (Simberloff and Dayan 1991; Vázquez 2002; Nuñez et al. 2010; Jaksic and Castro 2021). Effects including competition for trophic and spatial resources between native and non-native herbivores may occur, particularly if the sympatric species involved are of similar size and share similar feeding strategies (Owen-Smith 2002; Young et al. 2005). These effects are more accentuated in arid regions characterized by unpredictable and markedly seasonal rainfall, where landscapes are complex mosaics of interlocking habitats that physically and/or by activities of the inhabiting organisms modify the patterns of availability of key resources such as water and nutrients (Whitford 2002), especially during the dry season (Danell et al. 2006).

According to Hutchinson (1957), the niche concept is defined as an *n*-hyperdimensional volume, where *n* is the number of dimensions that compose the niche (i.e., resources such as habitat or food and conditions that a species exploits and that affect the fitness of its population). Theoretically, two species cannot occupy the same *n*-dimensional ecological niche (niche overlap) without exerting strong competition on each other (MacArthur and Levis 1967). Thus, under community ecology theory, the niche partitioning hypothesis predicts that the coexistence of ecologically similar species should show differentiation in at least one of the main niche dimensions to avoid or reduce competition (Schoener 1974). However, non-native species with a recent history of co-occurrence among them and with native species may show less resource partitioning than species with common evolutionary histories, as they have not had the opportunity to evolve mechanisms of resource partitioning (Stewart et al. 2002; Jaksic and Castro 2021). Overlap in habitat and diet is critical to understand the mechanisms that facilitate coexistence of mixed assemblages of herbivores (Schoener 1974; Jaksic and Marone 2007).

As in many arid regions, mammal assemblages in arid Argentina are composed of native and non-native herbivores (Reus et al. 2017). In these regions, herbivores face selective pressures related to water scarcity, extreme temperatures, low primary productivity, and the presence of shrubs with anti-herbivore components (Ojeda and Tabeni 2009). Rabbit, *Oryctolagus cuniculus*, and hare, *Lepus europaeus*, are introduced invasive herbivores that occur in arid regions of Argentina (Jaksic et al. 2002; Bonino 2006; Bobadilla et al. 2021). Even though these lagomorphs are ecologically similar, the rabbit is a semi-fossorial species that forms colonies in warrens (Gálvez Bravo et al. 2009), while the hare is a ground dwelling, solitary, and highly mobile species (Schai-Braun et al. 2015). These species are sympatric in many areas of the world in agricultural or pastoral habitats, and their diets when studied in the same locations are remarkably similar (Chapman and Flux 2008). Thus, they can exhibit direct or indirect competition for resources (Flux 2008; Lush et al. 2017) as well as with native herbivores (Cooke and Mutze 2018). Nevertheless, in an agroecosystem of Australia hare and rabbit used the same daytime sheltering areas but there is a degree of fine-scale separation that maintained a mutual tolerance between them (Stott 2003). In arid regions of Argentina, at least at a regional scale, there is sympatry associated with the preferred habitat of both lagomorphs (Bonino and Borrelli 2006). Previous studies in northwest Patagonia indicate that they exhibit important dietary similarities with plains viscacha (*Lagostomus maximus*) and domestic herbivores, suggesting that interspecific competition is likely to take place (Bonino 2006; Puig et al. 2007).

Medium-sized herbivores are represented in Argentina's arid regions by caviomorph rodents which coexist due to differential use of food resources and microhabitats (Campos et al. 2001; Ojeda and Tabeni 2009). Among these, plains viscacha reaches its westernmost distribution limit in northwest Patagonia (Puig et al. 1998). This native rodent is coprophagous and a generalist herbivore (Puig et al. 1998). It lives in social groups forming a burrow system around which it generates heavily grazed areas, where species richness of forbs is higher than that of grasses (Branch et al. 1994). Besides, it shows a great ability to survive in disturbed areas, which has enabled it to expand into new areas with native habitats, but that are undergoing anthropogenic intervention (Spotorno and Patton 2015).

Virtually all grasslands and arid shrublands in Argentina have been subjected to domestic livestock grazing for many decades (Fernández and Busso 1999). Accordingly, extensive livestock grazing by sheep, cattle, and goat occurs in about 60% of these arid areas and has important consequences in shaping and modifying landscape structure and species diversity (Villagra et al. 2009). Particularly in northwest Patagonia, the dominant land use is livestock farming and the vegetation has been degraded by overgrazing, causing changes in the composition of domestic herbivores, where cattle and sheep have been replaced by goats (*Capra hircus*; Guevara et al. 1997). Goats have diverse adaptations to harsh environments that involve integrated physiological and behavioral mechanisms that, for example, allow for grazing while perceiving the complexity of the food resource through chemosensory stimuli, or show less water dependence than larger ungulates (Puig et al. 2001; Egea et al. 2014). In general, the diet of goats has a strong component of woody plants (Pelliza et al. 2001; Villagra et al. 2013). Bucher (1987) proposed that habitat modification by livestock grazing might favor establishment of native species such as plains viscacha, but more studies about the dietary overlap of herbivores and their capacity for habitat modification are needed to test this assertion (Puig et al. 1998).

In arid regions of northwestern Patagonia there is co-occurrence of native, non-native, and domestic herbivores, which offers a unique opportunity to test coexistence mechanisms among these mammalian assemblages. In particular, we hypothesize that this assembly of native and non-native herbivores may coexist by having different responses in the use of at least one of two niche axes (habitat and/or trophic) associated with seasonal changes in food availability (Schoener 1974) and according to the native or non-native status of the species (Stewart et al. 2002). We predict that in the period of higher availability of resources (wet season), a high degree of spatial and food resource overlap will occur, while during the period of resource limitation (dry season), niche segregation will be higher. Furthermore, we expect that non-native herbivores, with a recent history of co-occurrence, will exhibit less clear-cut spatial distribution than the native herbivore, which co-evolved with its environment. Therefore, the purpose of this study is to characterize the use of habitat and food resources by each species and compare results among native and non-native herbivorous mammals in an arid region of Argentina.

## MATERIALS AND METHODS

*Study area.*—Our study area was located in the Laguna de Llancanelo Provincial Reserve (35°45′S to 69°08′W, 1,270–1,500 m elevation) in a border area between phytogeographic units of the Monte and Patagonia in central western Argentina (Cabrera 1994). The Reserve is a Ramsar site encompassing approximately 90,000 ha with public and private land and includes one of the largest endorheic lagoons of the region with permanent (rivers and streams) as well as temporary water inputs (fluctuations in neighboring water bodies that flood the areas closest to the lagoon) (Palma-Leotta et al. 2019; Fig. 1). Within the Reserve anthropic activities occur such as livestock (goat) production with extensive management (grazing in the open field; Palma-Leotta et al. 2019) and in co-occurrence with rabbit, hare, and plains viscacha. The climate is characterized by marked seasonality with humid summers averaging 19.5°C (wet season) and dry winters with average temperatures of 3°C (dry season), while annual rainfall ranges from 215 to 240 mm (De Fina et al. 1964). The area is characterized by five main habitat types: (i) shrublands, characterized by soils of volcanic origin and dominated by *Prosopis flexuosa*, *Bougainvillea spinosa*, and *Chuquiraga erinacea*; (ii) pichanal,

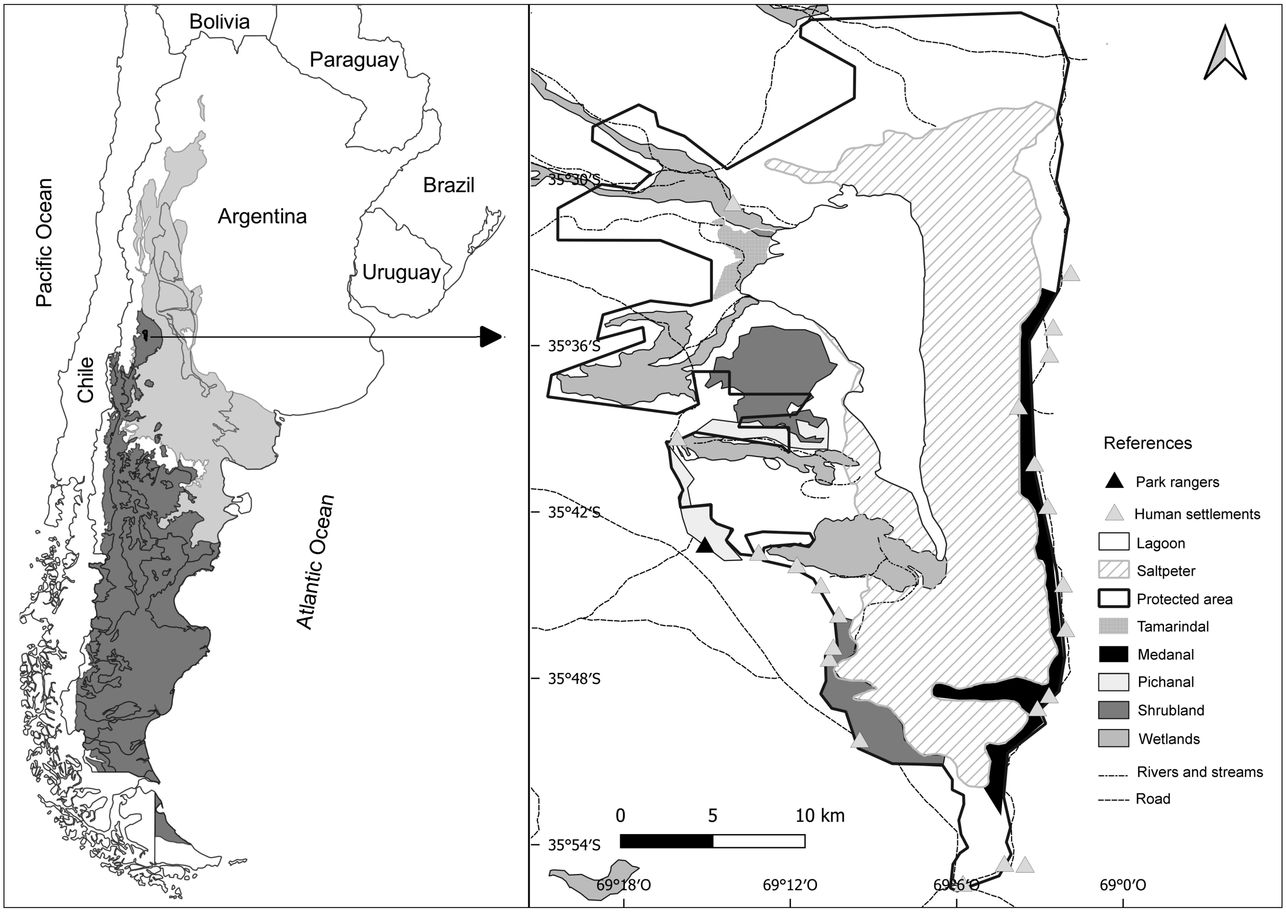

**Fig. 1.**—A) Map of Argentina showing the phytogeographical provinces of the Monte (light gray) and Patagonia (dark gray) and the location of Laguna de Llancanelo Reserve (black mark). B) Zoom of the study area showing the matrix of five available habitat types in the study site and water-covered surface (white area).

a shrub formation located over the gently sloping drainage network to the east and dominated by *Baccharis spartioides*; (iii) sand dunes, built up by the dynamics of wind transport and accumulation, and characterized by *Sporobolus rigens*, *Suaeda divaricata*, and *Atriplex lampa*; (iv) wetlands, where there is water accumulation, with soils of fine texture, clayey, and a flat relief and dominated by *Distichlis spicata*, *Distichlis scoparia*, *Frankenia juniperioides*, and *Cortaderia rudiuscula*; and (v) tamarindal, which are forests of substantial extension in the northern part of the Reserve, dominated by the invasive species *Tamarix* spp. (Méndez 2005).

*Sampling design.*—Sampling was conducted during the wet (December to February) and dry (June to August) season of 2017. We used a stratified random sampling model for 70 fixed strip transects of 1,000 m$^2$ (5 m × 200 m) established throughout the study area on the basis of the habitat types recognized. The number of transects in each habitat was estimated by taking the surface that allowed us to characterize the different environments and considering the logistics of access to them (shrublands 3,900 ha, pichanal 2,600 ha, sand dunes 3,300 ha, wetlands 4,000 ha, and tamarindal 1,000 ha). Number of transects varied from 10 (for tamarindal) to 15 (for the rest of the habitat types). The transects were placed randomly and at least 500 m apart within each habitat type and with a minimum distance of 2 km between transects in different habitats (Fig. 1). To minimize bias in feces detectability (Cortázar-Chinarro et al. 2019) within and among habitat types, two expert observers walked along the strip transects, one observer searching up to 2.5 m on one side of the transect and another on the opposite side. Fecal pellets of the four herbivores are easy to identify in the field observing their sizes, colors, shapes, and rugosity (Galende and Raffaele 2008; Salgado 2016) and we recorded the presence or absence of feces of the four species along the strip transects and also collected fresh feces. All feces collected in one transect were identified to the species level in the field, observing their size, color, shape, and constituted one sample for diet analysis. In the middle of each transect we established one vegetation transect 50 m long, where we measured the specific composition of plants and vegetation cover for each sampling season. For this, we used a 2-m graduated rod (modified Point Quadrat method; Passera et al. 1986). We measured 168 points separated 30 cm in each vegetation transect. We recorded species, percent cover of bare soil, litter, forbs, graminoids (Juncaceae and Ciperaceae), grasses, subshrubs (shrubs < 100 cm tall), and woody species (shrubs > 100 cm tall, and trees), hereafter called environmental variables. We also collected leaves, flowers, fruits, and seeds of all plants present in the study area to develop a reference collection. Other variables recorded at each transect included distance to nearest water source (considered as an environmental variable) and anthropogenic variables such as nearest human settlement and nearest road. These variables were measured using QGIS 3.12 Bucuresti software, taking the distance from the midpoint of each transect to the contact with the points of interest (nearest water source, nearest human settlement, and nearest road). We used the GIS hydrology layer (that included for this study lagoon, rivers, streams, and water wells), GIS population layer, and GIS road network layer of the study area.

*Spatial analysis.*—We used two different approaches to the spatial analysis: use and selection of habitat types (habitat type defined by dominant cover type) and factors shaping habitat selection (particular components of the habitat used by an individual within its activity area; Garshelis 2000; Stabach et al. 2017). We used fecal counts as a measure of spatial activity (Jaksic et al. 1979; Jaksic and Soriguer 1981). To analyze habitat selection we considered the five main habitat types (shrubland, pichanal, sand dune, wetland, tamarindal). To detect patterns of habitat selection, we used the Chi-squared goodness-of-fit test to determine whether there was a significant difference between the observed fecal frequencies along transects with those expected by availability of the different habitat types. Expected frequencies were calculated considering the total number of transects measured at each habitat type. When significant differences were found, we applied Bonferroni confidence intervals (CIs) for each frequency of occurrence of each type of herbivore based on fecal counts in each habitat (Broomhall et al. 2003; Liu et al. 2005). This analysis allowed us to determine which type of habitat was selected or not (i.e., if the use was proportional or not to what was available) by each herbivore during sampling. If the expected frequency lay outside the interval, we concluded that the expected and actual use was significantly different which thus allowed us to qualify preference by the species (if the frequency of usage was greater than expected) or avoidance (if the frequency of usage was lower than expected; Neu et al. 1974; López-Cortés et al. 2007).

To assess particular components of the habitat that influenced the presence of each species, we examined environmental and anthropogenic variables measured at each transect in the five habitats types. We applied generalized linear mixed-effects models, fitted by the function glmer (package lme4; Bates et al. 2015) in environment R 3.6.1 software (R Development Core Team 2019) with logit link function and binomial error distribution. We built one model for each herbivore and for each sampling season using as response variable the presence/absence of their feces. For models fitted, we selected 10 quantitative habitat variables as the fixed effects: environmental (percent cover of bare soil, litter, forbs, graminoids, grasses, subshrubs, woody species, and distance to nearest water source) and anthropogenic variables (nearest human settlement and nearest road). We only added to the model those variables which were not correlated to each other (see Supplementary Data SD1). We considered transects nested in the environment as random effects. Akaike's Information Criterion corrected for small sample size (AICc) was used to determine the best model. Model comparison was based on the differences in AICc values (ΔAICc) and Akaike weight ($w_i$; Symonds and Moussalli 2011). We also estimated the relative importance of each variable (RIV) under consideration by summing the Akaike weights for each model in which that variable appeared (Symonds and Moussalli 2011). Fixed effects with RIV > 0.5 were considered the most statistically informative (Barbieri and Berger 2004).

*Trophic analysis.*—All fecal pellets collected from each transect were assigned to the corresponding species by stereoscopic microscope inspection in the laboratory. In this manner, we corroborated the species identification of the samples obtained in the field. We only used feces collected in the habitat type where we had co-occurrences of the four herbivorous mammals. Samples were analyzed using the microhistological technique by Dacar and Giannoni (2001). For each sample, we prepared five microscope slides and systematically examined 50 fields under microscope at ×400 magnification. In previous studies, the quantity of 50 fields proved to be adequate for this purpose (Cuevas et al. 2013; Bobadilla et al. 2020). Food items in the fecal samples were identified by comparison of fragments with a reference collection of epidermic tissues of leaves, stems, seed teguments, and fruits, following Dacar and Giannoni (2001). When possible, the material was identified to species level. Presence of food items was recorded and diet composition was then calculated estimating the relative frequency of occurrence per slide by dividing the number of microscope fields in which an item occurred by the total number of microscope fields observed ×100 (Holechek and Gross 1982). We used Kruskal–Wallis ANOVA (*H*) and the post hoc pairwise Wilcox test with Holm correction ($P < 0.05$) to perform all the comparisons based on plant life forms (forbs, graminoids, grasses, subshrubs, woody species), and the four herbivorous mammals (native and non-native) for each of two seasons (Zar 2010).

To determine if there was selection of food resources by the herbivores, we used data on availability obtained from measurements of the vegetation transects. Selectivity of food items was estimated using Manly's Selectivity Index ( $\alpha_i = \mathrm{Pu}_i/\mathrm{Pa}_i \times 1/\sum \mathrm{Pu}_i/\mathrm{Pa}_i$, where $\mathrm{Pu}_i$ is the observed proportion of item *i* in the herbivores' diet and $\mathrm{Pa}_i$ is the available proportion of item *i* in the environment; Manly et al. 2002). If $\alpha_i$ is greater than $1/k$, *k* being the number of food items, it indicates selection (consumption greater than random). If $\alpha_i$ is less than $1/k$, it indicates avoidance (Manly et al. 2002). To test the reliability of Manly's Index, we resampled the data 1,000 times by nonparametric bootstrapping (package boot; Canty and Ripley 2021). This technique allows estimating the bias and variance of a given statistic and also provides a CI (Davison and Hinkley 1997). In this manner, we calculated the average values and the 95% CI of Manly's Index. The 95% CI that includes the value $1/k$ indicates a resource use that is proportional to its availability. In order to determine variation in the feeding strategy, we calculated richness and trophic niche breadth for each species in each season, using Levins' *B* index as standardized by Hurlbert (1978; $\mathrm{BS} = \left(1/\sum p_i^2\right) 1/(n-1)$, where $p_i$ is the relative proportion of item *i* in the diet of each herbivore, and *n* is the number of items; this index ranges from zero to one). To analyze niche overlap between species we used the Proportional Similarity Index ($\mathrm{PSI}_{ih} = 1\ {}^{1}/_{2} \sum |p_{ij}\ p_{hj}|$, where $\mathrm{PSI}_{ih}$ is the degree of overlap between the species *i* and *h*, $p_{ij}$ and $p_{hj}$ are the proportions of the resource *j* used by the species *i* and *h*, respectively; Colwell and Futuyma 1971). This index takes its minimum value of 0 when species *i* and *h* share no resource states (= ecological categories, e.g., food items), and its maximum value of 1 when the proportional distributions of the two species among the resource states are the same (Colwell and Futuyma 1971). We based calculations of niche breadth and diet overlap on the proportion of fragments identified in samples of each species from each plant functional group. We used Kruskal–Wallis ANOVA (*H*) and the post hoc pairwise Wilcox test with Holm correction ($P < 0.05$) to perform all comparisons based on richness and BS of the four herbivores in each season. We used the Mann–Whitney *U*-test (*W*) to perform pairwise comparisons of richness and BS of each herbivore and PSI of herbivore pairs between seasons (Zar 2010).

## RESULTS

*Spatial analysis.*—Of the five habitat types, only in wetland did the four herbivores occur sympatrically during both seasons (Table 1). The observed frequency of rabbit feces was significantly different from that expected during the two seasons (wet season 2017: $\chi^2 = 15.36$, *d.f.* = 4, $P = 0.004$; dry season 2017: $\chi^2 = 11.33$, *d.f.* = 4, $P = 0.023$; Table 2). Wetlands were used by rabbit more than expected by chance (Bonferroni CI) during the entire study period, indicating positive selection for this habitat. In the case of plains viscacha, even when the observed frequency of feces was significantly different from that expected for the five habitat types (wet season: $\chi^2 = 14.45$, *d.f.* = 4, $P = 0.006$; dry season: $\chi^2 = 12.66$, *d.f.* = 4, $P = 0.013$), the Bonferroni CI included the expected proportion of use, indicating that there was no selection for those habitats. For hare and goat, no significant differences were found among the available habitat in both seasons (hare: wet season: $\chi^2 = 4.98$, *d.f.* = 4, $P = 0.29$; dry season: $\chi^2 = 7.08$, *d.f.* = 4, $P = 0.132$; goat: wet season: $\chi^2 = 1.28$, *d.f.* = 4, $P = 0.864$; dry season: $\chi^2 = 7.04$, *d.f.* = 4, $P = 0.134$).

The models that best predicted the probability of presence of herbivores for each sampling season based on the

**Table 1.**—Number of transects with feces/number of transects for five habitat types during wet and dry seasons in Laguna de Llancanelo Reserve.

| Habitat type | Rabbit | | Hare | | Goat | | Plains viscacha | |
|---|---|---|---|---|---|---|---|---|
| | Wet | Dry | Wet | Dry | Wet | Dry | Wet | Dry |
| Shrublands | — | — | 12/15 | 12/15 | 8/15 | 9/15 | — | — |
| Pichanal | 3/15 | — | 11/15 | 6/15 | 8/15 | 9/15 | — | — |
| Sand dunes | — | — | 4/15 | 3/15 | 11/15 | 11/15 | — | — |
| Wetlands | 8/15 | 7/15 | 11/15 | 5/15 | 7/15 | 7/15 | 5/15 | 7/15 |
| Tamarindal | 2/10 | — | 9/10 | 6/10 | 7/10 | — | 3/10 | — |

**Table 2.—**Simultaneous confidence intervals using the Bonferroni approach for habitat use and selection, based on rabbit (*Oryctolagus cuniculus*) feces during wet and dry seasons in Laguna de Llancanelo Reserve. An asterisk indicates the expected frequency of use that fell outside the confidence interval. (−) = negative sign.

| Season | Category | Expected proportion of use | Observed proportion of use | 95% confidence interval |
|---|---|---|---|---|
| Wet | Shrubland | 0.21 | 0 | — |
| | Pichanal | 0.21 | 0.23 | (−) 0.10–0.41 |
| | Medanal | 0.21 | 0 | — |
| | Wetland | 0.21 | 0.61 | 0.27–0.96* |
| | Tamarindal | 0.14 | 0.15 | (−) 0.07–0.53 |
| Dry | Shrubland | 0.21 | 0 | — |
| | Pichanal | 0.21 | 0.14 | (−) 0.19–0.48 |
| | Medanal | 0.21 | 0 | — |
| | Wetland | 0.21 | 0.71 | 0.27–1.15* |
| | Tamarindal | 0.14 | 0.14 | (−) 0.19–0.48 |

**Table 3.—** Top generalized linear mixed-effects models (GLMMs) examining which factors affect the presence of four herbivore species during wet and dry seasons in Laguna de Llancanelo Reserve. Transects nested in the environment are fitted as random effects. Only models with ΔAICc < 2 are shown. RIV = relative importance of each variable; Dist. = distance; AICc = Akaike's Information Criterion corrected for small sample size.

| Herbivore | Season | Model rank | Dist. water | Dist. human | Dist. road | Grasses | Graminoids | Forbs | Sub-shrubs | Woody spp. | d.f. | AICc | ΔAICc | $w_i$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Rabbit | Wet | 1 | −1.245 | 1.082 | | | | | | | 4 | 74.3 | 0.00 | 0.467 |
| | | RVI | 0.918 | 0.745 | | | | | | | | | | |
| Hare | | 1 | | | | 0.646 | | | | | 3 | 89.1 | 0.00 | 0.310 |
| | | 2 | | | | 0.626 | | | | −0.264 | 4 | 90.7 | 1.59 | 0.140 |
| | | RVI | | | | 0.793 | | | | 0.315 | | | | |
| Goat | | 1 | | | −3.091 | | | | | | 3 | 99.5 | 0.00 | 0.266 |
| | | 2 | | | −2.958 | | | | −0.356 | | 4 | 99.8 | 0.32 | 0.226 |
| | | 3 | | | | | | | −0.426 | | 3 | 100.9 | 1.47 | 0.127 |
| | | 4 | | | −3.123 | | | | −0.417 | −0.258 | 5 | 101.1 | 1.64 | 0.117 |
| | | RVI | | | 0.610 | | | | 0.594 | 0.241 | | | | |
| Plains viscacha | | 1 | | 1.914 | | | −1.778 | −0.289 | | | 5 | 48.8 | 0.00 | 0.848 |
| | | RVI | | 0.959 | | | 0.872 | 0.764 | | | | | | |
| Rabbit | Dry | 1 | −1.741 | | 8.456 | | | | | | 4 | 63.0 | 0.00 | 0.522 |
| | | 2 | −1.778 | | 8.883 | −0.263 | | | | | 5 | 64.0 | 1.86 | 0.206 |
| | | RVI | 0.916 | | 0.734 | 0.309 | | | | | | | | |
| Hare | | 1 | 0.928 | 0.668 | | | | | | | 4 | 93.9 | 0.00 | 0.487 |
| | | 2 | 0.937 | 0.715 | | | −0.215 | | | | 5 | 95.7 | 1.80 | 0.198 |
| | | RVI | 0.889 | 0.686 | | | 0.241 | | | | | | | |
| Goat | | 1 | | −1.145 | | 0.529 | | | | | 4 | 89.7 | 0.00 | 0.349 |
| | | 2 | 0.583 | −1.104 | | 0.566 | | | | | 5 | 90.0 | 0.31 | 0.298 |
| | | 3 | | −1.079 | | | | | | | 3 | 90.6 | 0.92 | 0.220 |
| | | RVI | 0.413 | 0.964 | | 0.764 | | | | | | | | |
| Plains viscacha | | 1 | | 3.236 | | | | | 0.950 | | 4 | 47.0 | 0.00 | 0.349 |
| | | 2 | | 3.197 | | | | | | | 3 | 47.5 | 0.46 | 0.278 |
| | | RVI | | 0.898 | | | | | 0.527 | | | | | |

ΔAICc and Akaike weights ($w_i$) are shown in Table 3 and Supplementary Data SD2 and SD3. During the wet season, distance to water source had the largest effect in the model for rabbit, with a negative association between this parameter and rabbit presence. Distance to human settlement was also an important factor, which showed a positive association with rabbit presence. The presence of hare was positively associated with grass cover, and negatively with woody species cover. The presence of goat was negatively associated with distance to road, subshrubs cover, and woody species cover. The presence of plains viscacha was positively associated with distance to human settlement and negatively associated with graminoids and forbs cover.

During the dry season, negative associations were observed in relation to distance to water source and grass cover with presence of rabbits. To the contrary, distance to roads was positively associated with their presence. The models for hare revealed that the distance to water sources as well as to human settlements were positively associated with their presence, while the graminoids cover was negatively associated. The presence of goat was positively associated with distance to water source and with grass cover, and negatively associated with distance to human settlement. For plains viscacha, the models revealed that there was an effect positively associated with distance to the nearest human settlement and to subshrubs cover.

*Dietary analyses.*—For dietary analyses, we used all fecal samples collected in the wetlands because the four herbivores were found in sympatry only in this habitat type (Table 1). During the wet season, dietary analyses showed that grasses were the main food item consumed by plains viscacha, goat, rabbit, and hare (57%, 43%, 41%, and 39%, respectively; Fig. 2). The second most consumed food item by hare were

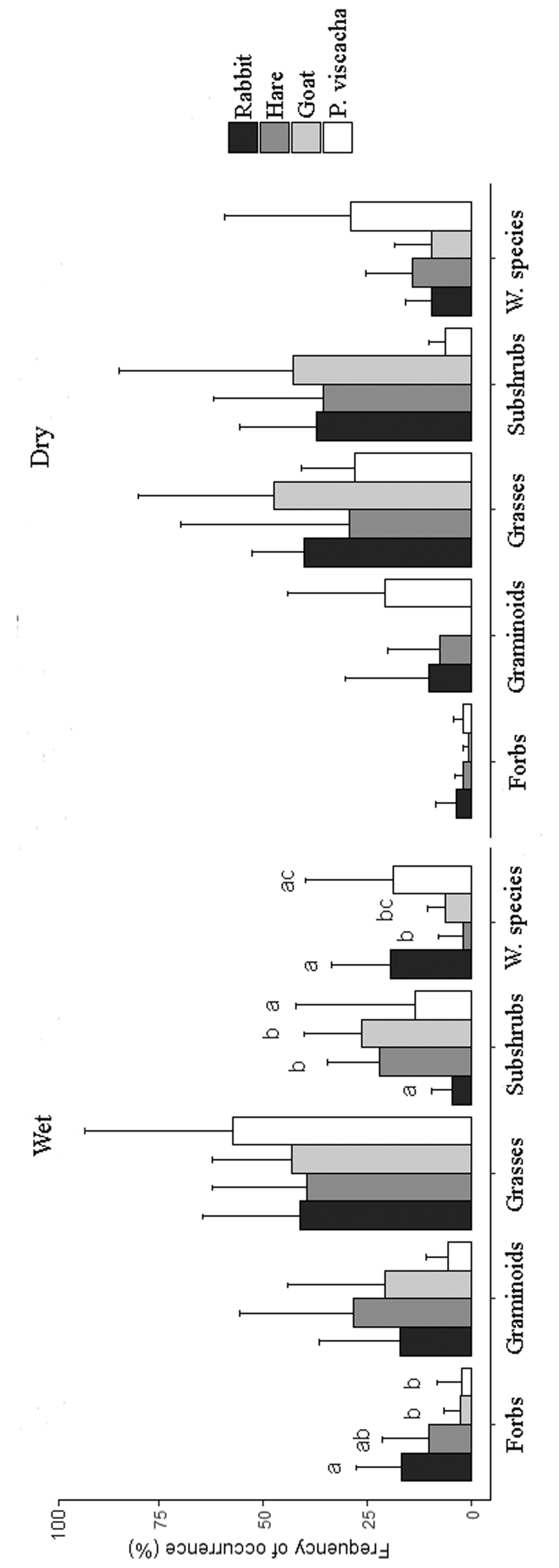

**Fig. 2.**—Seasonal variation in frequency of occurrence (mean ± *SD*) of each food category for rabbit, hare, goat, and plains viscacha in Laguna de Llancanelo Reserve. Shared letters indicate no significant differences among herbivores within each functional group by season. P. viscacha = plains viscacha; W. species = woody species.

graminoids (28%), whereas by goat were subshrubs (26%), and by rabbit and plains viscacha were woody species (31% and 19%, respectively; Fig. 2). The plant species most consumed by rabbit were the grass *D. spicata* and the forb *Cressa truxillensis*, while hare consumed mainly the grass *D. spicata* and the graminoid *Eleocharis albibracteata* (Supplementary Data SD4). In the case of goat, the grass *D. spicata* and the subshrub *F. juniperioides* were the most frequent food items. Plains viscacha's diet primarily included the grass *D. spicata* and the woody species *Capparis atamisquea* (Supplementary Data SD4).

During the dry season, grasses were the main food item category consumed by goat and rabbit (47% and 42%, respectively), followed by subshrubs (43% and 38%, respectively). For plains viscacha, woody species were the main food consumed (29%), while by hare they were subshrubs (35%; Fig. 2). The second most consumed food for hare and plains viscacha were grasses (29% and 28%, respectively; Fig. 2). The diet of rabbit was composed mainly of grasses such as *D. spicata* and *Poa* sp., while hare consumed chiefly the grasses *Poa* sp. and *Atriplex* sp. The major species consumed by goat were grasses *Poa* spp. and the woody species *F. juniperioides.* Plains viscacha's diet included mainly the grass *D. spicata* and the graminoid *E. albibracteata* (Supplementary Data SD4).

The composition of the diet of the four herbivores during the wet season was significantly different by functional groups between forbs ($H$ = 13.32, $P$ = 0.003, *d.f.* = 3), subshrubs ($H$ = 14.67, $P$ = 0.002, *d.f.* = 3), and woody species ($H$ = 17.46, $P$ = 0.0005, *d.f.* = 3; Fig. 2). Rabbits consumed significantly more forbs than did goats and plains viscacha, while goats and hares consumed significantly more subshrubs than did rabbits and plains viscacha (Fig. 2). Addionally, rabbits consumed significantly more woody species than did hares and goats, and plains viscacha consumed significantly more woody species than did hares (Fig. 2). The composition of the diet of the four herbivores during the dry season was not significantly different for any plant functional group (Fig. 2).

Manly's Index showed that diet selection varied as a function of species and by season. During the wet season, rabbits, hares, and goats selected graminoids and avoided woody species (Fig. 3). Rabbits avoided subshrubs while hares and goats consumed them proportionally to their availability in the field. The three non-native herbivores consumed forbs and grasses proportional to their availability (Fig. 3). Plains viscacha used all categories of food proportional to their availability (Fig. 3). During the dry season, rabbits and hares used all categories of available food proportional to their availability, while plains viscacha avoided subshrubs, and consumed the other food categories in proportion to their availability in the field. Goats did not consume graminoids and used the remaining categories in proportion to their availability (Fig. 3).

*Trophic niche.*—We found no statistically significant differences when comparing species richness of the four herbivores in the seasonal diets (wet season, $H$ = 7.49, $P$ = 0.053, *d.f.* = 3; dry season, $H$ = 5.75, $P$ = 0.115, *d.f.* = 3) and trophic niche breadth (wet season, $H$ = 1.75, $P$ = 0.627, *d.f.* = 3; dry

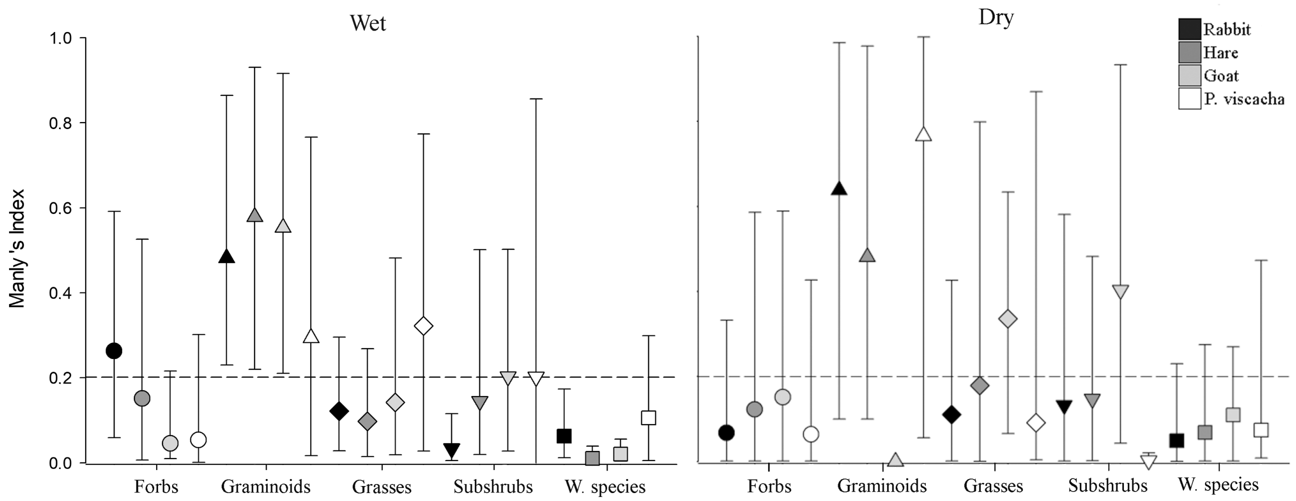

**Fig. 3.**—Manly's Selectivity Index (±95% confidence interval [CI]) for food categories consumed during wet and dry seasons by the four herbivores studied in Laguna de Llancanelo Reserve. P. viscacha = plains viscacha. The dotted line indicates $1/k = 0.2$, for a proportional use of food availability.

**Table 4.**—Plant species richness in diet and Levins' measure of trophic niche breadth (BS) (mean ± $SE$) of four herbivore species during wet and dry seasons in Laguna de Llancanelo Reserve. Different letters indicate significant differences between seasons by species.

| Season | Variables | Herbivores | | | |
|---|---|---|---|---|---|
| | | Rabbit | Hare | Goat | Plains viscacha |
| Wet | Richness | 7.20 (±2.60) | 6 (±1.49) | 5.43 (±1.13) | 4.33 (±1.75)$^{a}$ |
| | BS | 0.40 (±0.18) | 0.40 (±0.15) | 0.38 (±0.12) | 0.29 (±0.19) |
| Dry | Richness | 7.17 (±1.60) | 6 (±2.00) | 4.33 (±2.08) | 6.85 (±1.57)$^{b}$ |
| | BS | 0.38 (±0.11) | 0.35 (±0.12) | 0.31 (±0.10) | 0.39 (±0.09) |

**Table 5.**—Values of the Proportional Similarity Index (PSI) between pairs of herbivore species during wet and dry seasons in Laguna de Llancanelo Reserve. Different letters indicate significant differences between seasons.

| Herbivore | Wet | | | Dry | | |
|---|---|---|---|---|---|---|
| | Plains viscacha | Rabbit | Hare | Plains viscacha | Rabbit | Hare |
| Rabbit | 0.49 (±0.26) | | | 0.39 (±0.11) | | |
| Hare | 0.29 (±0.14) | 0.53 (±0.22) | | 0.31 (±0.16) | 0.48 (±0.04) | |
| Goat | 0.45 (±0.22)$^{a}$ | 0.48 (±0.07) | 0.35 (±0.26) | 0.05 (±0.03)$^{b}$ | 0.22 (±0.21) | 0.41 (±0.27) |

season, $H = 2.32$, $P = 0.509$, $d.f. = 3$; Table 4). Nevertheless, the viscacha's diet presented higher species richness during the dry season in comparison to the wet season ($W = 25$, $P = 0.007$; Table 4). Only in the case of plains viscacha versus goats did we detect significant differences between seasons for the values of the PSI ($W = 6$, $P = 0.036$; Table 5). During the wet season, the overlap in diet between goats and plains viscacha was 45%, while in the dry season they overlapped only 5% in diet (Table 5).

## Discussion

At the study area, the assemblage of herbivores did not segregate markedly in habitat use (shrublands, pichanal, sand dunes, wetlands, and tamarindal). Nevertheless, habitat use patterns varied among the four herbivore species, rabbits being more selective than plains viscachas, with hares and goats being the most generalist habitat users. This is consistent with previous studies in other environments showing that rabbits have a greater degree of selectivity in habitat use, whereas hares use a broader variety of habitats (Hulbert et al. 1996; Galende and Raffaele 2008). Plains viscacha have been reported in lowland habitats that include subtropical, humid grasslands, dry thorn scrub, and desert scrub (Spotorno and Patton 2015). Within the latter habitat, plains viscacha preference was for open plains (Puig et al. 1998). Although our result did not statistically detect selection for a specific habitat type, plains viscacha mainly used wetlands during both seasons.

Native and non-native herbivores showed different seasonal responses to particular components of the habitat. Rabbits are known to be associated with places having rivers, streams, or moister areas in other arid environments (Bonino and Soriguer 2009; Cuevas et al. 2011), and to select habitat primarily by antipredator considerations rather than by food abundance (Jaksic and Soriguer 1981; Jaksic and Ostfeld 1983; Iason et al. 2002). This is in line with the selection of wetland by rabbits, associated not only with proximity to water bodies but also with subshrub cover and remoteness from human settlements or roads, all components related to shelter for rabbits when they are out of their burrows (Dellafiore et al. 2008) and a lower risk of predation by wildlife or human hunting. For hares, both the positive response to grass cover and the negative response to woody species during the wet season likely indicate that suitability for forage has a strong effect (Schai-Braun et al. 2013). Nonetheless, the components of habitat not associated with their diet—distance to human settlements and to water—were more important during the dry season, suggesting that other habitat features were relevant. The negative association of goats with distance to roads and to human settlements possibly is linked with their choice of areas for livestock raising (nearness to farm). During the dry season, the occurrence of goats was positively associated with distance to water. In general, goats stand out for their better productive performance in arid and semiarid rangelands because of behavioral and physiological strategies; for example, showing less water dependence than larger ungulates (Puig et al. 2001; Egea et al. 2014). In our study, the low cover of subshrubs and of woody species detected during the wet season indicate the use of open areas by goats; while during the dry season, high grass cover was a relevant variable linked possibly with food availability. For native plains viscacha, distance to human settlements had strong effects in determining occurrence during both seasons. The response to this anthropic variable likely indicates that this species responds to increased hunting risk (Spotorno and Patton 2015) and to potential competition with livestock (Pereira et al. 2003). During the wet season, the negative association with graminoid and forb cover may be linked with feeding, because both were the least represented food categories in its diet. Given that rabbits and plains viscacha used mainly wetlands during both seasons, that their association with habitat components differed in the models could be revealing spatial segregation of these two herbivores within wetlands.

Several studies have described the diets of rabbits, hares, goats, and plains viscacha from elsewhere in the arid regions of Argentina, but not under the condition of sympatry. During the wet season, rabbit diet consisted predominantly of grasses, followed by forbs. These results are consistent with a report showing that rabbits are primarily a grass feeder throughout the year in Argentina's Patagonia (Bonino and Borrelli 2006), but they contrast with another report from the Monte Desert, in which forbs represented the main food category consumed (Bobadilla et al. 2020). The difference between these studies could be that when forbs are scarce due to the presence of other herbivores, rabbits consume mainly grasses; if alone, they prefer forbs (Soriguer 1988; Bobadilla et al. 2020). Even so, under dry conditions in arid Australia, grasses and forbs were replaced by shrub species, with rabbits behaving like opportunistic herbivores that adjusted their diet to the available food supply (Robley et al. 2001). This could also be happening in our study area, where we observed high consumption of grasses by rabbits, as well as selection of graminoids during the wet season; their being replaced by subshrubs under dry conditions.

Consistent with previous studies (Puig et al. 2007), hares in our study site consumed predominantly grasses but also high proportions of graminoids during the wet season. The diet of goats in our study area showed a seasonal alternation between the use of graminoids and subshrubs. Such alternation is consistent with this herbivore being labeled an "intermediate feeder" (Puig et al. 2001). In agreement with other studies of plains viscacha's diet in arid environments (Branch et al. 1994; Puig et al. 1998; Bontti et al. 1999; Pereira et al. 2003), grasses were the main forage throughout the year in our study site. Still, plains viscacha consumed higher species richness during the dry than during the wet season; this feeding trait has also been shown in other habitats of Argentina (Branch et al. 1994; Hagen et al. 2015).

We expected higher trophic niche overlaps between all herbivores during the wet season, because of increased food abundance. Nevertheless, we did not detect seasonal differences in trophic overlap among the four herbivores. The native plains viscacha broadened its trophic niche (higher diet richness) when items were less abundant (dry season), while plant species richness in the diets of non-native herbivores did not vary between seasons. It has been argued that the native herbivore shows a narrower trophic niche during the wet season because it feeds on the few most nutritious plants available (Pascual-Rico et al. 2020). This proposed feeding strategy for plains viscacha concurs with previous work (Branch et al. 1994) and could explain our results. For this reason, further studies should consider the nutritional quality of plants for these herbivores. Thus, the diet of the plains viscacha possibly reflects not only a change in feeding behavior in response to food availability (Puig et al. 2007), but a trophic niche adjustment in the presence of non-native herbivores when food is scarce. Still, the overlap in food use between goats and plains viscacha was larger during the wet than during the dry season. This result reinforces our contention that non-native herbivores display a minor adjustment in food consumed versus that available in comparison with the native herbivore, especially during the dry season (Reus et al. 2017).

In conclusion, the coexistence of herbivores in this arid region is facilitated by differential use of resources along with habitat, diet, and/or temporal gradients (i.e., between wet and dry seasons; Schoener 1974; Whitfield 2002; Jaksic and Marone 2007). Native and non-native herbivores overlap markedly in their trophic niche but segregate to some degree in their use of space between the two seasons. Under conditions of resource limitation (dry season), the only native herbivore examined differs in feeding strategy from the remaining three non-native herbivores. These results deepen our understanding of likely underlying mechanisms that allow coexistence of native–non-native herbivores in an arid ecosystem.

## Acknowledgments

We thank a long list of assistants for helping us with the fieldwork. We also thank the community of Laguna de Llancanelo. Lucrecia Pearson assisted with the English version. We are very grateful to the staff of Natural Reserve of Laguna de Llancanelo and Recursos Naturales Renovables of Mendoza province. We also thank to anonymous reviewers who provided valuable suggestions that greatly improved the final version of this manuscript.

Also, to the continuous support of our respective institutions: IADIZA CONICET, CCT Mendoza, Argentina and Center of Applied Ecology and Sustainability (CAPES), Santiago, Chile.

## FUNDING

This study was supported by the Rufford Foundation (21499-1), Sociedad Argentina para el Estudio de los Mamíferos (Osvaldo Reig Postgraduate Award 2018), Agencia Nacional de Promoción Científica y Tecnológica (PICT 4504/2017), and Agencia Nacional de Investigación y Desarrollo (PIA/BASAL FB0002).

## Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**—Results of pairwise correlation analysis comparing continuous variables included in analysis of generalized linear mixed-effects models.

**Supplementary Data SD2.**—Environmental (percent cover of forbs, graminoids, grasses, subshrubs, woody species, and distance to nearest water source) and anthropogenic variables (nearest human settlement and nearest road) associated with the presence of four herbivore species during the wet season in Laguna de Llancanelo Reserve, Mendoza province, Argentina. Only the significant variables of the generalized linear mixed-effects models are presented.

**Supplementary Data SD3.**—Environmental (percent cover of forbs, graminoids, grasses, subshrubs, woody species, and distance to nearest water source) and anthropogenic variables (nearest human settlement and nearest road) associated with the presence of four herbivore species during the dry season in Laguna de Llancanelo Reserve, Mendoza province, Argentina. Only the significant variables of the generalized linear mixed-effects models are presented.

**Supplementary Data SD4.**—Composition of diets (mean ± *SE* of percent frequency of occurrence by food items) of rabbit (*Oryctolagus cuniculus*), hare (*Lepus europeaus*), goat (*Capra hircus*), and plains viscacha (*Lagostomus maximus*), during the wet and dry seasons of 2017 in Laguna de Llancanelo Reserve, Mendoza province, Argentina.

## Literature Cited

Barbieri M., Berger J. 2004. Optimal predictive model selection. The Annals of Statistics 32:870–897.

Bates D., Machler M., Bolker B., Walker S. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 1:1–48.

Bobadilla S.Y., Marchetta A., Dacar M.A., Ojeda R.A., Cuevas M.F. 2020. Food habits of European rabbit and its role as seed dispersal of two Mosqueta roses: facilitation among non-native species in a semiarid protected area of Argentina? Biological Invasions 22:1565–1571.

Bobadilla S.Y., Ojeda R.A., Cuevas M.F. 2021. Invasive European wild rabbits (*Oryctolagus cuniculus*) in Argentina: state of the art and prospects for research. In: Jaksic F.M., Castro S.A., editors. Biological invasions in the South American Anthropocene: global causes and local impacts. Springer Nature; p. 187–201.

Bonino N. 2006. Estado actual del conocimiento sobre la liebre europea y el conejo europeo introducidos en la Argentina. Comunicaciones Técnicas N°61. Instituto Nacional de Tecnología Agropecuaria (INTA), Estación Experimental Agropecuaria Bariloche, Argentina.

Bonino N.A., Borrelli L. 2006. Variación estacional de la dieta del conejo silvestre europeo (*Oryctolagus cuniculus*) en la región andina de Neuquén, Argentina. Ecología Austral 16:7–13.

Bonino N., Soriguer R. 2009. The invasion of Argentina by the European wild rabbit *Oryctolagus cuniculus*. Mammal Review 39:159–166.

Bontti E.E., Boo R.M., Lindstrom L.I., Elia O.R. 1999. Botanical composition of cattle and vizcacha diets in central Argentina. Journal of Range Management 52:370–377.

Branch L.C., Villarreal D., Sbriller A.P., Sosa R.A. 1994. Diet selection of the plains vizcacha (*Lagostomus maximus*, family Chinchillidae) in relation to resource abundance in semi-arid scrub. Canadian Journal of Zoology 72:2210–2216.

Broomhall L.S., Mills M.G.L., Du Toit J.T. 2003. Home range and habitat use by cheetahs (*Acinonyx jubatus*) in the Kruger National Park. Journal of Zoology 261:119–128.

Bucher E.H. 1987. Herbivory in arid and semi-arid regions of Argentina. Revista Chilena de Historia Natural 60:265–273.

Cabrera Á.L. 1994. Regiones fitogeográficas argentinas. In: Kugler W.F., editor. Enciclopedia argentina de agricultura y jardinería. Tomo 2. 2da ed., 1ra reimpresión. Acme, Buenos Aires, Argentina; p. 1–85.

Campos C.M., Ojeda R., Monge S., Dacar M. 2001. Utilization of food resources by small- and medium-sized mammals in the Monte Desert biome, Argentina. Austral Ecology 26:142–149.

Canty A., Ripley B.D. 2021. boot: bootstrap R (S-Plus) functions. R package version 1.3-28.

Chapman J.A., Flux J.E. 2008. Introduction to the Lagomorpha. In: Alves P.C., Ferrand N., Hackländer K., editors. Lagomorph biology, evolution, ecology, and conservation. Springer Berlin, Heidelberg; p. 1–9.

Colwell R.K., Futuyma D.J. 1971. On the measurement of niche breadth and overlap. Ecology 52:567–576.

Cooke B.D., Mutze G.J. 2018. How introduced rabbits *Oryctolagus cuniculus* limit the abundance of red kangaroos *Macropus rufus* and other native grazers in Australia. Food Webs 15:e00079.

Cortázar-Chinarro M., Halvarsson P., Virgós E. 2019. Sign surveys for red fox (*Vulpes vulpes*) censuses: evaluating different sources of variation in scat detectability. Mammal Research 64:183–190.

Cuevas M.F., Chillo V., Marchetta A., Ojeda R.A. 2011. Mammalia, Lagomorpha, Leporidae, *Oryctolagus cuniculus* Linneaus, 1758: new record and its potential dispersal corridors for northern Mendoza, Argentina. Check List 7:565–566.

Cuevas M.F., Ojeda R.A., Dacar M.A., Jaksic F.M. 2013. Seasonal variation in feeding habits and diet selection by wild boars in a semi-arid environment of Argentina. Acta Theriologica 58:63–72.

Dacar M.A., Giannoni S.M. 2001. A simple method for preparing reference slides of seed. Journal of Range Management 54:191–193.

Danell K., Bergström R., Duncan P., Pastor J. 2006. Large herbivore ecology, ecosystem dynamics and conservation. Cambridge University Press, Cambridge.

Davison A.C., Hinkley D.V. 1997. Bootstrap methods and their application. Cambridge University Press, Cambridge.

De Fina A.L., Giannetto F., Richard A.E., Sabella L.S. 1964. Difusión geográfica de los cultivos índices de la provincia de Mendoza y sus causas. INTA, Instituto de Suelos y Agrotecnia, Mendoza, Argentina.

Dellafiore C.M., Fernández J.B.G., Valles S.M. 2008. Habitat use for warren building by European rabbits (*Oryctolagus cuniculus*) in relation to landscape structure in a sand dune system. Acta Oecologica 33:372–379.

Egea A.V., Allegretti L., Paez Lama S., Grilli D., Sartor C., Fucili M., Guevara J.C., Passera C. 2014. Selective behavior of Creole goats in response to the functional heterogeneity of native forage species in the central Monte desert, Argentina. Small Ruminant Research 120:90–99.

Fernández O.A., Busso C.A. 1999. Arid and semi-arid rangelands: two thirds of Argentina. The Agricultural Research Institute 200:41–60.

Flux J.E. 2008. A review of competition between rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*). In: Alves P.C., Ferrand N., Hackländer K., editors. Lagomorph biology, evolution, ecology, and conservation. Springer Berlin, Heidelberg; p. 241–249.

Galende G.I., Raffaele E. 2008. Space use of a non-native species, the European hare (*Lepus europaeus*), in habitats of the southern vizcacha (*Lagidium viscacia*) in Northwestern Patagonia, Argentina. European Journal of Wildlife Research 54:299–304.

Gálvez Bravo L.G., Belliure J., Rebollo S. 2009. European rabbits as ecosystem engineers: warrens increase lizard density and diversity. Biodiversity and Conservation 18:869–885.

Garshelis D.L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. In: Pearl M.C., editor. Research techniques in animal ecology: methods and cases in conservation science. Columbia University Press; p. 111–164.

Guevara J.C., Cavagnaro J.B., Estevez O.R., Le Houérou H.N., Stasi C.R. 1997. Productivity, management and development problems in the arid rangelands of the central Mendoza plains (Argentina). Journal of Arid Environments 35:575–600.

Hagen K.B., Besselmann D., Cyrus-Eulenberger U., Vendl C., Ortmann S., Zingg R., Kienzle E., Kreuzer M., Hatt J.M., Clauss M. 2015. Digestive physiology of the plains viscacha (*Lagostomus maximus*): a large herbivorous hystricomorph rodent. Zoo Biology 34:345–359.

Holechek J., Gross B. 1982. Evaluation of different calculation procedures for microhistological analysis. Journal of Range Management 35:721–723.

Hulbert I.A.R., Iason G.R., Racey P.A. 1996. Habitat utilization in a stratified upland landscape by two lagomorphs with different feeding strategies. Journal of Applied Ecology 33:315–324.

Hurlbert S.H. 1978. The measurement of niche overlap and some relatives. Ecology 59:67–77.

Hutchinson G.E. 1957. The multivariate niche. Cold Spring Harbor Symposia Quantitative Biology 22:415–427.

Iason G.R., Manso T., Sim D.A., Hartley F.G. 2002. The functional response does not predict the local distribution of European rabbits (*Oryctolagus cuniculus*) on grass swards: experimental evidence. Functional Ecology 16:394–402.

Jaksic F.M., Castro S.A. 2021. Biological invasions in the South American Anthropocene: global causes and local impacts. Springer Nature.

Jaksic F.M., Fuentes E.R., Yañez J.L. 1979. Spatial distribution of the Old World rabbit (*Oryctolagus cuniculus*) in central Chile. Journal of Mammalogy 60:207–209.

Jaksic F.M., Iriarte J.A., Jiménez J.E., Martínez D.R. 2002. Invaders without frontiers: cross-border invasions of exotic mammals. Biological Invasions 4:157–173.

Jaksic F.M., Marone L. 2007. Ecología de comunidades. 2da ed. Ediciones Universidad Católica de Chile, Santiago, Chile.

Jaksic F.M., Ostfeld R.S. 1983. Numerical and behavioral estimates of predation upon rabbits in Mediterranean-type shrublands: a paradoxical case. Revista Chilena de Historia Natural 56:39–49.

Jaksic F.M., Soriguer R.C. 1981. Predation upon the European rabbit (*Oryctolagus cuniculus*) in Mediterranean habitats of Chile and Spain: a comparative analysis. The Journal of Animal Ecology 50:269–281.

Liu X., Toxopeus A.G., Skidmore A.K., Shao X., Dang G., Wang T., Prins H.H. 2005. Giant panda habitat selection in Foping Nature Reserve, China. Journal of Wildlife Management 69:1623–1632.

López-Cortés F., Cortés A., Miranda E., Rau J.R. 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.

Lush L., Ward A.L., Wheeler P. 2017. Dietary niche partitioning between sympatric brown hares and rabbits. Journal of Zoology 303:36–45.

MacArthur R., Levis R. 1967. The limiting similarity, convergence and divergence of coexisting species. American Naturalist 101:377–385.

Manly B.F.J., Mc Donald L.L., Thomas D.L. 2002. Resource selection by animals. Statistical design and analysis for field studies. 2nd ed. Chapman and Hall, London, United Kingdom.

Méndez E. 2005. La vegetación de la Reserva Provincial Laguna de Llancanelo (Mendoza, Argentina). Candollea 60:123–148.

Neu C.W., Randall Byers C., Peek J.M. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38:541–545.

Nuñez M.A., Bailey J.K., Schweitzer J.A. 2010. Population, community and ecosystem effects of exotic herbivores: a growing global concern. Biological Invasions 12:297–301.

Ojeda R.A., Tabeni S. 2009. The mammals of the Monte Desert revisited. Journal of Arid Environments 73:173–181.

Owen-Smith N. 2002. Adaptative herbivore ecology. from resources to populations in variable environments. Wits University Press, Johannesburg, South Africa.

Palma-Leotta M., Torres J., Cisneros H., Caliri M., Ordoñez M., Gorla N.B.M. 2019. Aportes de la teledetección para la caracterización de amenazas para la conservación del sitio Ramsar humedal Llancanelo, Malargüe, Argentina. Boletín de Estudios Geográficos 112:83–113.

Pascual-Rico R., Sánchez-Zapata J.A., Navarro J., Eguía S., Anadón J.D., Botella F. 2020. Ecological niche overlap between co-occurring native and exotic ungulates: insights for a conservation conflict. Biological Invasions 22:2497–2508.

Passera C.B., Dalmasso A.D., Borsetto O. 1986. Método de “Point Quadrat Modificado”. In: Candia R.J., Braun R.H., editors. Taller de Arbustos Forrajeros para Zonas Áridas y Semiáridas. Subcomité Asesor del Árido Subtropical Argentino, Buenos Aires, Argentina; p. 71–79.

Pelliza A., Willems P., Manacorda M. 2001. Dietary structural types of polygastric herbivores at different environments and seasons. Journal of Range Management 54:330–337.

Pereira J.A., Quintana R.D., Monge S. 2003. Diets of plains vizcacha, greater rhea and cattle in Argentina. Journal of Range Management 56:13–20.

Puig S., Videla F., Cona M.I., Monge S.A. 2001. Use of food availability by guanacos (*Lama guanicoe*) and livestock in Northern Patagonia (Mendoza, Argentina). Journal of Arid Environments 47:291–308.

Puig S., Videla F., Cona M.I., Monge S.A. 2007. Diet of the brown hare (*Lepus europaeus*) and food availability in northern Patagonia (Mendoza, Argentina). Mammalian Biology 72:240–250.

Puig S., Videla F., Cona M.I., Monge S.A., Roig V. 1998. Diet of the vizcacha *Lagostomus maximus* (Rodentia, Chinchillidae), habitat preferences and food availability in Northern Patagonia, Argentina. Mammalia 62:191–204.

R Development Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. www.R-project.org/. Accessed 20 September 2020.

Reus M.L., De los Ríos C., Peco B., Giannoni S.M., Campos C.M. 2017. Relaciones tróficas entre mamíferos herbívoros nativos y exóticos del Parque Provincial Ischigualasto (San Juan, Argentina). Ecología Austral 27:392–403.

Robley A.J., Short J., Bradley S. 2001. Dietary overlap between the burrowing bettong (*Bettongia lesueur*) and the European rabbit (*Oryctolagus cuniculus*) in semi-arid coastal Western Australia. Wildlife Research 28:341–349.

Salgado I. 2016. Conejo *Oryctolagus cuniculus* (Linnaeus, 1758). In: Calzada J., Clavero M., Fernández A., editors. Guía virtual de los indicios de los mamíferos de la Península Ibérica, Islas Baleares y Canarias. Sociedad Española para la Conservación y Estudio de los Mamíferos (SECEM). http://www.secem.es/guiadeindiciosmamiferos. Accessed 21 November 2021.

Schai-Braun S.C., Reichlin T.S., Ruf T., Klansek E., Tataruch F., Arnold W., Hackländer K. 2015. The European hare (*Lepus europaeus*): a picky herbivore searching for plant parts rich in fat. PLoS One 10:e0134278.

Schai-Braun S.C., Weber D., Hackländer K. 2013. Spring and autumn habitat preferences of active European hares (*Lepus europaeus*) in an agricultural area with low hare density. European Journal of Wildlife Research 59:387–397.

Schoener T.W. 1974. Resource partitioning in ecological communities. Science 185:27–39.

Simberloff D., Dayan T. 1991. The guild concept and the structure of ecological communities. Annual Reviews of Ecology and Systematics 22:115–143.

Soriguer R.C. 1988. Alimentación del conejo (*Oryctolagus cuniculus* L. 1758) en Doñana. SO, España. Doñana Acta Vertebrata 15:141–150.

Spotorno A.E., Patton J.L. 2015. Superfamily Chinchilloidea Bennett, 1833. In: Patton J.L., Pardiñas U.F.J., D'Elia G., editors. Mammals of South America, vol. 2: rodents. University of Chicago Press; p. 762–783.

Stabach J.A., Rabeil T., Turmine V., Wacher T., Mueller T., Leimgruber P. 2017. On the brink of extinction—habitat selection of addax and dorcas gazelle across the Tin Toumma desert, Niger. Diversity and Distributions 23:581–591.

Stewart K.M., Bowyer R.T., Kie J.G., Cimon N.J., Johnson B.K. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. Journal of Mammalogy 83:229–244.

Stott P.A. 2003. Use of space by sympatric European hares (*Lepus europaeus*) and European rabbits (*Oryctolagus cuniculus*) in Australia. Mammalian Biology 68:317–327.

Symonds M.R.E., Moussalli A. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology Sociobiology 65:13–21.

Vázquez D.P. 2002. Multiple effects of introduced mammalian herbivores in a temperate forest. Biological Invasions 4:175–191.

Villagra P.E., Defossé G.E., Del Valle H.F., Tabeni S., Rostagno M., Cesca E., Abraham E. 2009. Land use and disturbance effects on the dynamics of natural ecosystems of the Monte Desert: implications for their management. Journal of Arid Environments 73:202–211.

Villagra E.S., Pelliza A., Willems P., Siffredi G., Bonvissuto G. 2013. What do domestic livestock eat in northern Patagonian rangelands? Animal Production Science 53:360–367.

Whitfield J. 2002. Neutrality versus the niche. Nature. 417:480–481.

Whitford W. 2002. Ecology of desert systems. Academic Press, London, United Kingdom and San Diego, California, USA.

Young T.P., Palmer T.M., Gadd M.E. 2005. Competition and compensation among cattle, zebras and elephants in a semi-arid savanna in Laikipia, Kenya. Biological Conservation 122:351–359.

Zar J.H. 2010. Biostatistical analysis. 5th ed. Pearson Education, Upper Saddle River, New Jersey, USA.

*Submitted 17 September 2020. Accepted 18 December 2021.*

*Associate Editor was Ariovaldo Cruz.*