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# Habitat and food preferences of European rabbits in core and edge populations along the invasion front Patagonia-Monte, Argentina

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## Abstract

The European rabbit *Oryctolagus cuniculus* is an exotic herbivorous mammal undergoing an active phase of geographical expansion in the arid ecosystems of Argentina. The Adaptive Flexibility Hypothesis states that populations at the range edge (new populations) will exhibit greater flexibility in the use of resources compared with populations located in the range core (older populations). The objective of this work was to compare the rabbit's use of spatial and trophic resources in relation to the establishment time of their populations. The sampling was carried out for 2 years (2017 and 2018) in sites with different establishment times for rabbit populations. Random sampling stratified by type of habitat was applied using 115 fixed strip transects of 1,000 m² laid out across the study areas. Fresh rabbit signs were recorded in each transect, and environmental and anthropic variables were measured. Our results show that the individuals from the range edge are more selective in the use of habitat than those from the range core. At the microhabitat level, we observed a pattern in the particular components of habitat use by rabbits mainly linked to food availability and proximity to water. From a trophic perspective, rabbits could show flexible adjustment to novel conditions and environments in the range edge. The variability in resource use by the European rabbit confirms its ecological flexibility, pivotal for their advance toward new environments in Argentina.

**Key words:** Arid ecosystems, invasive species, novel environments, range invasion, spatial use, trophic use.

Biological invasions are considered one of the main drivers of global change, generating problems for the conservation of biodiversity and natural resources (Sala et al. 2000; Simberloff et al. 2013). Of the 4 stages of an invasion (i.e., transport, introduction, establishment, and range expansion), the latter is arguably the most important because it is when an invading species causes its largest impacts (Liebl and Martin 2012). In this late stage of the invasion process, geographic range shifts occur rapidly, which is of great interest in studying geographic range expansion processes (Sax et al. 2007). When populations expand, individuals face different selection pressures. Toward this, they may present relevant morphological (e.g., longer limb segments), physiological (e.g., stressor hyper-responsiveness), or behavioral (e.g., exploration) traits that allow them to cope with new conditions in novel environments at the edge of the range (Liebl and Martin 2012; Louppe et al. 2017). Behavioral traits may be especially important during range expansion because they are often more labile than other traits, and thus more apt to match local environment conditions (Snell-Rood 2013).

From a behavioral approach to biological invasions, Wright et al. (2010) proposed that invasive species may change the degree to which they express behavioral flexibility in an adaptive manner during the different stages of the invasion process, favoring the invasion of new habitats (Adaptive Flexibility Hypothesis). They hypothesized that during the initial introduction stage, when founding individuals are exploring a new environment, innovation will be favored, and the expression of flexibility will be high. Later, in established populations, copying the more successful behavioral variants will be favored over exploration and innovation due to the risks associated with exploration, as well as the opportunity costs of foregoing behavioral alternatives that other individuals have demonstrated to be successful (Wright et al. 2010). Finally, in the invasion stage, the populations in the range edge will occupy novel environments that offer new resources to be exploited and new dangers to be faced; therefore, behavioral flexibility will again be favored among dispersers (Wright et al. 2010). Thus, populations at the range edge should express greater behavioral

innovation; for example, flexibility in foraging strategies, diet or habitat choice, nesting or burrowing site choice, or anti-parasite strategies, than older populations or those located in the core of the range (Wright et al. 2010). Several studies with invasive species have shown that different levels of behavioral features are expressed when comparing populations with different establishment times (individuals in new populations—range edge—with those in older populations—range core) (Liebl and Martin 2012, 2014; Webb et al. 2014; Gruber et al. 2017). There are good empirical advances in understanding the role of flexible behavior in the invasion process among various vertebrate taxa such as fish, amphibians, reptiles, and birds (Shine 2017). In particular, invasive mammals stand out for being more invasive than other vertebrates (Jeschke 2008), and thus assessing the role of flexible behavior among these invasive species may deepen our understanding of the role of flexible behavior in the invasion process.

The European rabbit *Oryctolagus cuniculus* is considered one of the 100 most harmful invasive alien species in the world due to its high plasticity and its negative impact on biological diversity and human activities (Lowe et al. 2000). This rabbit became established and successfully invaded central Chile (Jaksic et al. 2002). From there, it slowly expanded its distribution from east of the Andes mountains toward the provinces of Neuquén and Mendoza, in the arid ecosystems of central-west of Argentina (Figure 1). Like many arid regions, livestock farming is the predominant land use in Argentina drylands, and the vegetation has been degraded as a result of overgrazing, forcing changes in the composition of domestic herbivores, where cattle and sheep have been replaced by goats (*Capra hircus*; Guevara et al. 1997). The pastoralism carried out in these areas is based on the exploitation of primary productivity (natural pastures) through seasonal transhumance, a grazing modality linked to the activity of goat

fattening, prioritizing the use of tender pastures in mountain ranges during the wet season, while lowland pastures recover from being used during the dry season (Baied 1989). However, there is a degree of residential mobility of positions that fluctuates from annual permanence in the plains areas to transhumant pastoralists up in the Andes (Otaola et al. 2016).

In Argentina, European rabbits are known to be associated with places hosting rivers, streams, or moister areas that provide them with feeding and sheltering sites (Bonino and Soriguer 2009; Bobadilla et al. 2022). In relation to the use of trophic resources, in the central Andean region of Argentina rabbits mainly feed on grasses. However, when grasses are scarce, they exhibit a flexible behavior by consuming woody vegetation, adapting and adjusting their diet to the available food supply (Bonino and Borrelli 2006).

The European rabbit was first recorded in the arid region of Argentina in the 1970s. The diverse mosaic of habitats in this region constitutes an important scenario for the evolution of the biota and supports more species and endemic genera than other macrohabitats or biomes (Ojeda and Tabeni 2009). In these arid ecosystems, European rabbit populations are in an active process of expansion of the invaded area according to surveys carried out between 1969–1972 (Howard and Amaya 1975) and 1986–2003 (Bonino and Soriguer 2004). The first available record of the European rabbit's advance in Mendoza province dates back to 1972 in the locality of Bardas Blancas (35°52′S - 69°48′W, 1,420 to 2,800 m elevation), near the Grande River at the northern limit of their distribution (Howard and Amaya 1975) (Figure 1). In a survey conducted in 1986, it was determined that rabbit distribution in the southwest of Mendoza province extended to the Malargüe and Grande Rivers as its northern and eastern limits, respectively, occupying an area of 6,200 km², including the town of Bardas Blancas to the east (Bonino and Soriguer



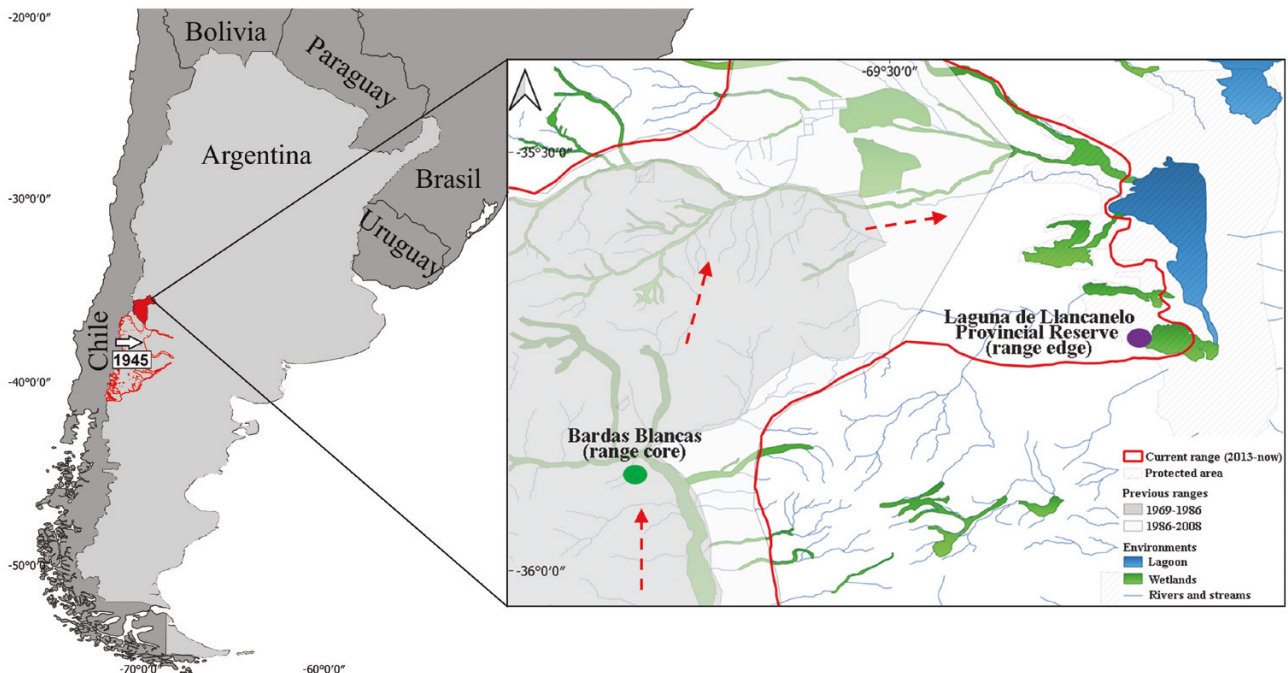**Figure 1.** Left: Map of Argentina showing the location of range distribution of European rabbit in the province of Neuquén (red-line area) (Guichón et al. 2016) and expansion to arid ecosystems of Mendoza, Argentina (red-filled area) (Cuevas et al. 2019). Right: Zoom of the study area showing previous and current distribution ranges of European rabbit and the location of the sites "range core" and "range edge."

2004). By 2003, the total occupied area in Mendoza province increased to 11,000 km², with the Salado River valley becoming the northern limit of their distribution (Bonino and Soriguer 2004). A more recent update of rabbit's distribution in this area was performed by Bonino and Soriguer (2009), noting that the rabbit is currently undergoing a dispersal process. Afterward, in 2013, rabbits were observed within the limits of Laguna de Llancanelo Provincial Reserve (35°45´S - 69°08´W, 1,270 to 1,500 m elevation) according to the information provided by park rangers (personal communication). In 2017, European rabbits were present in the wetlands of the Reserve, which is a Ramsar site encompassing approximately 90,000 ha that includes one of the largest endorheic lagoons of the region with both permanent (rivers and streams) and temporary water inputs (Bobadilla et al. 2022) (Figure 1).

In addition to these previous reports about rabbit ecology and distribution, to our knowledge, no studies have been conducted to evaluate the use of resources and their variation in relation to rabbit establishment and expansion as linked to behavioral flexibility. To assess the advance of this species to new ecoregions, such as the Monte Desert, it is important to understand the ecological strategies that rabbits use to survive extreme and variable conditions in xeric habitats. In this regard, we hypothesize that according to the Adaptive Flexibility Hypothesis, variability in the use of spatial and trophic resources by the European rabbit should change according to the establishment time at different sites. Comparing individuals belonging to core and edge populations across the range, we predict that rabbits at the edge will 1) use spatial resources (habitat and microhabitat) in a more diversified manner and 2) use trophic resources in a more diversified way. Thus, we aim to compare the use of resources (spatial and trophic) by European rabbits with different residence times (range core vs. range edge).

## Material and Methods

### Study areas

We set up sampling in the wet (December to February) and dry (June to August) seasons of 2017 and 2018 in 2 areas with different rabbit population's residence times within 2 arid ecosystems of Argentina: 1) Bardas Blancas, the core area of the rabbit's expansion range (residence time over 45 years), hereafter called range core and 2) Laguna de Llancanelo Provincial Reserve, the easternmost edge of the rabbit's expansion range (residence time 5 years), hereafter called range edge (Figure 1).

### Sampling design

For the quantification of spatial and trophic use, we recorded fresh rabbit signs (feces, latrines, and warrens) using a stratified random sampling model for 115 fixed strip transects of 1,000 m² (5 m × 200 m) laid out across the study areas on the habitat types recognized. We covered a total area of approximately 20 km² in range core (45 transects) and 66 km² in range edge (70 transects). The number of transects in each habitat was set by considering the surface that allowed to characterize the different environments and the access logistics. Number of transects varied from 10 (for tamarindal) to 15 (for the rest of the habitat types). They 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. The criterion of a minimum distance of 500 meters between transects was adopted to consider them as independent sampling units (Dellafiore et al. 2008). Thereby, in each transect, we recorded the presence or absence of feces along each transect and collected fresh feces that constituted a single sample for diet analysis. Fecal pellets of European rabbits are easy to identify in the field by observing their sizes, colors, shapes, and rugosity (Salgado 2016). 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.

In the middle of each study transect, we established one vegetation transect 50 m long, where we measured the specific composition of plants and vegetation cover for each sampling season (Passera et al. 1986). We recorded species, percent cover of bare soil, litter, forbs, graminoids (Juncaceae and Ciperaceae), grasses, sub-shrubs (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 areas to create a reference collection. Other variables recorded at each transect included distance to the nearest water body (considered it as an environmental variable) and anthropogenic variables such as the nearest human settlement and the 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 body, nearest human settlement, and nearest road). We used the GIS hydrology layer (that for this study included lagoons, rivers, streams, and water wells), GIS population layer, and GIS road network layer of the study area.

### Spatial analysis

We used 2 different approaches for spatial analysis: Use and selection of habitat types (habitat type defined by dominant cover) and factors shaping habitat selection (particular components of the habitat used by an individual within its activity area; Garshelis 2000; Stabach et al. 2017). To analyze habitat selection, we considered the 3 main habitat types in range core (shrubland, wetland, and pastureland) and the 5 main habitat types in range edge (shrubland, pichanal, sand dune, wetland, and tamarindal). To assess variation in habitat types, we used the Shannon-Wiener diversity index (Magurran 1988). We used Kruskal–Wallis ANOVA (*H*) and the post hoc pairwise Wilcox test with Holm correction (*P* < 0.05) to perform all comparisons among habitat types within the same season (Zar 2010). 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 frequencies along transects with those expected by the proportional availability of the different habitat types. Expected frequencies were calculated considering the total number of transects measured at each habitat type by study area and sampling season. When significant differences were found, we applied Bonferroni confidence intervals (CIs) for each frequency of occurrence in each type of habitat (Broomhall et al. 2003; Liu et al. 2005). This analysis allowed us to determine which—if any—habitat type was selected (i.e., if the use was proportional or not to what was available) by European rabbit in each study area and sampling season. 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 (if the frequency of usage was greater than expected) or avoidance (if the frequency of usage was lower than expected) by rabbits (Neu et al. 1974; López-Cortés et al. 2007).

To assess particular components of the habitat that influenced the presence of rabbits, 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 sampling season, using as response variable the presence/absence of rabbit signs. For models fitted, we selected 11 fixed effects: 1 qualitative variable (establishment time at range core or range edge), 8 quantitative environmental variables, and 2 anthropogenic variables as fixed effects. We only added to the model those variables which were not correlated to each other. We considered transects nested in the habitat types and year as random effects. This structure of random effects allows modeling the spatial correlation that may exist between transects due to sampling design (Zuur et al. 2009). 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's weight (*wi*; Symonds and Moussalli 2011). The most representative candidate models were considered, presenting as a whole an accumulated weight of 0.95, ordered from highest to lowest (Burnham and Anderson 2002). We also estimated the relative importance of each variable (RIV) (Symonds and Moussalli 2011). Fixed effects with RIV > 0.5 were considered the most statistically informative (Barbieri and Berger 2004).

### Trophic analysis

To determine the composition of the rabbit diet, we used all feces collected during each season (wet and dry) of the year 2017 in both study areas. Samples were analyzed using the microhistological technique by Dacar and Giannoni (2001) that permits the identification of leaf epidermis, stems, seed teguments, fruits, and rhizome tissues, which is widely used to study the diet of herbivores (Borgnia et al. 2010; Reus et al. 2013). For each sample, we prepared 5 microscope slides and systematically examined 50 fields under the 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 comparing fragments with a reference collection of epidermic tissues of leaves, stems, seed teguments, and fruits. When possible, the material was identified to the species level. The 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). Foods were grouped into 5 categories based on plant life forms: Forbs, graminoids, grasses, sub-shrubs, and woody species. We used Kruskal–Wallis ANOVA (*H*) and the post hoc pairwise Wilcox test with Holm correction (*P* < 0.05) to perform all the comparisons of food categories within the same season and study area (Zar 2010). We used the Mann–Whitney (W) test to make pairwise comparisons of each food category between study areas for the same season (*P* < 0.05) (Zar 2010).

To determine variation in the niche breadth for each sample at each site and season, we used the Shannon Wiener diversity index (H′ = −Σ $p_i$ × ln $p_i$, where pi is the proportion of item i in the total number of items found in the sample (*N*) and is calculated as follows: ni/*N* (Magurran 1988). We used the Mann–Whitney *U*-test (W) to perform pairwise comparisons between-study areas and seasons (Zar 2010). To determine if there was a selection of food resources, we used data on their availability obtained from measurements of the vegetation transects. Selectivity of food categories was estimated using Manly's Selectivity Index ($\alpha_i$ = $Pu_i$/$Pa_i$ × 1/$\Sigma Pu_i$/$Pa_i$, where $Pu_i$ is the observed proportion of item i in rabbit diet and $Pa_i$ 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 2019). 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 mean 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.

## Results

A total of 77 sampled transects had rabbit feces at both establishment times for the 2 years of sampling (Table 1). On average for both years, 20% of the sampled transects had rabbit feces in the wet season and 17% in the dry season at the range core. For the range edge, on average for both years, 16% of sampled transects had rabbit feces in the wet season and 15% in the dry season (Table 1).

### Spatial analysis

Habitat diversity used by rabbits was similar for wetland, pastureland, and tamarindal between establishment times in each season. Nevertheless, shrubland and pichanal had significantly more habitat diversity used by rabbits (Supplementary Material 1).

At the range core, we did not find any difference between frequencies of rabbit feces in the different habitat types, both for the wet (2017: *n* = 12, χ² = 2.2, *df* = 2, *P* = 0.33; 2018: *n* = 6, χ² = 1.68, *df* = 2, *P* = 0.43) and dry seasons (2017: *n* = 3, χ² = 0.75, *df* = 2, *P* = 0.69; 2018: *n* = 12, χ² = 2.67, *df* = 2, *P* = 0.26). To the contrary, in the range edge, the observed frequency of rabbit feces was significantly different from that expected during the wet season of 2017 (*n* = 14, χ² = 12.12, *df* = 4, *P* < 0.05) and the dry season of 2018 (*n* = 15, χ² = 21, *df* = 4, *P* < 0.001; Table 2). Wetlands were used by rabbits more

**Table 1.** Number of transects with feces/number of transects total for two study sites during wet and dry in 2017 and 2018

| Site | 2017 | | 2018 | |
|---|---|---|---|---|
| | Wet | Dry | Wet | Dry |
| Range core | 12/45 | 3/45 | 6/45 | 12/45 |
| Range edge | 14/70 | 6/70 | 9/70 | 15/70 |

than expected by chance (Bonferroni CI), indicating positive selection for this habitat (Table 2).

The models that best predicted the probability of rabbit presence for each season, based on the ΔAICc and Akaike weights (*wi*), are shown in Table 3. In all these models, the RIV of variable time (establishment times) was high (>0.90). For both establishment times and seasons, the distance to the water body had the largest effect in the models, with a negative association between this parameter and rabbit presence (Table 3, Figure 2). The presence of rabbits was also positively associated with forb cover during both seasons. Besides, in the dry season, RIV of grass cover was high, which showed a positive association with rabbit presence (Table 3).

## Trophic analysis

Rabbit diet during the wet season was composed of different parts of 35 plant species in range core and of 18 plant species in range edge (Supplementary Material 2). Rabbits consumed mainly grasses, followed by woody species, graminoids, and forbs, in both establishment times (Figure 3A). During the dry season, the diet was composed of 13 plant species in range core and of 17 plant species in range edge (Supplementary Material 3). Grasses and woody species were the main food categories consumed in the range core (Figure 3A), whereas grasses and sub-shrubs were the most consumed in the range edge (Figure 3A). The diet composition of rabbits was significantly different by food categories for the same season between establishment times (Figure 3A).

Trophic niche breadth was greater in range core that in range edge during the wet season (*W* = 149, *P* < 0.01; Figure 3B). During this season, trophic selection by food categories was positive for forbs, while sub-shrubs were avoided (Figure 3C). In the range edge, rabbits selected graminoids while avoiding woody species and sub-shrubs (Figure 3C).

**Table 2.** Simultaneous confidence intervals using the Bonferroni approach for habitat use and selection, based on European rabbit (*Oryctolagus cuniculus*) feces during wet 2017 and dry 2018 seasons in site edge range

| Season | Year | Habitat type | Expected proportion of use | Observed proportion of use | 95% Confidence interval |
|---|---|---|---|---|---|
| Wet | 2017 | Shrubland | 0.21 | 0 | - |
| | | Pichanal | 0.21 | 0.23 | (–) 0.103–0.411 |
| | | Sand dune | 0.21 | 0 | - |
| | | Wetland | 0.21 | 0.61 | **0.269–0.962*** |
| | | Tamarindal | 0.14 | 0.15 | (–) 0.069–0.531 |
| Dry | 2018 | Shrubland | 0.21 | 0.06 | (–) 0.099–0.232 |
| | | Pichanal | 0.21 | 0.2 | (–) 0.066–0.466 |
| | | Sand dune | 0.21 | 0 | - |
| | | Wetland | 0.21 | 0.73 | **0.439–1.027*** |
| | | Tamarindal | 0.14 | 0.0 | - |

An asterisk indicates the expected frequency of use that fell outside the confidence interval. (–) = negative sign.

**Table 3.** Top generalized linear mixed-effects models examining which factors affect the presence of European rabbit during wet and dry seasons

| Season | Model rank | Time: range Core | Time: range Edge | D. Water | D. Human | Grass | Graminoids | Herbs | Sub- Shrubs | Woody spp. | df | AICc | ΔAICc | wi | Cumulative Weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Wet** | 1 | –2.511 | –2.251 | –1.164 | — | — | — | 0.229 | — | — | 7 | 207.2 | 0 | 0.38 | 0.39 |
| | 2 | –2.582 | –2.135 | –1.229 | — | — | — | — | –0.014 | — | 7 | 208.4 | 1.18 | 0.21 | 0.60 |
| | 3 | –2.514 | –2.251 | –1.163 | — | 0.012 | — | 0.229 | — | — | 8 | 209.4 | 2.14 | 0.13 | 0.73 |
| | 4 | –2.642 | –2.184 | –1.210 | — | — | — | — | –0.033 | –0.343 | 8 | 209.4 | 2.17 | 0.13 | 0.86 |
| | 5 | –2.564 | –2.281 | –1.155 | — | –0.031 | — | 0.189 | — | –0.283 | 9 | 210.8 | 3.59 | 0.06 | 0.92 |
| | 6 | –2.442 | –2.306 | –1.151 | –0.085 | 0.017 | — | 0.227 | — | — | 9 | 211.4 | 4.22 | 0.05 | 0.97 |
| | RIV | **0.99** | **0.99** | **0.99** | 0.03 | 0.27 | 0.02 | **0.65** | 0.36 | 0.22 | | | | | |
| **Dry** | 1 | –3.294 | –2.725 | –2.288 | — | — | — | 0.180 | — | — | 7 | 173.8 | 0 | 0.35 | 0.35 |
| | 2 | –3.260 | –2.750 | –2.227 | — | 0.118 | — | — | — | — | 7 | 174.5 | 0.69 | 0.25 | 0.60 |
| | 3 | –3.148 | –2.773 | –2.349 | — | 0.178 | — | — | — | 0.310 | 8 | 175.5 | 1.71 | 0.15 | 0.75 |
| | 4 | –3.331 | –2.689 | –2.255 | — | 0.157 | — | 0.199 | — | — | 8 | 175.5 | 1.74 | 0.15 | 0.90 |
| | 5 | –3.217 | –2.831 | –2.226 | — | — | — | — | –0.137 | — | 8 | 176.9 | 2.79 | 0.09 | 0.99 |
| | RIV | **0.99** | **0.99** | **0.99** | 0.10 | **0.56** | 0.00 | **0.51** | 0.10 | 0.16 | | | | | |

Transects nested in the environment were fitted as random effects. Models that collectively represent a cumulative weight of 0.95 are shown in the table. Values greater than zero indicate a positive association between the variables, while lower values indicate a negative relationship. AICc = Akaike's Information Criterion corrected for small sample size; D. = distance; RIV = relative importance of each variable. RIV > 0.5 is shown in bold values.
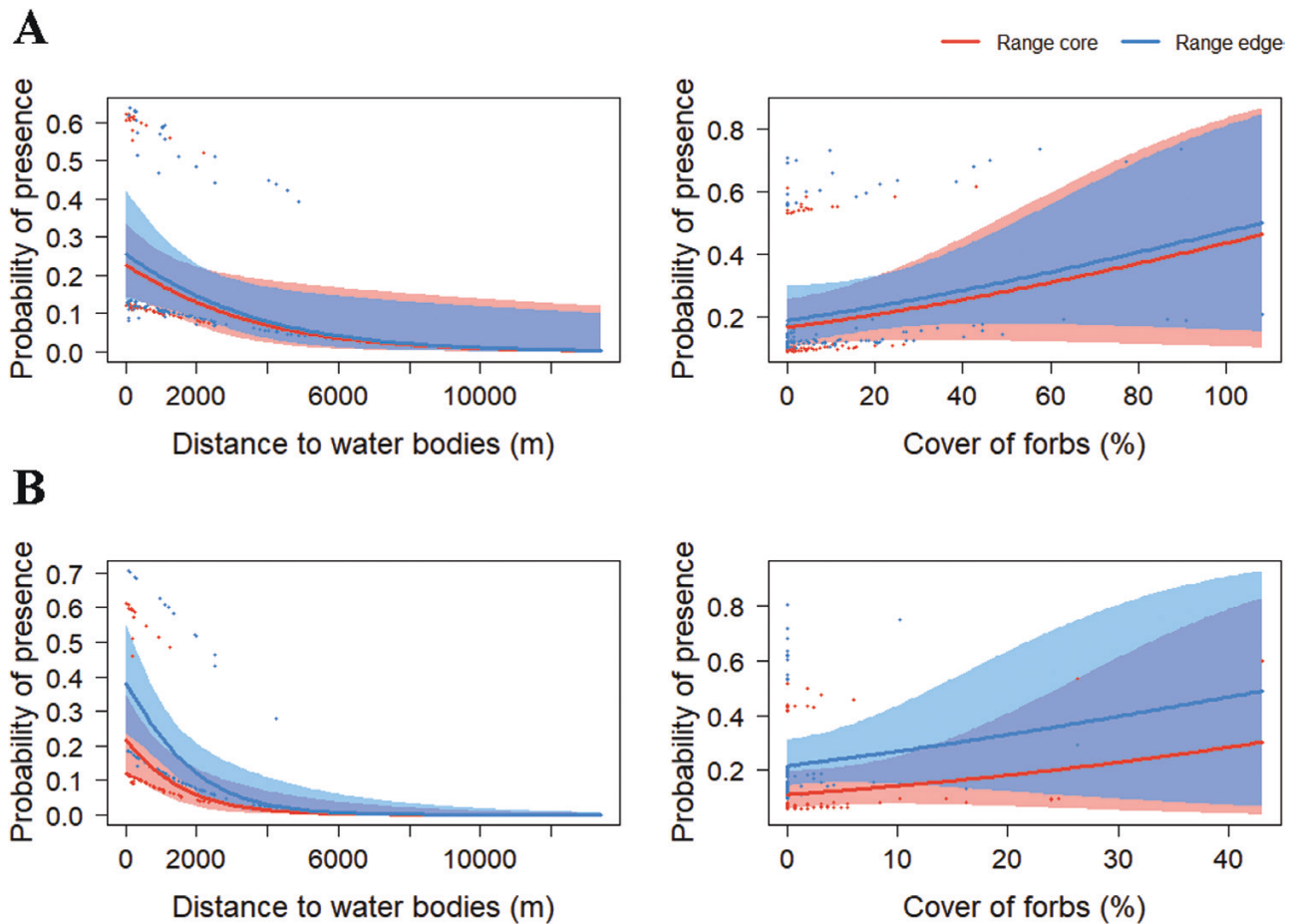
**Figure 2.** Probability of presence of European rabbit by distance to nearest water bodies and percent cover of forbs during wet (A) and dry (B) seasons in range core and edge core for the most representative candidate models.

During the dry season, only in the range core, the graminoids were avoided, while at the range edge, all food categories were consumed proportionally to their availability (Figure 3C).

## Discussion

This is the first study that evaluates ecological traits in core and edge populations of an invasive herbivorous mammal in the arid ecosystems of Argentina. Our results show that rabbits from edge populations exhibit somewhat different responses in spatial and trophic resource use compared with the core population. Nevertheless, we detected a similar pattern of habitat use at the microhabitat level for both populations, with a strong association with places closer to water resources. This indicates that the distance to water bodies could act as a limiting factor for the establishment and dispersal of rabbits in arid environments.

We expected that at the range edge, rabbits would use the environments in a more diversified manner compared to the range core. However, contrary to our expectations, rabbits were more selective in habitat use at the range edge, positively selecting the wetlands. At the microhabitat level, we observed a pattern in the particular components of habitat use by rabbits mainly linked to food availability. During the wet season, the presence of rabbits showed a positive association with herb cover, while

in the dry season, it also showed a positive association with grass cover. In the Mediterranean environments of Europe, the habitats occupied by rabbits also depend on food resources, shelter availability, and predator pressure (Lombardi et al. 2007). In range edge, the habitat components selected by rabbits were associated with wetlands for both seasons. This habitat type was characterized by presenting fine-textured, clayey soils, with highly palatable vegetation associated with stream water margins or channel edges; it included grass, graminoid, and subshrub cover (Bobadilla et al. 2022). According to Guo et al. (2005), edge populations, which are exposed to potentially higher stress levels, respond to changing environmental conditions by tracking favorable environments, such as the wetlands in this arid biome.

A strong pattern at the microhabitat level was observed for both establishment times and between wet and dry seasons: The probability of rabbit presence increased with proximity to water. Because European rabbits physiologically are not well adapted to dry conditions (Correa-Cuadros et al. 2022 and references therein), their occurrence in arid ecosystems could be restricted to areas close to water resources. The association of rabbits to wetlands or places with rivers, streams, or high humidity has been previously reported (Fernández 2005; Rueda et al. 2008; Bonino and Soriguer 2009; Cuevas et al. 2011). Indeed, Bonino and Soriguer (2004) highlighted the importance of watercourses as dispersal routes for this invasive species, especially in arid environments.
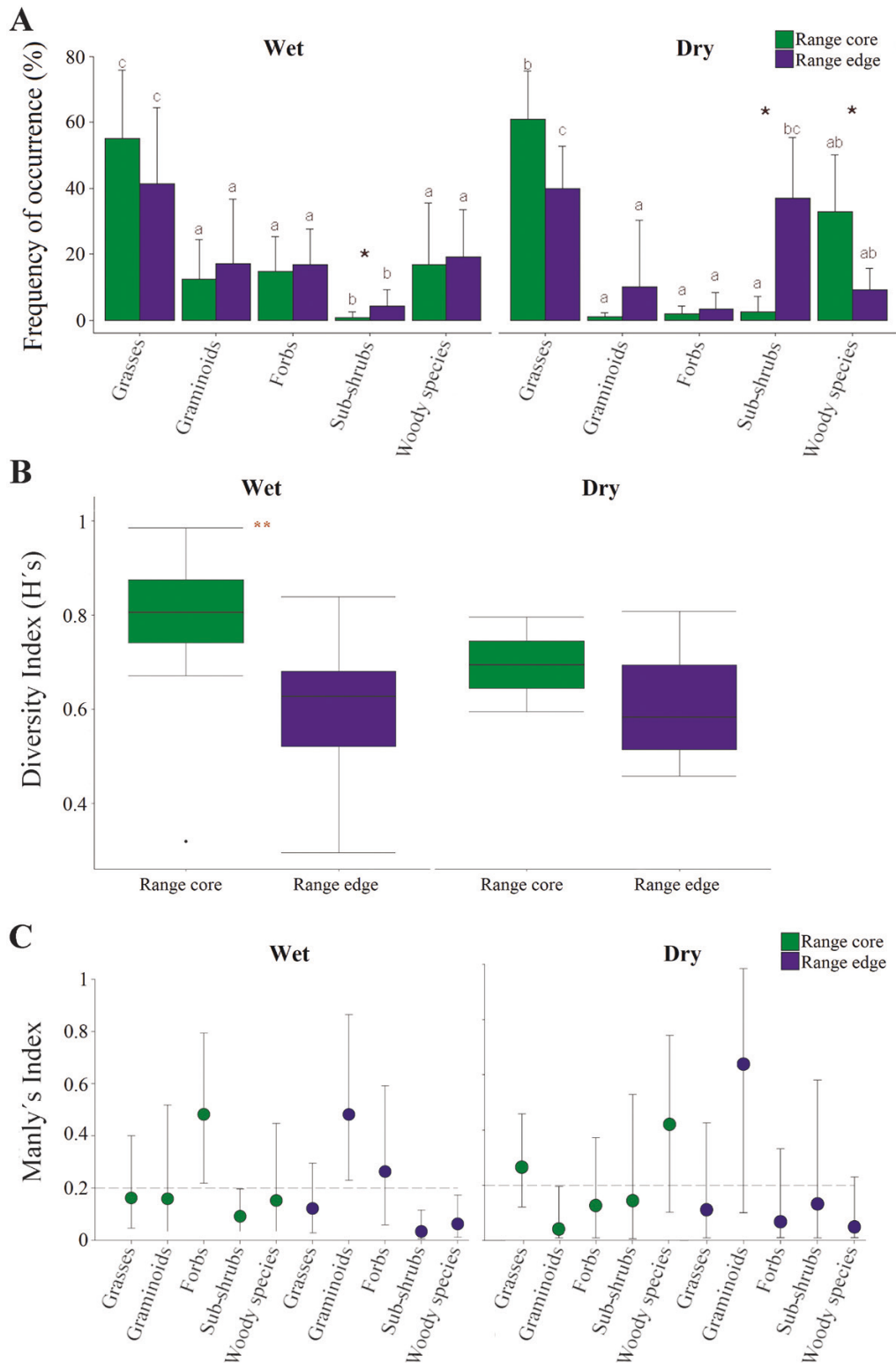
**Figure 3.** (A) Seasonal variation in frequency of occurrence (mean ± SD) of each food category for European rabbit in range core (green) and range edge (purple) during wet and dry seasons. W. species = woody species. Different letters indicate significant differences between food categories in same establishment time and season ($P < 0.05$). * indicates significant differences ($P < 0.05$) for the same food category between establishment times. (B) Shannon diversity Index of trophic niche breadth for European rabbit during wet and dry seasons. ** indicates significant differences ($P < 0.01$) between establishment times. C) Manly's Selectivity Index (± 95% confidence interval [CI]) for food categories consumed by European rabbit during wet and dry seasons. The dotted line indicates $1/k = 0.2$, for a proportional use of food availability.

In relation to trophic resources, the rabbit diet consisted predominantly of grasses throughout the year in both establishment times, while under dry conditions, graminoids and forbs were replaced by woody species (range core) and subshrubs (range edge). These results are consistent with previous work in arid environments of Argentina and Australia, where

under dry conditions, rabbits adjust their diet to the available food supply (Robley et al. 2001; Bonino and Borrelli 2006). On the other hand, we expected that at the range edge, rabbits would use trophic resources in a more diversified way than at the range core. However, our results showed that during the wet season, rabbits reduced their trophic breadth at the range edge as compared to the core. This outcome can be explained by 2 factors: (1) Potential competition for trophic resources with goats at the range edge (Bobadilla et al. 2022), whereas rabbits in range core are not cohabiting with these medium herbivores due to transhumant pastoralism. (2) Rabbits use the environments in a more diversified manner in range core, while at the range edge, they show a preference for wetland with lower diversity. On the other hand, during the dry season, the trophic breadth of rabbits decreased in the range core, while it remained constant at the range edge. This suggests that at the range edge, when food availability is less abundant, rabbits exhibit a different feeding strategy compared to the range core due to remain the diversify their diet.

Exploiting new habitats and resources are relevant features among individuals found in invasion fronts as these traits are associated with the dispersal capacity of species, favoring geographic range expansion (Liebl and Martin 2012; Gruber et al. 2017). Nevertheless, contrary to our predictions, rabbits from the range edge were more selective in their use of space at the habitat level. This expression of rabbit ecological traits, contrary to that expected for core versus edge populations, could be because the behavioral repertoire of individuals is influenced by factors not included in our study, such as anti-predator responses, anti-parasitic strategies, or hormonal stress responses (Wright et al. 2010; Martin 2015). We hope that ongoing research on corticosterone response to stress and anti-parasitic strategies (Moreno et al. 2021) could aid our understanding about the use of arid ecosystems by European rabbits.

Similar to other invasive vertebrates (DeVore et al. 2021), the European rabbit exhibits flexibility in ecological traits, which may be a key predictor of successful invasions. The pattern here reported for European rabbits regarding ecological traits further confirms their ecological flexibility. From a trophic perspective, rabbits could show flexible adjustment to novel conditions and environments in the range edge. While our results do not fully support the predictions of the Adaptive Flexibility Hypothesis (Wright et al. 2010) for ecological traits, they show that edge populations respond to changing environmental conditions by tracking favorable environments. In addition, at a local scale, distance to water resources could be a limiting factor for the establishment and dispersal of rabbits. Thus, for rabbits at the invasion front, these responses may aid colonization of new environments.

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## Conflict of Interest

The authors declare that they have no conflict of interest.

## Author Contributions

The authors have no relevant financial or non-financial interests to disclose. All authors have materially participated in the research and article preparation. The first draft of the manuscript was written by S.Y.B. and all authors commented on several versions of the manuscript. All authors read and approved the final manuscript.

## Data Availability

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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