Living on the edge: Heterogeneity in vegetation type cover as key factor of the habitat occupied by *Dolichotis patagonum* at landscape scale

Virginia Alonso Roldán [a, *], Ricardo Baldi [a, b], Héctor Del Valle [a], Douglas Deutschman [c]

[a] *Instituto Patagónico para el Estudio de los Ecosistemas Continentales (IPEEC) — CONICET, Boulevard Brown 2915, Puerto Madryn 9120, Argentina*
[b] *Programa Estepa Patagónica y Andina, Wildlife Conservation Society, Puerto Madryn, Argentina*
[c] *San Diego State University, 5500 Campanile Dr., San Diego, CA 92182, USA*

ABSTRACT

There is an urgent need to characterize the relationships between endangered species and their habitats in response to the accelerating pace of habitat transformation by humans. Mara *(Dolichotis patagonum)* is a large rodent endemic to the Argentine semi-deserts. It has been classified as "Near Threatened" by IUCN mainly as the result of habitat loss. There is contradictory evidence about the impact of human activities on mara and further information is needed to develop effective conservation strategies. We describe the main environmental factors, both natural and human, that are associated with warren presence as an indicator of the habitat selected by maras at the landscape scale. Habitat selected by maras was characterized by a high proportion of bare soil, low β diversity, open herbaceous steppe, and proximity to fences. The relationship of warren presence to the proportion of shrubby steppe in the broader landscape was variable across environments being positive in grasslands, and negative in shrubbier habitats. This supports the hypothesis that mara's preference for open areas depends on the level of shrubs in the surrounding habitat. As a result, conservation efforts will need to be tailored to the amount and structure of vegetation in any given area.

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1. Introduction

The habitat requirements of a species and its relation to the species' abundance and distribution have interested biologists since Darwin (1859). Now it is urgent that we understand these relationships in order to conserve biodiversity in a rapidly changing world (MA, 2005). Suitable habitat is required to meet the species needs for reproduction and survival and the inability to fulfill these needs because of habitat loss contributes to population decline. As a result, understanding the habitat preferences of a species is important to assessing extinction risk and to developing effective conservation and management actions (Battin, 2004; Ben-Shahar and Skinner, 1988).

In arid systems, the vegetation structure and spatial distribution are naturally heterogeneous enhancing biodiversity. The contrasting mix of environmental conditions created by patches of vegetation scattered in a matrix with low cover provide habitat for species with differing ecological requirements (Aguiar and Sala, 1999). Vegetated patches serve as protection from predation for small animals and low cover areas are used by species with strategies to escape predators based on visual detection. Human population growth coupled with expectations for increased standards of living are driving rapid changes in land use and exploitation of ecosystem services in arid and semi-arid lands more than in many other ecosystems (MA, 2005). Changes in land use alter the disturbance regime and modify the spatial structure of the vegetation, usually simplifying habitat structure (Tabeni and Ojeda, 2003). This habitat simplification can have direct effects on species that depend on heterogeneity to fulfill habitat requirements and on ecological communities because the populations of rare and opportunistic species could increase. However, the relationship of animal species with habitat structure is complex and varies among species in ways that often dependent on spatial scale (Tews et al., 2004). Information about the nature and scale of a species' response to changes in vegetation structure is key to regional planning efforts that allow sustainable development while

conserving biodiversity and valuable ecosystem services.

The mara (*Dolichotis patagonum*) is a deer-like rodent species that is endemic to the Argentine semi-deserts. Maras are the second largest members of the Cavidae family and are unique due to their particular morphology and behavior combining monogamy with communal denning (Taber and MacDonald, 1992a, b). They are also an important component of the ecosystem as an herbivore (Bertiller et al., 2009), as prey for carnivores (Palacios et al., 2012), and as potential ecosystem engineers resulting from their burrowing activities (Alonso Roldán and Udrizar Sauthier, 2016). Maras have been classified as "Near Threatened" by IUCN. The main threat to Maras is habitat loss related to human activities (Ojeda and Pardiñas, 2008). However, these same human activities can also create open areas which are often associated with the presence of Maras (Baldi, 2007; Kufner and Chambouleyron, 1991; Rodríguez, 2009; Taber and MacDonald, 1992b). They prefer open habitat because of their predator avoidance strategy which is based on early detection (Baldi, 2007; Taber and MacDonald, 1992b).This apparent contradiction between the positive and negative consequences of habitat changes may be an artifact of the scale at which most research has been conducted. Research on habitat characteristics related to the presence of Maras has focused on the microhabitat scale without considering habitat configuration at larger scales.

Habitat structure is an important factor determining activity patterns, behavior and habitat selection by other rodents in arid environments (Hughes and Ward, 1993; Taraborelli et al., 2003). This is likely a consequence of higher predation risk for animals in open areas compared to the relative safety of hiding under bushes (Hughes and Ward, 1993). Although maras are not small mammals, they also use bushes to hide in response to perceived threats and predation risk. Thus our hypothesis is that vegetation heterogeneity at landscape scale is a key factor in habitat selection and the preference of maras for open areas would be mediated by other elements providing shelter across the landscape.

The objective of this study was to describe the main environmental factors, whether natural or human, that are associated with warren presence as an indicator of the habitat selected by maras. This description uses the concept of landscape from the species' perspective (Dunning et al., 1992) which is defined as study areas large enough to encompass multiple home ranges.

2. Methods

2.1. Study site

The study was conducted in the Península Valdés in southern Argentina (Appendix 1, electronic version only). The climate is temperate semi-arid, with an average annual rainfall of 230 mm concentrated in the cold season (May–September) and high interannual variation. The mean annual temperature is 12.9 °C (6 °C in the coldest month, 21 °C in the warmest). The vegetation is characteristic of the southern Monte Phytogeographic Province, but shares some plant species with the northern Patagonian Province (León et al., 1998). The Monte is characterized by tall shrubland covering 40–60% of the soil surface. Foliage cover varies from 35% to 65% in the Patagonian Province, but it may increase substantially in rainy periods when annual plants constitute a large proportion of the total cover (Beeskow et al., 1995). Península Valdés is a provincial protected area and a UNESCO World Natural Heritage Site. The land is mainly devoted to extensive sheep ranching, and most of the effective conservation activities are targeted towards coastal areas where marine mammals and birds predominate.

2.2. Sampling design

We established six macroplots across three different environments within Península Valdés: shrubland, mosaic of shrubland and grassland, and grassland (Appendix 1, electronic version only). Two 4 × 5 km macroplots (2000 ha) were placed in each environment. Within each macroplot we searched for mara warrens following the protocol described in Alonso Roldán et al. (2015). We used warrens as indicators of the habitat selected by maras because there is evidence that they remain within an 800 m radius home range all year long (Alonso Roldán and Baldi, 2016; Taber and MacDonald, 1992b). Thus, the areas within-macroplot used by maras were defined by an 800 m buffer around warrens.

We sampled 10 warrens (hereafter referred to as mara points) randomly selected from those found in each macroplot. We then located the same number of random points in the portions of the macroplot outside the 800 m buffers (hereafter referred as random points). We used the type of point (mara or random) as a binary response variable for statistical modeling. Complete sampling was not possible in the shrubland. We found only four warrens in one macroplot and none in the other because mara and their warren's were scarce in this environment.

2.3. Predictor variables

We measured environmental variables in the field and from satellite images in order to characterize the habitat around the sampling points at multiple scales (Table 1). We selected a range of variables that reflect the presence or relative abundance of habitat requirements and resources such as food and shelter, and human related features like roads and fences. We described the spatial configuration of these resources which may be important to the mara's predator avoidance strategy which is based on early visual detection.

2.3.1. Field-based measurements

We measured the mean distance to, and mean height of, the 12 nearest shrubs to the sampling point, three in each quadrant delimited by the cardinal directions, to characterize the "openness" of each point. We used this method because it is not possible to account for the spatial distribution of shrubs with a simple measurement of average shrub cover. We also calculated the mean distance to the highest point of the 12 nearest shrubs, because the height of vegetation varies (Campanella and Bertiller, 2008) and affects the behavior of rodents (Ebensperger and Hurtado, 2005). Using both measurements we calculated the tangent of the triangle whose sides are the height and the distance of each plant, in order to characterize the visual obstruction in each sampling point. This is based on evidence that indices that integrate vertical and horizontal dimensions performs better that individual variables to characterize vegetation structure (Harrell and Fuhlendorf, 2002).

We estimated relative cover of bare soil and the main plant life forms (i.e. grasses and shrubs) as a proxy to the relative abundance of food and shelter resources. Cover was estimated from photographs taken 2.5 m above ground level in five random sites located within 50 m of the warren/random point. The effective ground area sampled in the pictures was approximately 3 m^2. Pictures were then sampled using a 100-point rectangular grid (SamplePoint v1.48; see Booth et al., 2006). We estimated the proportion of four major categories within each sample that represent 99.3% of the cover: bare soil, grasses, shrubs, and mulch/moss/feces (MMF). We averaged the cover of each category across the five photographs around each sampling point. In addition we calculated the β diversity, which takes into account the diversity in cover type among photographs from each sampling point.

Table 1
Names, definition, habitat requirements and features, and data source for all variables included in the models.

Variable	Definition	Habitat requirement	Source
Mean distance to nearest shrubs	Mean distance to the 12 nearest shrubs (3 in each quadrant)	Shelter/early detection of predators	Field
Mean height of nearest shrubs	Mean height of the 12 nearest shrubs (3 in each quadrant)	Shelter/early detection of predators	Field
Visual obstruction or tangent	Mean distance to the highest point of the 12 nearest shrubs, calculated as the tangent of the triangle which sides are the hight and the distance	Early detection of predators	Calculated from other
Proportion of bare soil	Mean number of points with bare soil in 5 rectangular grids of 100 points	Early detection of predators	5 photos within 50 m radius
Proportion of shrub cover	Mean number of points with shrub in 5 rectangular grids of 100 points	Shelter	5 photos within 50 m radius
Proportion of grass cover	Mean number of points with grass in 5 rectangular grids of 100 points	Food	5 photos within 50 m radius
Proportion of mulch, moss and feces cover	Mean number of points with mulch, moss and/or feces in 5 rectangular grids of 100 points	Early detection of predators	5 photos within 50 m radius
Beta diversity	Beta diversity in mean proportion of cover across 5 sampled points in 50 m radius	Heterogeneity	Calculated from other
Distance to point infrastructure elements	Minimum distance to a point infrastructure	Shelter/early detection of predators	Field mapping and GIS
Distance to fences	Minimum dDistance to a the nearest fence	Shelter/early detection of predators	Field mapping and GIS
Distance to roads	Minimum dDistance to a the nearest road	Shelter/early detection of predators	Field mapping and GIS
Proportion of bare soil	Proportion of pixels classified as bare soil in 500 m radius	Early detection of predators	Clasified satellite image
Proportion of shrubby steppe	Proportion of pixels classified as shrubby steppe in 500 m radius	Shelter/early detection of predators	Clasified satellite image
Proportion of shrubby steppe with short and scattered shrubs	Proportion of pixels classified as shrubby steppe with short and scattered shrubs in 500 m radius	Shelter/early detection of predators	Clasified satellite image
Proportion of herbaceous steppe	Proportion pixels classified as herbaceous steppe in 500 m radius	Food	Clasified satellite image
Proportion of low cover herbaceous steppe	Proportion pixels classified as cover herbaceous steppe in 500 m radius	Food	Clasified satellite image
Number of patches	Number of patches in 500 m radius	Heterogeneity	Clasified satellite image
Mean area of patches	Mean area of patches in 500 m radius	Heterogeneity	Clasified satellite image
Weighted mean area of patches	The sum, across all patches in the 500 m radius landscape, of the corresponding patch metric value multiplied by the proportional abundance of the patch	Heterogeneity	Clasified satellite image
Agregation index	Frequency with which adjacencies between the same patch type appear side-by-side on the map	Heterogeneity	Clasified satellite image
Contagion	The observed contagion over the maximum possible contagion for the given number of patch types	Heterogeneity	Clasified satellite image
Percentage of like adjacencies	Proportion of adjacent pixels that are alike. number of like adjacencies involving the corresponding class, divided by the maximum possible number of like adjacencies involving the corresponding class, which is achieved when the class is maximally clumped into a single, compact patch; multiplied by 100 (to convert to a percentage).	Heterogeneity	Clasified satellite image
Interspersion and juxtaposition index	The observed interspersion over the maximum possible interspersion for the given number of patch types	Heterogeneity	Clasified satellite image
Patch richness	Number of patch types	Heterogeneity	Clasified satellite image

We also considered three distance-related variables: 1) distance to point infrastructure elements (e.g. windmills, sheep outstations), where natural predators might be deterred due to human presence, 2) distance to fences and 3) distance to roads, which may serve as corridors with good visibility. We recorded the position or track of these elements in the field using a Garmin e-trex hand-held GPS unit. Then, we measured the minimum distance from each sampling point to these features using ArcView 3.2 (Environmental Systems Research Institute, Redlands, CA).

2.3.2. Landscape variables

A Landsat 5TM image from Península Valdés in January 2001 was analyzed performing an unsupervised classification (Jensen, 2007) and five classes of vegetation structure were identified: shrubby steppe, open shrubby steppe, herbaceous steppe, open herbaceous steppe and bare soil. Using Fragstats v3.3 (McGarigal et al., 2002), we measured the proportion of pixels in each of these classes in clips of the image of 500 m radius around the sampling points, representing the most intensively used portion of the home range (Alonso Roldán and Baldi, 2016). We calculated

several landscape metrics designed to assess habitat heterogeneity including: number of patches, mean area of patches, weighted mean area of patches, aggregation index, contagion, percentage of like adjacencies, interspersion-juxtaposition index and patch richness. There is no concordance in literature about which metrics are best able to characterize the heterogeneity or texture of a landscape (Cushman et al., 2008) and different metrics have been correlated to habitat preferences of several mammal species (Uuemaa et al., 2009). We selected several commonly-used metrics of landscape texture that we thought would be relevant to habitat selection by mara.

2.4. Statistical analysis

We identified variables that best explained habitat use by maras by fitting generalized linear mixed models with a binomial error distribution and a logit link function (Zuur et al., 2009). We tested for collinearity of predictors (r > 0.5) using Spearman's rank correlation index (Rhodes et al., 2009). When collinearity was detected we fitted single variable models and retained the variable that explained the largest portion of the variance. The ID of environments and macroplots inside each environment were included as random effects.

To identify parsimonious models we applied a backward elimination procedure (Zuur et al., 2009). We initially fit complete models including all non-collinear predictors and tested for alternative structures for random factors by comparing AIC values. Among the random factors we tested variable slope structures in relation to the proportion of shrub within 50 m radius, the proportion of shrubby steppe within 500 m radius and proportion of bare soil within 500 m radius. These models allowed us to evaluate whether habitat selection varied relative to the scale and structure of the patch-matrix in the sampled environments. We then proceeded to eliminate non-significant predictors (P > 0.05) one at a time while keeping the random component structure and checked if the elimination of each of the variables significantly modified model fitting by comparing residual deviances using a χ^2 test (Zuur et al., 2009). For predictors included in the final model, odds ratio were normalized by calculating the odds of detecting mara at the 10th and 90th percentile for each variable. Thus, odds ratios were compared based on the observed distribution of each metric rather than on an arbitrary value or unit. We used R (R Development Core Team, 2010) package lme4 (Bates et al., 2011) for model fitting and selection.

After testing for model fit, we checked for autocorrelation among residuals using Moran's I (Legendre and Fortin, 1989) calculated with the R package ape (Paradis et al., 2004). Finally, we assessed goodness of fit and departures from model assumptions by means of a quantile-quantile plot of fitted vs. simulated residuals and partial residuals plots (Rhodes et al., 2009). We obtained simulated residuals by generating 150 data sets of the same size as the original, sampling from a binomial distribution and using the probabilities estimated from the fitted model.

3. Results

Two pairs and two groups of predictor variables showed significant levels of collinearity (Table 2). Among these, the variables with the lowest residual deviances in single variable models were: distance to fences, proportion of bare soil and shrubs within 50 m radius, and proportion of bare soil within 500 m radius (Table 3). In addition, six other independent variables were used in the models: mean height of nearest shrubs, distance to point infrastructure elements, β diversity, proportion of open herbaceous steppe within 500 m radius, interspersion-juxtaposition index and contagion.

The best structure for the random components included variable slopes for the proportion of shrubby steppe within 500 m radius (Table 4 and Fig. 1). In the final simplified model the presence of warrens (mara points) was strongly and positively related to the proportion of shrubby steppe within 500 m radius in grassland, relatively flat in the mosaic of shrubland and grassland and strongly negative in shrubland. In general across the different environments the presence of warrens was positively related to the proportion of bare soil at the 50 m and 500 m radius, and negatively related to the distance to fences, β diversity and the proportion of open herbaceous steppe within 500 m radius (Table 5). An increase in open herbaceous steppe reduced the odds of detecting mara 612 fold (CI 106-3558; p = 0.0003). On the other hand, an increase in bare soil increased the odds of detecting mara 128 fold (CI 26-626; p = 0.0022). The large magnitude of these odds ratios indicates that our sampling covered the gradient from extremely good habitat to what is essentially non-habitat.

Residuals from the model did not show any major departure from the model assumptions. The quantile-quantile plot showed the points lying close to the 1:1 line and the partial residual plots only showed departures from linearity in extreme values (Fig. 2). The residuals from the final model didn't show evidence of autocorrelation (Moran's I = 0.018 ± 0.032; p = 0.359).

4. Discussion

The habitat selected by maras was characterized by high proportion of bare soil, low β diversity, low proportion of open herbaceous steppe, and proximity to fences. The relation to the proportion of shrubby steppe at the 500 m radius was variable across the environments, indicating that maras use heterogeneous habitats with a mix of open and shrubby areas. This is consistent with the hypothesis that heterogeneity is a key factor in habitat selection and that the preference of maras for open areas depends on the availability of shrubs in the surrounding habitat. Counter to what is generally accepted about this species, maras select shrubbier areas in open environments with little cover, likely for predator avoidance (i.e. shrubs to hide).

The patterns of habitat use at the broader landscape scale are consistent with the patterns observed at microhabitat or fine scale where the intensity of use was related to the proportion of bare soil and the proximity to human infrastructure (Alonso Roldán and Baldi, 2016). In general, these results on habitat utilization and their role in predator avoidance agree with previous studies conducted at microhabitat scale (Kufner and Chambouleyron, 1991; Rodríguez, 2009; Taber and MacDonald, 1992b). However, caution must be exercised when drawing conclusions about cause and effect from the final model because several of the predictor variables are collinear with other not included in the model. For example, the high proportion of bare soil could also be interpreted as an indicator of landscape heterogeneity since bare soil is strongly correlated with the patch richness. This relationship provides additional support for the selection of heterogeneous habitat by mara. Likewise, β diversity that was negatively related to mara presence apparently indicating avoidance of heterogeneity at local level, could be interpreted in a different way. In Península Valdés, β diversity is negatively correlated with the proportion of grasses in a 50 m radius. Thus The presence of mara in areas with lower β diversity could be related, at least in part, to increased grass cover, the preferred food for maras (Sombra and Mangione, 2005). This interpretation is not consistent with the conclusions of Kufner and Chambouleyron (1991) who reported that the use of habitat by maras was unrelated to grass cover and concluded that habitat selection was driven mainly by predator avoidance. In fact, our results show that maras could select an area with good

Table 2
Collinearity among predictor variables estimated with Spearman correlation index. Above the diagonal the correlation signs are highlighted if r > 0.5. Section a shows field-based variables and the landscape variables correlated with them; section b shows remaining landscape variables. Variables with r < 0.5 in all pairs are not included.

a

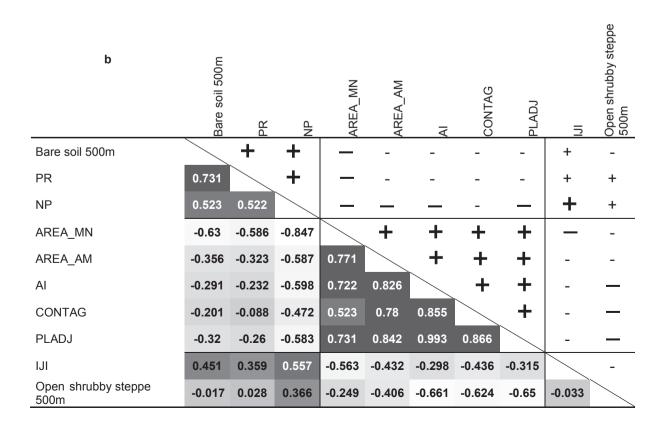|	Shrubs 50m	Shrubby steppe 500m	Tangent	Grasses 50m	Herbaceous steppe 500m	Distance to shrubs	Bare soil 500m	β diversity	Distance to fences	Distance to roads	Bare soil 50m	MMF 50m
Shrubs 50m		+	+	−	−	−	+	+	+	+	-	+
Shrubby steppe 500m	0.723		+	−	−	−	+	+	-	-	-	+
Tangent	0.839	0.641		−	-	−	+	+	+	+	-	+
Grasses 50m	-0.795	-0.585	-0.682		+	+	-	−	+	+	+	-
Herbaceous steppe 500m	-0.615	-0.557	-0.493	0.673		+	−	−	+	+	-	+
Distance to shrubs	-0.833	-0.621	-0.981	0.693	0.497		-	-	-	-	+	-
Bare soil 500m	0.228	0.190	0.134	-0.387	-0.578	-0.132		+	-	+	+	-
β diversity	0.499	0.386	0.427	-0.561	-0.585	-0.428	0.439		-	-	+	-
Distance to fences	0.053	-0.011	0.172	0.153	0.209	-0.189	-0.264	-0.263		+	-	+
Distance to roads	0.100	-0.020	0.185	0.060	0.197	-0.189	-0.415	-0.310	0.560		-	+
Bare soil 50m	-0.333	-0.341	-0.240	0.035	-0.040	0.248	0.218	0.130	-0.246	-0.164		−
MMF 50m	0.085	0.134	0.132	-0.091	0.121	-0.179	-0.166	-0.091	0.125	0.042	-0.716	

b

	Bare soil 500m	PR	NP	AREA_MN	AREA_AM	AI	CONTAG	PLADJ	IJI	Open shrubby steppe 500m
Bare soil 500m		+	+	−	-	-	-	-	+	-
PR	0.731		+	−	-	-	-	-	+	+
NP	0.523	0.522		−	−	−	-	−	+	+
AREA_MN	-0.63	-0.586	-0.847		+	+	+	+	−	-
AREA_AM	-0.356	-0.323	-0.587	0.771		+	+	+	-	-
AI	-0.291	-0.232	-0.598	0.722	0.826		+	+	-	−
CONTAG	-0.201	-0.088	-0.472	0.523	0.78	0.855		+	-	−
PLADJ	-0.32	-0.26	-0.583	0.731	0.842	0.993	0.866		-	−
IJI	0.451	0.359	0.557	-0.563	-0.432	-0.298	-0.436	-0.315		-
Open shrubby steppe 500m	-0.017	0.028	0.366	-0.249	-0.406	-0.661	-0.624	-0.65	-0.033	

Table 3
Residual deviance from single variance models fitted with variables that showed collinearity.

Single variable model	Residual deviance
Distance to fences	117.5
Distance to roads	118.9
Bare soil 50 m	122.9
MMF 50 m	124.7
Shrubs 50 m	118.9
Tangent	121.8
Distance to shrubs	123
Grasses 50 m	123.4
Shrubby steppe 500 m	123.4
Herbaceous steppe 500 m	124.6
β diversity	124.7
Percentage of bare soil within 500 m radius	116.5
Patch richness	116.7
Contagion	118.5
Percentage of like adjacencies	119.8
Agregation index	121
Interspersion and juxtaposition index	121.1
Weighted mean area of patches	121.8
Mean area of patches	122.6
open shrubby steppe 500 m	123.6
Number of patches	124.5

Table 4
Random component structures assessed showing the best in bold, the degrees of freedom (FD) needed and Akaike Information Criterion (AIC) for each structure relative to the best.

Random component structure	DF	AIC
**Bushland cover 500 m	Environment**	**0**	**0**
Without random factors	−3	6.39
Environment	−2	6.45
Macroplot	−2	8.39
Macroplot| Environment	−1	8.45
Bushland cover 500 m	Macroplot	0	3.80
Bushes cover 50 m	Environment	0	6.66
Bushes cover 50 m	Macroplot	0	8.82
Bushland cover 500 m + Bare soil Proportion 500 m|Environment	3	6.00
Bushes cover 50 m| Macroplot| Environment	3	12.79

opportunities for predator detection and ample food at the same time since low shrub cover is associated with high grass cover. The same argument is valid for sites with a high proportion of bare soil that provide good visibility since these areas often have abundant annual herbs and seedlings during spring, providing food for maras (Rodríguez and Dacar, 2008; Sombra and Mangione, 2005). This pattern of mara using areas with ephemeral springtime herbaceous cover was also reported by Taber and MacDonald (1992b). It is noteworthy that proportion of grasses and shrubs within 50 m radius are related with the proportion of herbaceous steppe and shrubby steppe within 500 m radius. In addition, the proportion of bare soil was a significant explanatory variable in models at both scales. These positive relationships suggest that mara habitat selection is associated with the environment at both scales.

The differing relationships between mara presence and the amount of shrubby steppe across the environments imply that maras use heterogeneous habitats, even when the indices of landscape heterogeneity were not a significant predictor of mara habitat use. Similar cases were reported for other mammals including the European rabbit (*Oriclolagus cuniculus*; Fernández, 2005), elk (*Cervus canadensis*; Boyce et al., 2003), moose (*Alces alces*; Maier et al., 2005) and several African ungulates (Ben-Shahar
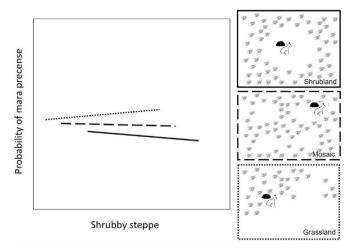

Fig. 1. Conceptual illustration of the interpretation of the variable slope random component structure in the final model.

and Skinner, 1988). The presence of these species is related to heterogeneous habitats including grasslands or open areas for food and woodland or areas more densely covered by shrubs for shelter from predators. In all these cases, the indices of landscape structure were less relevant to understanding habitat selection. This could mean that the landscape metrics, although good at describing the environment, are not capturing the factors to which the animals are responding.

Mara could be defined as an edge species (*sensu* Imbeau et al., 2003) given that its habitat includes open and shrubby areas. In this sense, and as indicated by the relation of warrens presence to fences, this species could actually benefit from shrubland fragmentation due to human infrastructure. Another implication of mara's requirement for heterogeneity is that croplands are not suitable habitat for this species, which could explain the range reductions in Córdoba and Buenos Aires provinces where agriculture area has been expanded during the last decades. In contrast, cattle or sheep ranching could be compatible with mara conservation. It is even possible that ranching benefits maras to some degree (Kufner and Chambouleyron, 1991) given that ranching produces areas of low vegetation cover (Bisigato and Bertiller, 1997; Cheli, 2009). This effect was also reported for other medium size rodents and the brown hare in Monte and Chaco regions (Tabeni and Ojeda, 2003) of South America. However over grazing could lead to shrub recruitment and reduction of grasses (Beeskow et al., 1995; Bucher, 1987), changes that would negatively impact mara.

The different relationships between mara presence and shrubby steppe in grassland environments highlight the need for further study of mara habitat use, distribution and response to human activities in multiple regions of Argentina. This is advisable because the Pampa and Patagonia Steppe regions have a more open vegetation structure than the Monte where a dense shrub matrix is predominant. Most of the previous studies on mara were performed in Monte (Kufner, 1995; Kufner and Chambouleyron, 1991; Rodríguez, 2009; Rodríguez and Dacar, 2008; Sombra and Mangione, 2005). This concentration of research in the Monte may explain only part of the mara-habitat interaction and could potentially lead to an overemphasis on the importance of open areas. Moreover, it is likely that habitat modification resulting from human activities varies both with the environment of a region as well as the extent and intensity of the impact. Specifically, activities that lead to small and medium size open areas in a shrub matrix like Monte vegetation could benefit mara but activities that create

Table 5
Estimated parameters for predictors of warren presence according to the selected model. The table shows: odds ratio (OR), limits of 95% confidence interval (L95 and U95), z statistic value (z) and associated probability (p) for each predictor.

Variable	OR	L95	U95	Z	p
Intercept	1.406	0.339	5.829	0.239	0.8108
Distance to fences	−27.12	9.332	78.79	−3.094	0.0020
β diversity	−53.94	14.63	198.9	−3.056	0.0022
Bare soil Proportion 50 m	128.0	26.16	626.0	3.056	0.0022
Bare soil Proportion 500 m	29.25	8.815	97.04	2.815	0.0049
Low cover grassland Proportion 500 m	−612.9	105.6	3558	−3.650	0.0003

Fig. 2. Assessment for departures from model assumptions. Quantile-quantile plot of fitted vs. simulated residuals with an envelope based on 1000 simulations (a) and partial residuals plots (b, c, d, e y f).

large open areas should be avoided because of the lack of shelter. On the other hand, because the different characteristics of vegetation activities with the same impact on shrubs that in Monte lead to small open areas could lead to the lack of shelter in Patagonia.

There are similar cases across the world where mammals respond in different way to habitat modification by human activities in arid and semi-arid biomes, especially in response to different intensities of cattle grazing (i.e. Table 1 in Tabeni and Ojeda, 2003). Although there seems to be agreement about negatives impacts of shrub encroachment by overgrazing, medium to low levels of grazing can have positive or negative effects depending on the particular habitat requirements of a species (Blaum et al., 2007; Hoffmann and Zeller, 2005; Tabeni and Ojeda,

2003). More drastic land-use changes such as urbanization or the conversion of rangelands to cropland have a stronger impact on biodiversity (MA, 2005) but they could be compatible with biodiversity conservation in a landscape context if species responses are considered across spatial scales (Tews et al., 2004) with land use diversification. The complexity and scale-dependence of these relationships make it difficult to generalize across species, activities, or environments. In addition, it underscores the need for land managers and biologists to understand the local response of a species. Conservation strategies that are responsive to these local species-habitat relationships within the broader landscape context may support economic development while protecting biodiversity and associated ecosystem services.

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2017.01.008.

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