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Location of breeding warrens as indicators of habitat use by maras (*Dolichotis patagonum*) in Península Valdés, Argentina

DOI 10.1515/mammalia-2015-0136

Received August 10, 2015; accepted May 4, 2016

Abstract: We characterized the habitat use by maras (*Dolichotis patagonum*) on a microhabitat scale in the area surrounding the warren, assessing the conditioning effect of the warren over space use and exploitation of other resources. We evaluated the relationships between the probability and intensity of use, habitat configuration and distance to the warren, counting feces along transects departing from each warren. Our results showed that the location of breeding warrens was positively associated with the habitat use by maras on a microhabitat scale. The core area of the annual activity of maras was concentrated around the warren and there was no evidence of alternative areas of activity. According to the fitted models, maras used microhabitats with a high proportion of bare soil and close to infrastructure elements. The spatial autocorrelation components indicated that intensively used patches are small and disperse. The patterns of habitat use observed in this study suggest that maras use multipurpose areas including the breeding site and resources needed throughout the year. These patterns suggest that warrens are good all year-round indicators of mara habitat use and spatial ecology.

Keywords: breeding site; generalized linear mixed models; landscape; resources configuration; rodent.

Introduction

The habitat selected by an animal should satisfy all its needs. However, resources are usually heterogeneously distributed over space and the availability of a particular resource may imply the scarcity of another. When a given resource has a limited distribution and it is repeatedly used, it will condition habitat use and the exploitation of other resources (Orians and Wittenberger 1991). Conditioned habitat use, in turn, would affect population distribution and intraspecific interactions. Thus, decisions made by organisms at a local scale may have an influence at higher scales and organizational levels (Holland et al. 2008, Roshier et al. 2008).

The breeding site is a critical resource to which animals become attached during the breeding season; its selection frequently prevails over other habitat selection considerations (Orians and Wittenberger 1991). The restrictions imposed by breeding site selection on the exploitation of other resources will depend on the mobility of the species. Some species may travel long distances between breeding sites and foraging areas (e.g. Garthe 1997, Falk et al. 2002), but exploiting distant resources imposes an energy cost. According to resource optimization theory, animals will select resource patches for inclusion in their home ranges depending on the balance between benefits and traveling costs (Mitchell and Powell 2004, Börger et al. 2008). Thus, resource distribution across the landscape significantly contributes towards determining the configuration of home ranges (Mitchell and Powell 2004).

The mara (*Dolichotis patagonum* Zimmermann, 1780) is an endemic caviomorph rodent of the Argentine semi-deserts, which uses warrens to lodge their newborn pups. Warrens are burrows dug in the ground by mara pups and basically consist of long tunnels (Taber and MacDonald 1992a). Only pups use the breeding warrens, as nursing adults remain in their proximity for 6–8 weeks during the breeding season (Taber and MacDonald 1992a,b, Baldi 2007). According to the resource optimization theory, warrens are expected to be central landmarks of the areas used by maras, at least during the breeding season.

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Outside the breeding season, the high mobility of the species (Taber and MacDonald 1992b) would allow for the exploitation of foraging areas far from warrens. Radiotracking data from Taber and MacDonald (1992b) suggest that mara couples remain within home ranges of nearly 200 ha including their breeding warrens all year round, even when they do not use the warrens or the closest surroundings. However, that study was focused on a single colony. Across Península Valdés, settlements of mara warrens are located in different contexts of either vegetation type, as the presence of lagoons and human infrastructure which could influence the patterns of habitat use by maras according Taber and MacDonald (1992b). Variation in other components of mara behavior such as group size (Taber and MacDonald 1992a) and reported changes in use of space under varying environmental conditions in other caviomorphs (Quirici et al. 2010, Maher and Robert Burger 2011), suggest that maras probably adapt their behavior to the environmental context. Thus, maras could move around in a multipurpose area around the warren, this being a conditioning point in the use of the surrounding area at microhabitat scale, or they could have different activity centers for the breeding and non-breeding seasons depending on the configuration of resources. It is important to understand the role of warren location in conditioning the areas used by maras, as it will allow to

use them as a landmark in studies of both spatial structure of populations and habitat use at different scales.

Our main objective was to assess the influence of the breeding warrens on the maras' annual range, and explore the main factors affecting the probability and intensity of use on a microhabitat scale in the areas surrounding warrens. We assessed the relationship between probability and intensity of use by maras and some habitat characteristics as potential explanatory variables across several settlements of mara with different configurations of resources, and constructed models to describe patterns of habitat use. If warren location was the sole conditioning factor for the use of other habitat resources, then probability and intensity of use should (1) decrease with distance from the warren and (2) be uniform in every direction away from the warren. Departures from those expected trends would be indicative of other landscape elements affecting habitat use.

Materials and methods

Study site

The study was conducted in the Península Valdés in southern Argentina (Figure 1). Climate is temperate semi-arid,

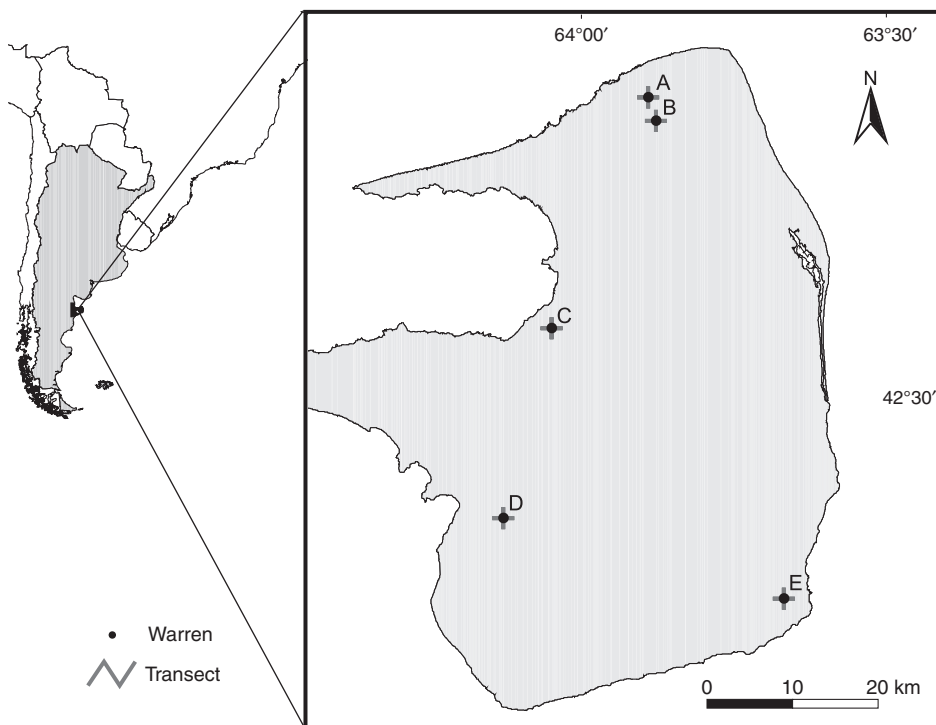


Figure 1: Study area, warrens and transects location. The warrens are named with consecutive capital letters.

with an average annual rainfall of 230 mm concentrated in the cold season (May – September) and high inter-annual variation (Prohaska 1976, Paruelo et al. 1998). 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 contribute 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 protection is targeted towards coastal areas where marine mammals and birds predominate. Although the area is under IUCN Category VI (Managed Resources), the management plan has not been properly implemented.

We surveyed the areas used by maras around five breeding warrens during February 2008 (Figure 1). We chose this time in the year for sampling because as it is the late dry season, the food availability is more restricted (Bertiller et al. 1991) and corresponded to the non-reproductive period. Warrens were randomly selected from a known set of warrens occupied by maras during the previous breeding season (August through December 2007). These areas contained variable configurations of landscape elements that could act as possible “attractors” for the species (e.g. infrastructure with a human presence, lagoons, or open vegetation patches; Kufner and Chambouleyron 1991, Taber and MacDonald 1992b, Rodríguez 2009).

Use assessment

We used the presence of feces as an indicator of the probability of use of a given sampling unit and the number of feces as a measure of use intensity. These indicators have been used for maras (Kufner and Chambouleyron 1991) and *Lagidium viscacia* Molina, 1782 (Walker et al. 2000). The survey was conducted in five warrens sparsely located inside the study site (Figure 1). In each warren we established four 1500 m transects departing from each warren and orientated towards each cardinal point. Each transect was divided into 75 consecutive sampling units of 20×4 m. We only considered feces dropped within approximately 1 year before sampling, which accumulated on the ground as they remain for a long time. These feces are recognizable by their brown coloration according to controlled

observations from a pilot study (Alonso Roldán, unpublished results). Looking at the distribution of the feces dropped during the whole year allows to describe the complete pattern of habitat use during the breeding and non-breeding season. If maras used only one area conditioned by their breeding activity, the presence and the number of feces should decrease with the distance from the warren. In contrast, if they have a different activity center when they are not breeding the presence and the number of feces accumulated through the year should present different patterns, likely affected by other factors. If, for example, maras have a center of activity at 1 km from the warren we expect to find at that distance a higher number of feces or probability of use than at points between it and the warren. Even if we cannot assign a date to this alternative center of activity we could spatially differentiate it and we can deduce that it is related with activities not related with the breeding season by exclusion of the “breeding related” activity center around the warren.

In order to describe the shape and extension of use areas around each warren we derived two descriptive variables from the number of feces. The total number of feces by transect was interpreted as an index of intensity of use in each direction, and the distance from the warren at which the accumulated proportion of feces in each transect reached 95% (0.95 distance) was interpreted as an index of the extension of the use area in each direction. Finally, with the number of feces recorded in all transects and warrens added up, we calculated the distance where the accumulated proportion of feces reached 50% as to characterize the “core” areas around warrens (overall 0.5 distance) and the 95% to represent the total area of use excluding extreme outlier values (overall 0.95 distance); those were our approximations to the size of use areas around warrens.

Landscape configuration

We utilized the distance from the warren as an explanatory variable. We also considered another four 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 linear infrastructure elements (e.g. roads), which may serve as corridors with good visibility, (3) distance to seasonal lagoons that represent large patches of habitat with good visibility and food availability during spring (when covered with soft sprouts relished by maras), and (4) distance to neighboring warrens that may influence space use because of social interactions. The distance to

neighboring warrens also account for possible contributions of individuals from these warrens to the number of feces. We recorded the position, shape of or path towards these elements using a Garmin e-trex hand-held GPS unit. Then, we measured the minimum distance from the end point of each sample unit to point infrastructure elements, roads, lagoon borders, or nearest known neighbor warren (distance to neighbor warren) using ArcView 3.2 (Environmental Systems Research Institute, Redlands, CA, USA), so we obtained one value of these variable for each of the 1500 sampling units (5 warrens \times 4 transects \times 75 sampling units=1500 values). With the distance to the road we built up a binary predictor (road presence) using 60 m as threshold distance, because we observed in the field that the side influence of this linear infrastructure element seemed to become less notorious around this distance.

Patches of vegetation allowing for an early detection of predators or providing cover may also influence space use by maras. We estimated relative cover of bare soil and main vegetation functional forms from photographs taken 2.5 m above ground level at the distal end of each sampling unit relative to the warren. The effective ground area sampled in the pictures was approximately 3 m². Pictures were then sampled over a 100-point rectangular grid using SamplePoint v1.48 (Booth et al. 2006). We estimated the proportion of seven categories within each sample: bare soil, grasses, shrubs, forbs, dwarf-shrubs, mulch, moss and feces (MMF), and other types of cover. The area covered with other types of cover was discarded so the total cover for some sampling units does not necessarily add to one.

Statistical analyses

In the explanatory phase of the analyses we aimed at identifying variables that best explained sampling unit use by maras and use intensity by fitting generalized linear mixed models (Zuur et al. 2009). The probability of a given sampling unit to be used by maras was modeled using presence of feces as the response variable; we assumed a binomial error distribution and used a logit link function because this is a binary variable (Zuur et al. 2009, Logan 2011). To model use intensity we took natural logarithms of the number of feces to control the over-variance and discarded samples without use (0 feces) thus focusing on the variation of intensity of use in areas effectively used by maras as indicated by the presence of feces; in this case we assumed normality of errors and used an identity link function because the transformed response variable is continuous (Zuur et al. 2009, Logan 2011). We tested

for collinearity of predictors ($r > 0.5$) using Spearman's rank correlation index (Rhodes et al. 2009). Warren and transect ID were included as random effects in order to account for possible dependencies.

The procedure to select the final model is a backward elimination method for generalized linear mixed effects models (Zuur et al. 2009). We initially composed complete models including all predictors and tested for alternative structures for random factors using Akaike's information criterion (AIC, Akaike 1973). 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). We used the R (R Development Core Team 2010) packages *lme4* (Bates et al. 2011), *MASS* (Venables and Ripley 2002) and *nlme* (Pinheiro et al. 2009) for model fitting and selection.

After testing for model fit, we checked for autocorrelation among residuals using Moran's I autocorrelation index (Legendre and Fortin 1989, Overmars et al. 2003) calculated with the R package *ape* (Paradis et al. 2004). When this test showed evidence of autocorrelation we refitted the model including a spatially structured variance term following Zuur et al. (2009) guidelines, using the "correlation" argument of the *lmn* functions of the R package *nlme*. To evaluate the presence of anisotropy we calculated partial variograms by transect using the R package *gstat* (Pebesma 2004) and the spherical model. Finally, we assessed goodness of fit and departures from model assumptions by different means depending on the error structure assumed. We graphically verified the logistic model of probability of use 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. Regarding the use intensity model, we performed a Shapiro-Wilk normality test over the residuals and evaluated its homogeneity by regressing the Pearson residuals and its absolute values on the fitted values (Jiao et al. 2004).

Results

The extension of use areas with respect to warren position showed heterogeneity given that distance 0.95 varied between 80 and 1460 m across transects and warrens (Figure 2). The intensity of use also showed

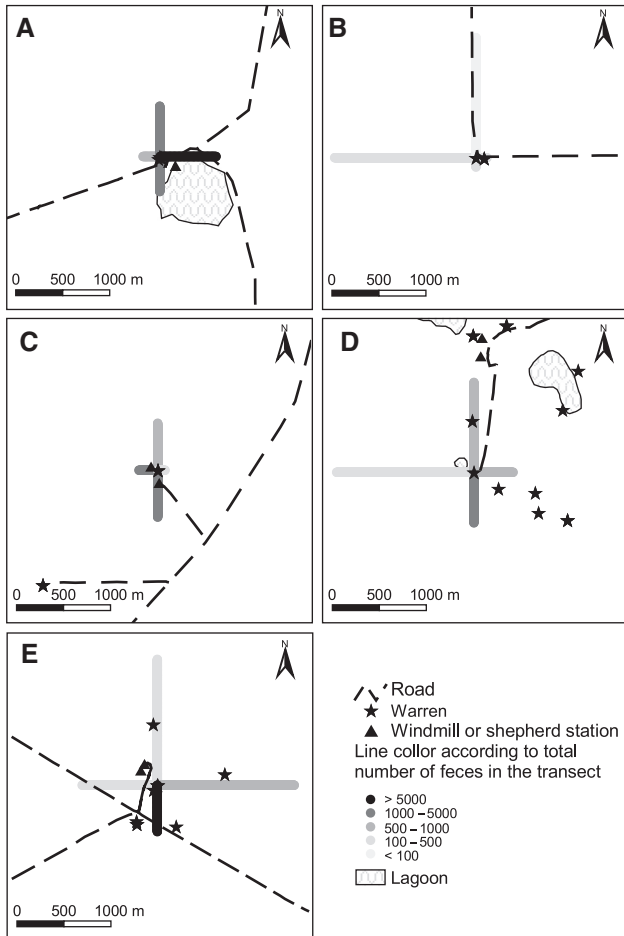


Figure 2: Maps of sampling sites showing the portion of transects where the accumulated proportion of feces registered in each transect reached 95%. Gray decreasing tones indicate the total number of feces registered in the transect according to the legend.

variation among transects within warrens (Figure 2). The radius of areas of use estimated by means of the overall distance 0.95 was 720 m, and the overall distance 0.5 was 240 m, indicating a concentration of use closer to the warren.

According to the models of probability of use (presence of feces) and use intensity (number of feces) the best structure of random components included only transects ID (Table 1). However, this structure of random effects did not take into account dependencies among sampling units because model residuals showed spatial autocorrelation. The Moran’s I for the residuals of the model fitted to the presence of feces was $0.11 \pm 4.86 \times 10^{-3}$ ($p < 0.001$) and for the residuals of the model fitted to the number of feces was $0.07 \pm 1.81 \times 10^{-2}$ ($p = 1.29 \times 10^{-5}$). The experimental partial variograms calculated for each transect within a warren showed anisotropy, so we kept transect identity as a random factor to refit the models.

Table 1: Akaike information criterion values for the random components structures evaluated to model presence of feces and number of feces.

Random components structure	Response variable modeled	
	Presence of feces	Number of feces
Transect warren	1251.00	1226.14
Warren	1299.97	1249.41
Transect	1249.00	1224.14
Without random factors	1297.97	1247.41

The hierarchical structure transect|warren models the effect of variation between warrens and the effect of variation between transects in a given warren. The values of the selected structure are in bold.

The probability of a sampling unit being used by maras (presence of feces) was negatively related to the distance to the warren (Table 2). However, the intercept of the lineal predictor was not significantly different than zero. According to the autocorrelation structure of the model fitted, the probability of use of a given sampling unit was independent of other sampling unit use beyond 487 m (range). The quantile-quantile plot showed the points lying close to the 1:1 line (Figure 3), suggesting there were no major departures from the model assumptions. The partial residual plot for the distance to the warren was moderately non-linear for distances >1000 m, but re-fitting the most parsimonious linear model with a quadratic term for this covariate did not improve the model.

The intensity of use (number of feces) was negatively related to the distance to the warren and the distance to point infrastructure elements, and positively associated with the proportion of bare soil and the presence of roads (Table 3). The model of autocorrelation structure estimated that use intensity in a given sampling unit was independent of other sampling unit use intensity beyond 83 m (range). The residuals of the selected model did not show evidence of departures from normality according to the Shapiro-Wilk test result ($W_{328} = 0.99$, $p = 0.71$), nor any tendency, given that regression parameters of Pearson’s residuals and their absolute values over fitted values were

Table 2: Estimated parameters for predictors of probability of use (presence of feces) according to the selected model.

Variable	b_i	SE	t_{1479}	p
Intercept	0.72	0.39	1.81	0.07
Distance from the warren	-2.77	0.62	-4.46	0

The table shows: the estimated parameter (b_i), standard error (SE), t statistic value ($t_{d,p}$) and associated probability (p) for each predictor.

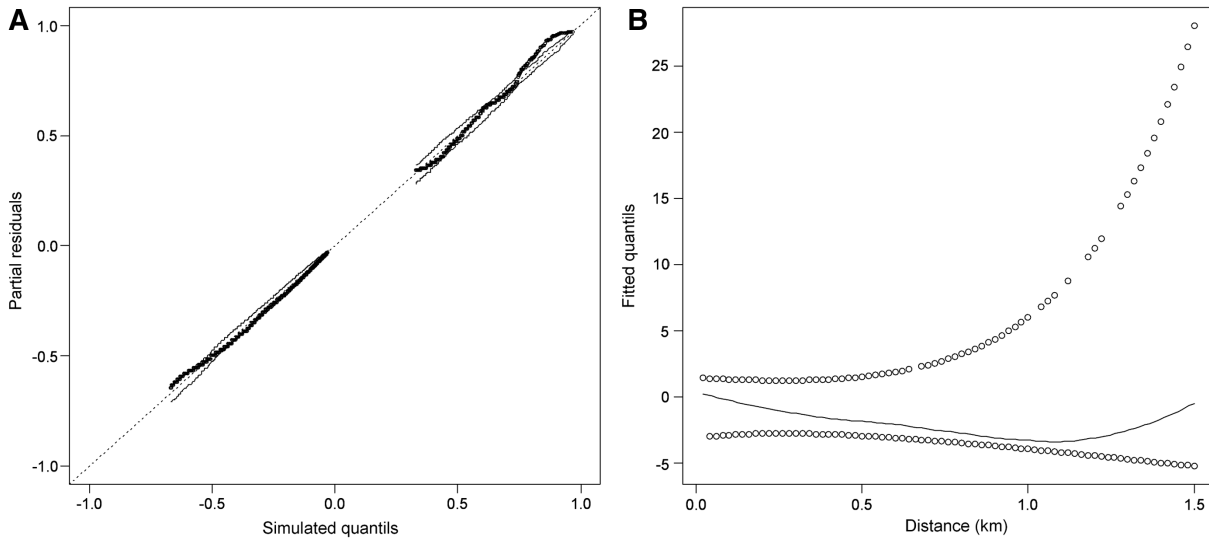


Figure 3: Quantil-quantil plot of fitted vs. simulated residuals (A) and partial residuals vs. distance to warren plot (B).

Table 3: Estimated parameters for predictors of use intensity (number of feces) according to the selected model.

Variable	b_i	SE	t_{305}	p
Intercept	3.730	0.278	13.426	0
Distance from the warren	-1.042	0.270	-3.859	0.0001
Proportion of bare soil	0.008	0.004	2.112	0.0355
Road presence	0.772	0.292	2.642	0.0087
Distance to point infrastructure elements	-0.571	0.162	-3.520	0.0005

The table shows: the estimated parameter (b_i), standard error (SE), t statistic value ($t_{d,f}$) and associated probability (p) for each predictor.

not significantly different from zero ($t_{327}=1.053$, $p=0.29$ and $t_{327}=0.549$, $p=0.58$, respectively).

Discussion and conclusion

The activity of maras was concentrated in the surroundings of the warren, the probability of use of a given site by maras was mainly explained by the distance to the warren, and the use intensity decreased in general when distance from warren increased. These results agree with the hypothesis that the location of the warren conditions the use of other resources (Mitchell and Powell 2004, Börger et al. 2008). Therefore, even when maras use the warrens temporarily and only for reproductive purposes, the location of warrens is a fundamental indicator and a factor positively associated with the annual home range. However, the warren would not be the center of use areas nor the only element conditioning the use of space because we found asymmetries in the extension of use areas as well as in the use intensity.

Other elements of the landscape, some of human origin, would be also influencing the way in which maras use the space around warrens. We found that the proportion of bare soil, the presence of roads and the distance to point infrastructure elements influence the use intensity as well as the distance to the warren. The relation of the microhabitats used by maras and the proportion of bare soil was reported in previous studies (Kufner and Chambouleyron 1991, Taber and MacDonald 1992b, Rodríguez 2009). Maras might intensively be using bare soil patches as resting areas with good visibility or because during spring these patches are covered with soft sprouts of annual forbs and grasses (Bertiller et al. 1991), representing concentrated food resources. Regarding the association with infrastructure, it has been observed previously that bigger colonies were localized close to shepherd stations (Taber 1987) and most areas used by maras were found at sites modified by humans (Rodríguez 2009). Our results confirmed this relation and, in addition, showed quantitatively that maras use areas close to human infrastructure elements more intensively. These results would be related to behaviors of early detection

of predators, given that in infrastructure surroundings bushes and tall grasses are systematically cut off, and exploitation of low predation pressure sites generated by human presence (Kufner and Chambouleyron 1991, Taber and MacDonald 1992b, Baldi 2007). In contrast, the distance to neighbor warrens did not significantly influence neither the probability nor the intensity of use.

The habitat use patterns at microhabitat scale observed in this study suggest that maras use multipurpose areas including the breeding site and the resources needed throughout the year. This space use pattern, as well as the association between use areas characteristics and environmental conditions, has also been observed in other caviomorph rodents (Maher and Robert Burger 2011). In contrast, studies about the relation between space use and warren position among the caviomorphs with comparable results are scarce. Among them, a characterization of spacing behavior within and among social groups of *Lagostomus maximus* reported that the warren was located at the center of residents' home ranges (Branch 1993). Space use studies in *Octodon degus* (Hayes et al. 2007, Quirici et al. 2010) and *Microcavia australis* (Ebensperger et al. 2006) using radio tracking suggest that the position and characteristics of burrow systems influence the activity development of their residents. However, these studies did not show or evaluate the relation between burrow location and the extension or orientation of home ranges, and were restricted to the breeding season. It is remarkable that space use patterns and its determining factors are similar in maras and the above-mentioned semifossorial rodents, which use the warren constantly as shelter and not only for reproductive purposes. The resource optimization theory could explain the restrictions imposed by the warren position to habitat use in other rodents and in maras during the breeding season, but it cannot explain the permanence of maras around the warren throughout the year. This permanence would be due to absence of incentive to change the use area, given that the cover from predators provided by habitat is a determining resource over mara space use according our results, which does not vary across seasons (Campanella and Bertiller 2008). Nevertheless, it can not be rejected that they could shift use areas facing environmental variation, as reported for *Cavia magna* (Kraus et al. 2003) and *Cavia aperea* (Bilenca et al. 1995), given that information about space use in relation with the warren in other sites of the species range is not available.

We found that the distribution and abundance of feces are good indicators of habitat use by maras, and help to identify the main conditioning factors. From

a methodological perspective the agreement between results obtained counting feces and with radio-tracking is remarkable. The distance where the accumulated proportion of total feces reached 0.95 (720 m) was close to the average radius of the annual home range reported by Taber and MacDonald (1992b) using telemetry (783, 79 m). Our results also agreed with this study regarding that maras would stay around the warren throughout the year and the spatial patterns of habitat use (see next paragraph). In addition, feces counting is cheaper, easy to perform and non-invasive, while the capturing of maras presents a high mortality rate (Taber 1987). Therefore, counting feces would be a good option in use areas surveys if it is not critical to discriminate between individuals or seasons.

The spatial autocorrelation models of use probability and intensity presented here are the first estimated for the mara. The results indicated that sites <500 m apart would be dependent in their use probability. This pattern could reflect the high mobility of maras as reported by Taber and MacDonald (1992b), who found that radio-tracked individuals traveled 1.7 km during daily forage trips, remaining for more than 30 min only in a few patches and using the extension between them as passing habitat. In addition, the use intensity showed independency beyond 80 m of lag, suggesting that intensively used patches are small and disperse. Our estimations will be relevant in future studies' design, allowing sampling efforts to be re-allocated in larger extent, increasing the grain of sampling without losing informative power. Besides, the development of studies at scales of larger extent and related to spatial ecology of such a cryptic and highly mobile species will be possible using warrens as a reference point, because our results confirmed the warren as a landmark of habitat use not only for reproductive purpose but in wider terms.

Acknowledgments: We are grateful to the owners of the ranches San Lorenzo, La Anita, Valdés Creek, La Pelada, San Felix and San Pablo de Valdés, for allowing us to conduct the sampling at their properties. To G. Zaperi, N. Kuzmanich and D. Galván for assistance in the field, to L. Beltramino, R. D'Agostino and L. Bossio for assistance during sample processing, and to G. Pazos for suggestions of valuable references. The Centro Nacional Patagónico, Fundación Patagonia Natural and Fundación Vida Silvestre Argentina provided logistical support. Funding for this work was provided by the Ministerio de Educación de la Provincia de Chubut. The study was authorized by the Dirección General de Conservación de Areas Protegidas del Chubut and the Dirección General de Fauna del Chubut.

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