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Factors influencing the location and number of entrances of European wild rabbit (*Oryctolagus cuniculus* L.) warrens in a Southern Portuguese montado

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Abstract

The importance of environmental variables related to vegetation, soils and topography on the distribution and number of entrances of wild rabbit warrens was investigated in a Mediterranean savannah-like ecosystem (montado in southern Portugal). Warren locations were obtained using the line transect method. Each warren was mapped on an orthophotomap and characterised in terms of total number of entrances. Estimates of warren density and average number of entrances were obtained, using Distance 3.5 software, for five different vegetation types - arable crops, pastures, tall scrub, average scrub and low scrub. Environmental variables were also measured at each warren location, either at the site or using GIS functions. These included distance to the nearest tree and percentage of vegetation cover, landscape diversity, exposure and slope. The importance of vegetation and environmental variables on warren location was assessed by comparison with random points within generalised linear models, allowing for bias due to detectability.

The importance of vegetation type and structure on warren location and the number of entrances, in terms of providing protective cover and feeding areas, was demonstrated. Warrens were more abundant in dense scrub vegetation and their location was positively correlated with height and percentage of scrub cover in the proximity, landscape diversity, tree cover and presence of a tree. The number of entrances was positively correlated with the tree diameter at 1.30 m (d.b.h.). The presence of trees was demonstrated as contributing significantly to the suitability of montados for wild rabbits. The results are discussed in relation to habitat management strategies for increasing or maintaining wild rabbit populations. A strategy of maintaining patches of dense scrub interspersed with areas of open vegetation is advocated.

Introduction

In Mediterranean areas, the wild rabbit (*Oryctolagus cuniculus* L.) is a popular game species and a key species in food webs, being the main prey of several predators, some of which are endangered (Jaksic & Soriguer, 1981; Iborra *et al.*, 1990; Palomares & Delibes, 1991; Ontiveros & Pleguezuelos, 2000). The decrease in Iberian wild rabbit populations due to habitat changes, diseases and excessive predation and hunting (e.g. Moreno *et al.*, 1996; Palomares *et al.*, 1996) heightens the importance of ecological information that can be used to improve habitat conditions and to recover population densities.

The European wild rabbit is the only lagomorph to build warrens. It has been argued that warrens may be a means of exploiting environmental heterogeneity (Rogers & Myers, 1979; Roberts, 1987) and are important as protective structures against predation and climatic extremes (Myers & Parker, 1965; Chapuis, 1980; Parer & Libke, 1985). Their spatial distribution has been related to vegetation cover (Myers & Parker, 1965; Myers *et al*., 1975; Parker *et al*., 1976; Rogers, 1981; Chapuis; 1980), local topography (Myers *et al*., 1975; Parker, 1977) and soil type (Parer & Libke, 1985).

The information on warren distribution has been mainly obtained from studies undertaken in areas where the rabbit was introduced and, therefore, where different adaptive strategies may be acting. There has been relatively little research on the distribution of warrens in the Iberian Peninsula where the species in endemic (eg: Jaksic & Soriguer, 1981; Villafuerte *et al*., 1993). Warren distribution has been characterised in relation to landscape types in one study in Spain (Soriguer & Rogers, 1981), and inconclusively in terms of vegetation height and cover, slope and distance to feeding areas in central Portugal (F. Monteiro, unpublished data).

The aim of the present study was to examine the environmental factors that may explain the location and the number of entrances of wild rabbit warrens in Southern Portuguese montados, savannah-like ecosystems of great ecological and economic interest (e.g. Joffre *et al*., 1999; Roberts & Nunes da Silva, 2000). Many of the management activities taking place in a montado, such as ploughing and scrub clearance, affect the structure of the vegetation cover. Therefore, in this study emphasis was given to the assessment of the importance of vegetation type and density, and related environmental factors, on warren location and the number of entrances. A second aim of the study was to provide guidelines for the improvement of habitats for wild rabbits in montado ecosystems.

Methodology

Study Area

The study area is a 270 ha hunting estate in south-east Portugal (38º47'N, 7º25'W), comprising a rolling landscape between 300 and 420 m in altitude (figure 1). The climate is Mediterranean with a strong seasonality, being characterised by hot and dry summers (average temperature of 25º C and average rainfall 2 mm in August) and rainy and mild winters (average temperature of 9º C and average rainfall 100 mm in January) (Rosário *et al*., 1983).

The vegetation consists mainly of cork oak (*Quercus suber* L.) and holm oak (*Quercus rotundifolia* L.) stands, some with arable crops of triticale (X *Triticosecale* Wittmack) and oats (*Avena sativa* L.) and characterised by a reduced tree cover in order to facilitate ploughing. The remaining understorey is dominated either by patches of gum cistus (*Cistus ladanifer* L.) or natural pasture.

Data collection

The location of 197 warrens was identified by use of the line transect method and respecting the underlying assumptions of Distance Sampling Theory (Buckland *et al*., 1993). An observer surveyed the study area along parallel lines with a 50 m interval between them, mapping all the warrens detected on both sides of the line, and recording the perpendicular distance from their geometric centre to the centre of the line. The first line was placed randomly, ensuring that lines were distributed independently with respect to the distribution of warrens (Buckland *et al.*, op. cit.). All the lines were perpendicular to the main tracks crossing the study area and, therefore, parallel to possible warren distribution gradients induced by human disturbance.

For each warren, environmental variables were either measured at the site or derived using functions of the Geographic Information Systems ArcInfo (ESRI, 1995a), ArcView (ESRI, 1995b) and ERDAS Imagine (ERDAS, 1995) (see Table 1).

Landscape diversity was described in relation to the proximity to the edge of a patch by developing an index that has a value of 1 if the warren is in the middle of the patch, 2 if the warren is at the edge of two different types of habitat, 3 if it is at the edge of three different vegetation types and so forth. Values of the index were obtained for circles around the warren, with a radius of 20 m up to a radius of 140 m, at increments of 10 m.

Measurements for the same variables were also collected at 197 random points. It was also recorded whether the warrens showed signs of being used (active) or inactive, and the total number of entrances.

Statistical analysis

The assumption of independence between detections is critical for the use of inference methods (Buckland *et al*., 1993; McCullagh & Nelder, 1989). Spatial dependence arises as an autocorrelation, i.e. a correlation between environmental variables that makes the presence of a warren likely in the neighbourhood (Smith, 1994). It can lead to a loss of power of the statistical models by reducing the number of degrees of freedom (Griffith, 1992; Legen-

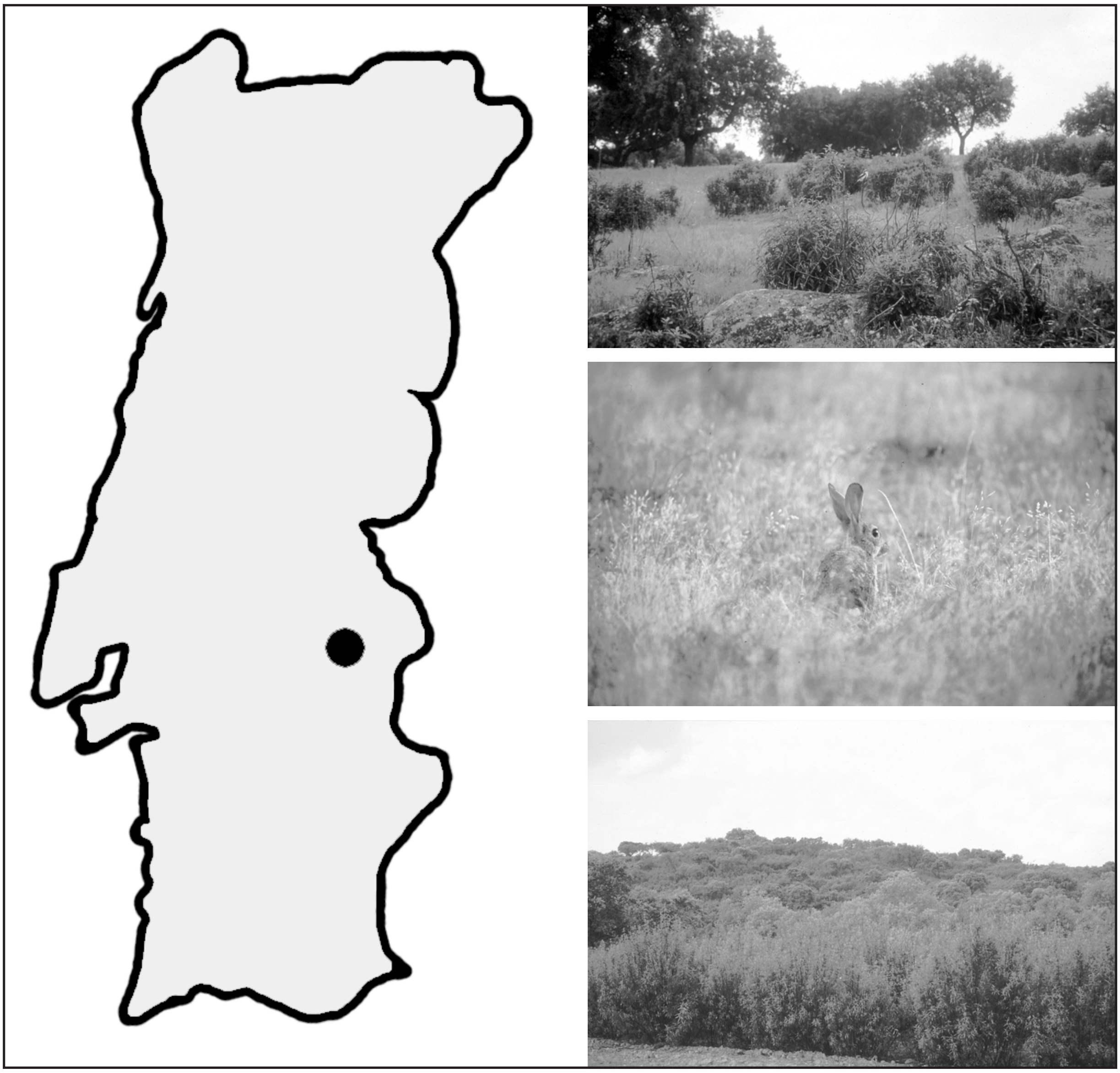

Figure 1. Study area

dre, 1993). Thus special attention was given to this issue before carrying out the analyses.

Spatial dependency of warrens at a scale of the study area was assessed with ArcInfo by calculating Moran's Spatial Autocorrelation Index considering a radius of 25 m, 50 m, 100 m, 150 m and 200 m with each warren as the centre (Moran's I; Goodchild, 1986). At the scale of the vegetation types, the method involved the use of generalised linear models to test the assumption that the number of warrens detected per transect replicate within a vegetation type followed a Poisson distribution (McCullagh & Nelder, 1989). The length of transects was accurately measured on an orthophotomap at the scale 1:40 000, with a resolution of 1 m. If the warrens are randomly distributed along the transects, it can be assumed that its number is directly proportional to the length of the transects. This relationship can be translated in the following model:

$$\log(\text{n°warrens}_{i,j}) = ß_0 + \log(\text{length}_{i,j})$$

where i is a transect replicate in vegetation type j, and the logarithm of its length was considered as the offset, whose regression coefficient is known to be 1.

Table 1. Specifications with respect to the environmental variables.

VARIABLE	CATEGORIES/UNITS
Vegetation type	crop, pasture, dense scrub cover, average scrub cover and sparse scrub cover.
Soil type	Soils reddish-grey, non-calcareous over schists (Px) Soils red, non-calcareous over schists (Vx) Alluvium (A) Colluvium (Sb) Skeletal soils of schists (Arx) Lithosol (Ex) Complex combinations of types
Herbaceous layer average height	Low: <5 cm Average: 5 cm-20 cm High: >20 cm
Shrub layer average height	Low: <50 cm Average: 50 cm-1.5 m High: >1.5 m
Aspect	N, S, E, W, NW, NE, SW, SE, flat
Drainage	1 - high probability of waterlogging 0 - low probability of waterlogging
Index of landscape diversity	Ii i= radius of 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 110, 120, 130 and 140 m The index has the value 1 if the warren is in the middle of the patch, 2 if the warren is at the edge of two different types of habitat, 3 if it is at the edge of three different vegetation types and so on.
Distance to the nearest tree	m
Diameter at breast height (DBH; 1.30 m) of the nearest tree	m
Proportion of herbaceous cover	%
Proportion of shrub cover	%
Proportion of tree cover	%
Slope	Degrees from horizontal
Altitude	m
Exposure to wind	Topex Units
Shortest distance to a stream	m
Shortest distance to a spring	
Shortest distance to a pond	
Shortest distance to water	
Shortest distance to crop	
Shortest distance to pasture	
Shortest distance to dense cover	
Shortest distance to sparse cover	
Shortest distance to average cover	

The residual deviance obtained for each vegetation type was compared with the χ^2 value for the same number of degrees of freedom. Departures from independence between detections would cause an increase of the residual deviance in relation to the χ^2 value, for which it is possible to check the level of significance (McCullagh & Nelder, 1989).

Assessment of the effect of vegetation type and density of cover on warren density and number of entrances

Estimates of warren density per vegetation type were obtained using Distance Sampling Theory (Buckland *et al*., 1993) implemented in the software Distance 3.5 (Thomas *et al*., 1998). The vegetation types identified in the study area were pooled into five categories reflecting the ecological needs of the wild rabbit in terms of vegetation cover (e.g. Rogers, 1981): arable crops, pasture, tall scrub, low scrub and average scrub. In most cases, the size of sample was at least 30 warrens, except for arable crops and pastures. However, pooling these two categories did not appear reasonable due to the differences in the structure of the vegetation cover. Moreover, arable crops have considerably lower tree cover to facilitate ploughing. Therefore, arable crops and pastures were considered individually, but acknowledging that the higher variability associated with the density estimates obtained from small samples makes the tests of statistical comparisons less robust.

In order to assess the influence of the environmental variables on the number of entrances, warrens were considered as clusters of entrances and the total number of entrances was included in the analysis as an ancillary variable. The number of entrances of the warrens might influence its own probability of detection, and the estimated average number of entrances might be biased towards the largest warrens. This was overcome by regressing *ln(cluster size)* against the detection function g*(x)*, when distance to line and number of entrances of the warren were significantly correlated (Buckland *et al*., 1993).

Several models were examined in modelling the detection function in each vegetation type. The selection of the most accurate model was made on the basis of the lowest value of the parsimonious Akaike´s Information Criterion (AIC; Burnham & Anderson, 1998). In order to obtain more accurate density estimates, perpendicular distances from the warrens to the transect line were truncated at 8 m for tall scrub, at 16 m for average scrub and at 25 m for the rest of the vegetation types. The estimates of warren density and average number of entrances obtained with the selected model for each vegetation type were compared using Beherens-Fischer t-tests (Zar, 1984) with Bonferroni correction of the level of significance, since multiple comparisons result in loss of degrees of freedom (Rice, 1989).

Vegetation type is a variable that changes with time due to management actions such as shrub clearance and ploughing. Therefore, the same analysis was carried out using only warrens with evidence of current use, since location of inactive warrens could reflect the past management. The density and the expected number of entrances of active warrens were estimated using the attribute active/inactive to post-stratify the Distance Sampling Analysis (Buckland *et al*., 1993).

Effect of other variables on warren density and number of entrances

The effect of soil type was assessed also by using Distance Sampling Theory (Buckland *et al*., 1993). The soil classes followed the classification suggested by Carvalho Cardoso (1965), which were pooled into three categories: lithosols (Ex), lithosols mixed with red soils, non-calcareous over schist (Ex+Vx), and others in order to have a sufficient sample size. Warren density and average number of entrances were estimated for each soil category by using Distance 3.5 (Thomas *et al*., 1998), and compared with the Behrens-Fisher t-test with Bonferroni correction of the level of significance.

The survey design selected to collect data for this study produces a bias associated with the detectability of warrens, related to their distance from the transect. This is especially important in the variables related to vegetation cover and, consequently, visibility. Therefore, the variables under study have to be always conditional on the perpendicular distance from transect line, which was included in the models as a covariate.

The influence of the categorical variables on the warren location was assessed by means of generalised linear models fitted with Genstat 5 (Genstat 5 Committee, 1993). The independent variables, apart from the distance from the transect line, are a factor *type* that assumes the labels either *warren* or *random point* and a factor named *class* that is the variable under study. For each warren or random point, the dependent variable, *data*, assumes per observation the value 1 for the correspondent level of the factor *class* and 0 for the others. The assumption of interaction between *type* and *class*, conditional to distance from transect, is tested with the Likelihood Ratio Test (McCullagh & Nelder, 1989) applied to the model:

$$data = b_0 + b_1 \cdot distance + b_2 \cdot type + b_3 \cdot class + b_4 \cdot distance \cdot class + b_5 \cdot type \cdot class$$

In relation to numerical variables, the approach selected was of testing the significance of b_2 in the model (Draper & Smith, 1981):

$$y = b_0 + b_1 \cdot distance + b_2 \cdot type$$

where *y* is the environmental variable under study, transformed for normality, *distance* the perpendicular distance from the transect line and *type* is the two-label factor that can be either *warren* or *random point*.

The study of the effect of the environmental variables on the location and number of entrances of the active warrens is only relevant for variables related to vegetation cover, since only they were affected in the recent past due to land management activities.

An exploratory analysis was carried out with the help of the Spearman Correlation Coefficient (Daniel, 1990) to understand the effect of the variables considered on the number of entrances of the warrens.

The effect of potential autocorrelation was investigated for numerical variables by fitting models using the Residual Maximum Likelihood (REML) facilities in Genstat 5 for modelling correlated error structures in spatial data (Reference Manual Supplement Genstat 5 Release 4.1, 1997). In the models fitted, the fixed effects were considered the *type* (*warren* or *random point*) and the *distance* (perpendicular distance from transect in metres). *Object* is the random effect and is a factor with as many levels as observations. The significance of the fixed term in the model was tested using the Wald test. The spatial pattern of covariance was modelled using the power model, because a distance-based covariance structure was assumed. Since the correlation between warrens depends on the distance between them, coordinates had to be provided for the calculation of the Euclidean distances (Horgan & Hunter, 1993).

Results

Spatial independence of detections

The calculation of the Moran's I at different distances showed that warren detections were strongly spatially correlated up to a distance of 50 m and then less strongly up to 100 m, being independent thereafter (Fig. 2). At the scale of the vegetation type, the value of the residual deviance for the generalised linear models fitted to a sequence of detections of warrens is always significantly higher than the critical value for randomness (Table 2). Thus the distribution of residuals is not random and confirms the spatial dependency of warren detections within each vegetation type.

Effect of vegetation type and density of cover on warren density and number of entrances

The detectability effort was proportional to the area of the vegetation patches (r^2=0.98, P<0.001) and therefore conclusions about habitat selection are valid. Tall scrub had significantly higher warren densities than arable crops (t_{58}=4.864, P<0.005, considering sequential Bonferroni's levels of significance), low scrub (t_{51}=4.467, P<0.006) and pasture (t_{77}=3.350, P<0.007) (Fig. 3). Average scrub had significantly higher warren density than arable crops (t_{75}=3.561, P<0.006) and low scrub (t_{61}=2.988, P<0.008). When the same analysis was repeated using only active warrens, the warren density was also significantly higher in tall scrub in relation to arable crops (t_{57}=4.166, P<0.005) and low scrub (t_{50}=3.676, P<0.006). Average scrub had significantly higher densities than arable crops (t_{75}=3.365, P<0.006). In terms of number of entrances, there was no significant difference between vegetation types, although there was a tendency for larger warrens in the pasture and low scrub categories.

Effect of other variables

Lithosols (Ex) and combination of lithosols with red, non-calcareous soils over schists (Ex+Vx) had significantly higher warren densities ($t_{126,(Ex,Others)}$=4.826,

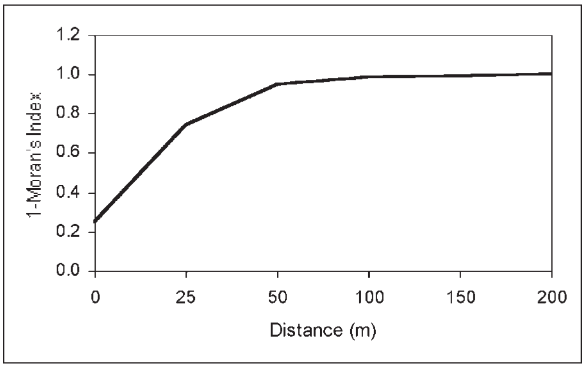

Figure 2. Spatial autocorrelation of warren detections measured by Moran's I in relation to distance from the warren.

Table 2. Results of the test of the assumption of randomness of warren locations on transects within each vegetation type.

Vegetation type	Residual Deviance	d.f.	p-value
Average scrub cover	89.02	38	<0.001
Low scrub cover	153.00	43	<0.001
Tall scrub cover	85.38	31	<0.001
Crop	79.86	25	<0.001
Pasture	56.73	23	<0.001

P<0.001; $t_{67,(Ex+Vx,Others)}$=3.019, P=0.004) than the other soil types (Fig. 4). Soil type did not have a significant effect on the number of entrances of warrens.

Warrens differed significantly from random points by having a higher shrub cover in their proximity (χ^2=42.048, df=3, P<0.001) and a higher vegetation diversity at a scale of 70-90m (χ^2=8.460 to χ^2=10.778, df=3 with P=0.037 to P=0.013) (Table 3).

The presence of warrens was positively associated with the percentage of shrub cover ($F_{1,391}$=17.72, P<0.001) and tree cover ($F_{1,391}$=28.94, P<0.001). The significant and negative coefficient of the distance to the nearest tree ($F_{1,391}$=22.00, P<0.001) implies that warrens are likely to be closer to trees. Warrens were near a cork oak in 45% of the cases, in 31% of the cases under a holm oak and in 23% of the cases under an olive tree. There was also a weak negative relationship with the distance to a stream ($F_{1,391}$=4.08, P=0.044) (Table 3).

The values of the correlation in one dimension (phi-estimate) showed high spatial autocorrelation (f=0.9) for altitude, distance to the nearest stream, distance to average and dense cover, distance to arable crop, distance to pasture, distance to sparse cover and distance to the nearest pond. The direction of the correlations between numerical variables and location of warrens mentioned above did not, however, change after filtering out the autocorrelation. In terms of warren locations, the Wald statistic showed that there was a significant negative correlation with the distance to the nearest tree (5.2 m for warrens *vs* 8.4 m for random points; Wald statistic=17.8, df=1, P<0.001), and a positive correlation with the percentage of scrub cover (40.45% for warrens *vs* 31.63% for random points; Wald statistic=31.5, df=1, P<0.001), and with the percentage of tree cover (43.66% for warrens *vs* 35.42% for random points; Wald statistic=56.5, df=1, P<0.001). It is possible to infer that results for categorical variables were also not affected.

The location of an active warren was also significantly and positively correlated with the average height of the shrub layer in the proximity of the warren (χ^2=22.703, df=3, P<0.001), with vegetation diversity at a scale of 70-90m (χ^2=8.020 to

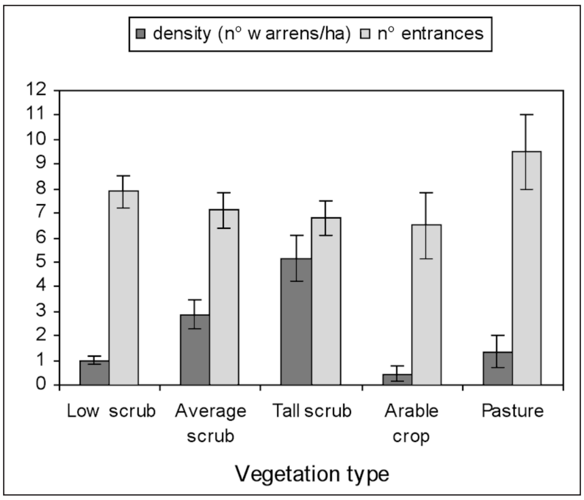

Figure 3. Estimates of density (nº warrens/ha) and number of entrances of all warrens for the different vegetation types.

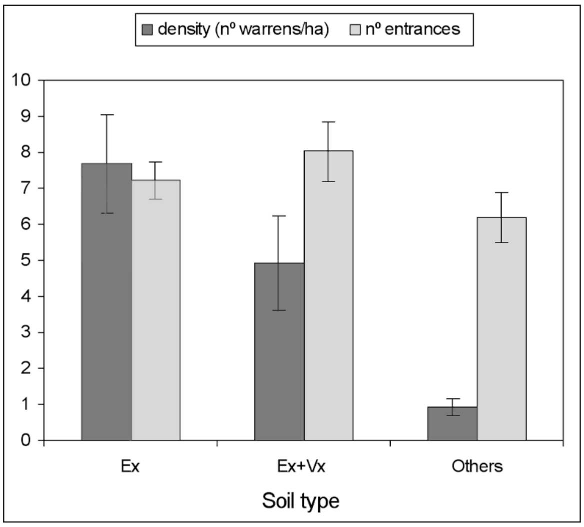

Figure 4. Estimates of warren density (nº warrens/ha) and number of entrances for the different soil types.

Table 3. Coefficients of the univariate models comparing warren locations and random points for significant environmental variables ($p<0.05$). A positive coefficient indicates a positive correlation between the variable and the warrens.

Variable	Model coefficients
Shrub layer average height	
Low	0.90
Average	0.91
Tall	2.01
Landscape diversity in a radius of 70 m	
edge of 2 vegetation types	0.20
edge of 3 vegetation types	0.83
edge of 4 vegetation types	0.38
Landscape diversity in a radius of 80 m	
edge of 2 vegetation types	0.05
edge of 3 vegetation types	0.79
edge of 4 vegetation types	0.11
Landscape diversity in a radius of 90 m	
edge of 2 vegetation types	0.22
edge of 3 vegetation types	0.79
edge of 4 vegetation types	0.12
Distance to the nearest tree (m)	-4.49
Percentage of shrub cover	11.80
Percentage of tree cover	9.49
Shortest distance to a stream (m)	-30.50

$\chi^2=10.320$, df=3, with P=0.005 to P=0.016), and with the percentage of shrub cover in the proximity of the warren ($F_{1,267}=5.107$, P=0.025).

In terms of number of entrances of the warrens, there was a weak positive correlation with the d.b.h. of the nearest tree (Spearman r=0.23, P<0.01, n=197) and a negative correlation with the distance to a pond (Spearman r=-0.15, P<0.05, n=197). The number of entrances of the active warrens was only positively correlated with the d.b.h. of the nearest tree (Spearman r=0.20, P<0.01, n=171).

Discussion

The use of Distance Sampling Theory (Buckland *et al*., 1993), as a method to describe the influence of environmental variables on the spatial distribution of warrens by inference from a sample of locations, has advantages over the census method in terms of costs, time spent and sampling effort. An intensive survey of an area of 270 ha would have been time-consuming and expensive. Moreover, where warrens are counted in different habitats, there are difficulties associated with the detectability allowed by the vegetation structure. For example, Rogers (1981) pointed out the limitations of conventional methods of conducting warren census, with a likelihood of bias in habitat selection occurring due to the difficulty of observing warrens where vegetation is taller. This bias can only be eliminated by intensifying the detection effort in these areas.

The spatial dependency of warrens may be a reflection of a heterogeneous environment or social processes inducing group-living (Roberts, 1987; Legendre, 1993). In this study, spatial autocorrelation might also have been generated by applying the line transect method. Warren detections were conditional on the detectability allowed by each vegetation type, which might have induced clustering near the transect line. The fact that Moran's I indicates that autocorrelation decreases between 50 and 100 m, which is exactly the distance that covers two consecutive transects, might be evidence of this. However, the results pointed to no bias in the results due to this lack of dependence, since the significance of the correlations between warren locations and environmental variables did not change after filtering the autocorrelation by modelling the error structure.

Jacksic & Soriguer (1981) compared habitat use in Southern Spain, where the species is native, and central Chile, where it had been introduced. They concluded that for rabbits in Spain protective cover was more used than open areas as opposed to rabbits in Chile, where predation pressure was lower. However, new data have demonstrated that Spanish rabbits use open areas more often than previously found, due to the presence of warrens that are used as protective structures (Palomares & Delibes, 1997). This role of warrens as alternative protection against predation and its supposedly higher availability in the open areas are not, although, supported by the results of this study. It seems more plausible that scrub cover is the main protection, and warrens offer a complementary protective structure. The few warrens observed in arable crops in this study may also be associated with periodic ploughing, and the low percentage of tree cover in this land use.

The results suggest that the location of warrens in Southern Portuguese montados is mainly influenced by availability and juxtaposition of protective cover and food resources (see also Queirós *et al*., 1991). Evidence for this is the significant positive correlation of warren locations with landscape diversity at a scale of 70 - 90 m, distances close to the 100 m suggested by Gibb (1993) as being the average home-range of wild rabbit. This diversity might allow more constant food supply in face of seasonal fluctuations in herbaceous biomass availability (Daly, 1981).

The characteristic tree canopy of this savannah-like ecosystem favours the presence of warrens, by providing shade during the hot and dry summers. At the same time, the root system allows the development of a soil structure suitable for burrowing. Trees with a high d.b.h. and, consequently, with a wider root system and shade, are particularly favourable for larger warrens (Southern, 1940; Parer & Libke, 1985).

Water has an important role in thermoregulation, being necessary for the dissipation of metabolic heat production, either through the ingestion of succulent plants or water from water supplies (Hayward, 1961). It is therefore reasonable to conclude that the hot and dry summers, characteristic of the study area, could induce such a dependency on water, which could explain the negative correlation with the distance to streams, which have water throughout the year.

It would have been interesting to assess the effect of the interaction of the environmental variables on the location and number of entrances of warrens, but the bias induced by distance to the transect line and by detectability, which is different from variable to variable, precluded the use of multiple linear models to explain such interactions. The importance of the variables related to vegetation type and structure, such as percentage of cover, landscape diversity and presence of trees, enhances, however, the confidence that can be placed in the conclusion that vegetation has a leading role in the location and size of warrens in the study area.

To conclude, Southern Portuguese montados, managed in order to maintain a diversity of vegetation types, appear to provide suitable habitats for the location of wild rabbit warrens. The results underline the importance of dense scrub for the location of the warrens, and this should be taken into consideration when management operations, which affect vegetation cover, such as scrub clearance, are carried out. The creation of open areas, with high herbaceous biomass availability, in the patches of tall and dense scrub, would also be favourable. The installation of water supplies scattered over the area might also have a positive effect, especially during the dry season.

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