Capítulo 3

Los mamíferos excavadores como ingenieros de ecosistemas: la construcción de vivares de conejo (*Oryctolagus cuniculus*) en una dehesa mediterránea

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

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Resumen

Algunos animales excavadores crean sistemas de madrigueras que pueden convertirse en una fuente importante de recursos para otras especies. Las propiedades de estos sistemas de madrigueras pueden ser muy diferentes del hábitat sin modificar que les rodea, por lo que las especies constructoras pueden ser consideradas como ingenieras de ecosistemas. La magnitud de los efectos ingenieriles en un lugar determinado depende de la abundancia, tamaño y persistencia de las estructuras físicas que crean, y el tipo de hábitat y características del lugar donde son construidas. Los objetivos principales de este capítulo fueron 1) examinar la ingeniería de ecosistemas a una escala amplia, e intentar describir la densidad y relevancia espacial de los sistemas de madrigueras creados por un animal excavador (los vivares de conejo europeo, Oryctolagus cuniculus); y 2) estudiar los factores del hábitat que determinan la densidad de estos sistemas de madrigueras y, por consiguiente, el lugar donde su influencia será mayor. El estudio se llevó a cabo en una dehesa de 300 ha en el centro de España. Se cartografiaron todos los vivares de conejo y se crearon capas de los factores ambientales que pudieran influir en su localización utilizando un Sistema de Información Geográfica (SIG). En base a esta información se intentaron derivar modelos para identificar los factores más importantes para explicar la densidad y tamaño (nº de entradas) de los vivares. También se registraron todos los elementos del microhábitat asociados a los vivares, como la vegetación leñosa y las rocas, y se investigaron las relaciones entre los elementos asociados y diferentes clases de tamaño. Los vivares de conejo pueden alcanzar altas densidades, y constituir un recurso fácilmente accesible. La densidad de vivares está determinada por la cobertura de rocas y encinas, y por una alta heterogeneidad del hábitat. La cobertura de las zonas inundables y el pastizal abierto estaban relacionadas negativamente con la densidad. Los elementos del microhábitat relacionados con la protección y soporte estructural de los vivares fueron los factores más importantes para explicar el tamaño de los vivares. Se discuten estos resultados considerando el papel del conejo como especie ingeniera de ecosistemas en sus ecosistemas nativos, y la importancia de los factores que controlan sus actividades excavadoras en relación a las ventajas que pudieran aportar para otras especies.

Burrowing mammals as ecosystem engineers: warren building by rabbits (*Oryctolagus cuniculus*) in a Mediterranean dehesa

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Abstract

Some burrowing mammals create open burrow systems that can become an important locus of resources for other species, especially in terms of refuge and soil characteristics. Conditions at open burrow systems can be very different from the unmodified habitat, so burrowing species may fit the definition of allogenic ecosystem engineers. The magnitude of ecosystem engineering effects at a given place depends on the abundance, size and persistence of the physical structures they create, and on habitat type and characteristics of the site where they are built. The main objectives of this investigation were 1) to examine ecosystem engineering at a wide scale, describing the density and spatial relevance of open burrow systems (warrens) created by a burrowing mammal (the European rabbit, *Oryctolagus cuniculus*), and 2) to study the habitat factors that determine their location and, therefore, where their effects will be exerted. The study was carried out in a 300 ha dehesa in Central Spain. We mapped all rabbit warrens and created layers of environmental factors that could be influencing warren location using Geographic Information Systems (GIS). From this information we attempted to derive models that identified the most important environmental factors for warren density and size (no. of burrows). We also recorded microhabitat elements such as woody vegetation and rocks which were found in association with rabbit warrens, and investigated the relationship between associated elements and different warren-size classes. Rabbit warrens can reach high densities and they can become a readily accessible resource. Warren density was mainly determined by rock and holm oak cover, and high habitat heterogeneity. Cover of flood-prone areas and open pastures were negative predictors. Microhabitat elements related with the physical protection and support of warrens appear to be the main factors explaining warren size. We discuss these results considering the potential role of rabbits as allogenic ecosystem engineers within their native ecosystems, and the importance of those factors controlling warren-building activities in relation to the 'services' warrens may provide for other species.

Keywords: open burrow systems, warren denisty, warren size, GIS, GLZ, heterogeneity

1. Introduction

Animal activities are potentially capable of altering habitat characteristics, and can play key roles in shaping the structure and function of ecosystems (Chapin *et al.* 1997). Burrowing mammals may induce strong changes in plant communities and biogeochemical cycling (Brown & Heske 1990); and may have further impacts on geomorphology, hydrology, soil dynamics, vegetation patterns, and animal community diversity (see Huntly & Reichman 1994, and Whitford & Kay 1999 for thorough reviews). Some semi-fossorial mammals (i.e. those which use burrows mainly as refuge and breeding quarters, but feed on above-ground vegetation) create large, persistent structures called open burrow systems. These structures are usually very important in terms of reproduction and species survival, but can also alter the spatial and temporal characteristics of soil patches, thus affecting productivity and spatial heterogeneity of resources, and may even have landscape level effects (Kinlaw 1999). Open burrow systems can also become an important locus of resources for other species, from fungi, microbes (fungi, Hawkins 1996; microbes, Ayarbe & Kieft 2000) and plants (Huntly 1987; Bagchi e*t al.* 2006; Davidson & Lightfoot 2006); to invertebrates (Bangert & Slobodchikoff 2004), reptiles (Shipley & Reading 2006), birds (Butts & Lewis 1982; Lai & Smith 2003) and even other mammals (Hawkins & Nicoletto 1992), including grazers (Hansen & Gold 1977; Fahnestock *et al.* 2003).

Organisms that can modulate the supply of resources for other species are often classified as ecosystem engineers (Jones *et al.* 1994). Burrowing mammals create habitat patches where environmental conditions and resource availability are very different from the unmodified habitat, thus fitting the definition of allogenic ecosystem engineers. This type of engineer "changes the environment by transforming living or non-living materials from one physical state to another", in contrast with autogenic ecosystem engineers, which change the environment through their own physical structures (e.g. trees) (Jones *et al.* 1994, 1997). Examples of burrowing mammals as allogenic ecosystem engineers include prairie dogs (*Cynomys* spp. Whicker & Detling 1998), pocket gophers (Geomydae, Reichman and Seabloom 2002) and plateau zokors (*Myospalax fontanierii*, Zhang *et al.* 2003).

The magnitude of ecosystem engineering effects at a given place depends on the abundance, size and persistence of the physical structures they create, and the habitat type and characteristics of where they are built. Open burrow systems can persist as significant structures in the landscape for long time periods (Whitford & Kay 1999), and their size and longevity will ultimately be determined by where the animal decides to burrow. Burrowing is very costly in energetic terms (Vleck 1981), so there must be clear advantages to an efficient location of burrows (Huntly & Reichman 1994), which suggests that certain identifiable landscape or habitat cues will encourage burrowing in certain patches. Despite the recognised engineering role of burrowing mammals, few studies have analysed the factors that determine the density and location of open burrow systems. Engineering effects may be different, and of different magnitude, depending on habitat factors. For example, the type of substrate (Jones *et al.* 1997), or whether they provide resources which are scarce in a given habitat (e.g. in an ecosystem dominated by predation pressure, engineers that offer effective refuges can be essential for maintaining species diversity) (Crain & Bertness 2006). Knowledge about the presence, density, size and distribution of open burrow systems within a landscape will not only give insights about the ecology and habitat priorities of the engineering species, but also about their potential influence on the spatial distribution of other taxa.

The main objective of this investigation was to examine ecosystem engineering at a wide scale, trying to describe the density and spatial relevance of open burrow systems (warrens) created by a burrowing mammal (the European rabbit, *Oryctolagus cuniculus*), and study the habitat factors that determine their location and, therefore, where their effects will be exerted. European rabbits are social lagomorphs and central place foragers, so several different activities take place around their warrens (herbivory, scraping, defecation, the generation of latrines and excavation). In Mediterranean environments, they are a keystone species (Delibes-Mateos *et al.* 2007), and can act as allogenic ecosystem engineers through warren building (Jones *et al.* 1994), although this role has hardly been studied within their native Mediterranean ecosystems (but see Gálvez *et al*. 2008; **chapters 4 & 5**). We used an extensive dataset of warren location in a Mediterranean dehesa to study warren distribution and the main habitat factors that determine rabbit warren density and size. We also investigated the relevance of microhabitat elements which may serve as protection and structural support for rabbit warrens. We discuss the implications of the most important factors for warren density and size for rabbits; the role of rabbits as allogenic ecosystem engineers within their native ecosystems, and the potential importance of those factors controlling warren-building activities in relation to the 'services' warrens may provide for other species.

2. Material and methods

Study area

The present study was carried out in a "dehesa" of approximately 300 ha near Madrid, central Spain (40º 23´ N, 4º 12´ W). Mean altitude is 670 m and climate is Mediterranean-continental, with mean annual temperature and precipitation of 12º C and 432.6 mm. Dehesas are man-made savannah-like landscapes, characterised by a mosaic of cleared holm oak woodlands with an annual grass understorey, and this arrangement is highly favoured by rabbit populations (Rogers & Myers, 1979; Wheeler *et al.* 1981). In the study area the substrate is sandy, and lays upon fractured granite bedrock; and the dominant tree species is *Quercus ilex* L. subsp. *rotundifolia* (Lam.), within a pasture matrix. There are also extensive areas of Mediterranean short scrub dominated by *Lavandula stoechas* L., and some patches where the tall shrub *Retama sphaerocarpa* (L.) Boiss. is dominant. The main herbivores are an abundant rabbit population, and a herd of about 600 transhumant sheep. The area is still under traditional management practices, with periodic ploughing, mowing of the most productive pastures, and small game hunting.

Mapping of rabbit warrens

In winter (February-March) 2002, all rabbit warrens were identified and geo-referenced, and their total number of entrances recorded. Warren density was very high and warrens were close together (**Figure 1**), making it difficult to discern one warren from another. It was decided that burrows (warren entrances) would be assigned as belonging to the same warren when they were within 2 m of each other. On average, 50% of all warren entrances were active when surveying took place.

Landscape variables

Several environmental variables thought to be relevant for explaining warren density (warrens/ha) and size (number of burrows) were derived from aerial orthophotos of the study area (1:5000), the Digital Elevation Model (DEM), and field verification. All maps were digitised and processed with ArcView GIS 3.2. Several properties of the predictor variables (colinearity, ecological redundancy, etc.) and parsimony considerations were taken into account, so we carried out a priori variable selection. If variables were strongly correlated (Spearman´s correlations, r > 0.70, Fowler & Cohen 1992), the variable which we considered

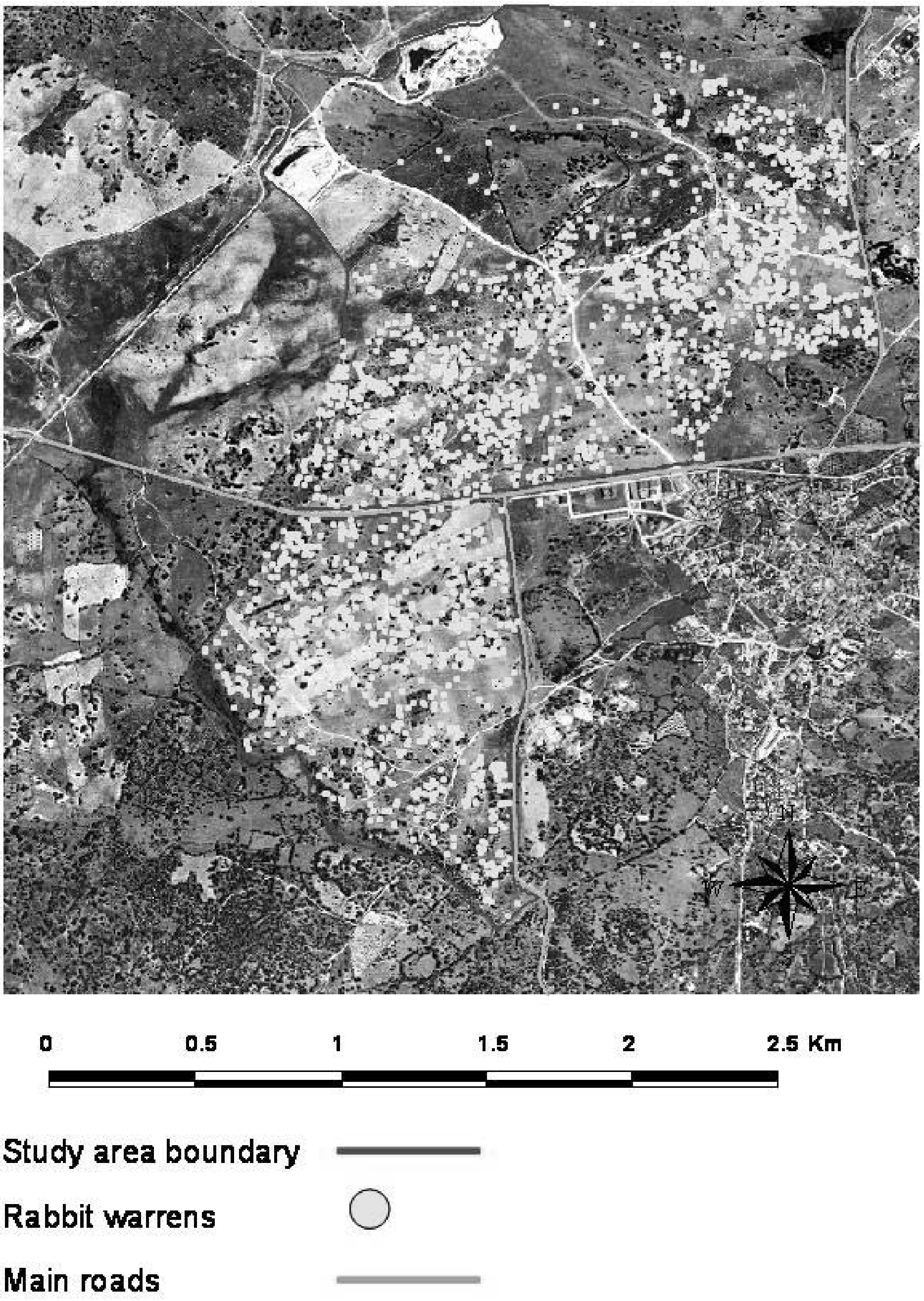

Figure 1. The study area, a 300 ha dehesa in Central Spain. Roads are shown in blue and the study site boundary is marked in red. Yellow circles represent all rabbit warrens found during the sampling period (Feb-March 2002).

most redundant in terms of its ecological meaning was eliminated from further analyses (**Appendix 1**). Finally, 13 variables were selected to be used for models of warren density and size:

Vegetation variables (1-3): Cover of (1) holm oaks (*Quercus ilex* subsp. *rotundifolia*); (2) tall shrubs, represented exclusively by *Retama sphaerocarpa* (*Retama*) (Martins *et al.* 2002; Dellafiore 2007); and (3) open pastures (as access to food), which refers to the herbaceous matrix within which holm oaks, short scrub and tall shrubs are embedded. These variables were chosen to represent both potential refuge from predators (holm oaks, *Retama*) and food resources (pastures).

Geomorphology variables (4-8): The study area was categorised into five large-scale geomorphological classes: (4) ridges (higher areas: dense woodland patches with scarce pasture areas (Ridges); (5) slopes (gently sloping areas, with alternating trees, scrub and pasture patches (Slopes); (6) high flat areas (flat areas in mid-slope: open habitat with some scrub and large xerophytic pasture patches) (High-flat), (7) low flat areas (flat open habitat with pastures, punctuated by trees and scrub) (Low-flat); and (8) Wet lowlands (highly productive open grasslands, close to a temporal stream bed that becomes dry in summer) (Wet-low). These geomorphological classes represent a gradient from ridges to wet lowlands of increasing pasture cover, primary productivity, perennial herbaceous cover and decreasing woody vegetation. They encompass the main habitat types found in the study area, and may have an influence on rabbit habitat use (Rueda 2006). The approximate percentage of the whole study area covered by each geomorphology class is: Ridges: 11.5%; Slopes: 42%; High-flat: 4.7%; Low-flat: 14.4%; Wet-low: 15.2%.

Ploughing (9): Ploughing maps were obtained from 6 sets of aerial photographs (1:18000 and 1:30000) of the area covering the last 20 years (1981-2001). A preliminary study (Gálvez *et al.* 2008) revealed that "time since last ploughing event" was the most relevant ploughing variable for rabbit warrens. The cover of the three main categories for this variable was estimated: ploughed > 15 years ago (Pl.>15); ploughed 4-15 years ago (Pl.4-15); ploughed <3 years ago (Pl. <3). Parsimony considerations induced us to summarise the ploughing variables by means of a PCA for all models. We used the Kaiser (1960) criterion (eigenvalue >1) to define the principal components which we should choose as our final ploughing variables. Although the first two factors had an eigenvalue >1, only Factor 2 was chosen as the final variable for all models, since it represented a gradient from more recent (<3 years) to older (>15 years) ploughing events (**Appendix 2a,b**).

Rock cover (10) (Rocks): Rocks have been identified by other authors as relevant structural elements for rabbit warrens (Myers et al. 1975; Gea-Izquierdo *et al.* 2005). The cover of large rocks and rocky outcrops was estimated from aerial photos and ground confirmation.

Flood-prone areas (11) (Flooded-area): Flooding can be very detrimental for rabbit warrens because it causes the collapse and blockage of burrows, affecting rabbit survival and reproductive success (Palomares 2003a), so the cover of flood-prone areas was assessed using aerial photographs and ground confirmation, which took place in the spring of 2002.

Habitat Heterogeneity (12) (Heterogeneity): All habitat diversity parameters considered were highly correlated (**Appendix 1**). Habitat Heterogeneity (E(P) = H'/ln total no. of vegetation patches, where H´ = Shannon´s diversity index), applied to the main vegetation types in each cell (Rescia *et al.* 1994), was chosen because other studies in the Mediterranean (Carvalho & Gomes 2004; Monzón *et al.* 2004; Fernández 2005) and our own preliminary work (Gálvez *et al.* 2008) highlight the importance of diverse, heterogeneous landscapes for rabbits.

Ecotone (13): GIS tools were used to calculate the total perimeter (m) of the contact area between the short scrub and open pasture layers, and this was considered as an indication of the "length of ecotone". The ecotone between two habitat types has been shown to be a preferred area for warren building, and harbour the highest numbers of burrow entrances (Lombardi *et al.* 2003).

Modelling and statistical analyses

First, we quantified overall warren density and studied their spatial pattern in the study area by calculating the Clark and Evans index of aggregation (R) (Krebs 1999), which uses nearest-neighbour distances. The significance of R with respect to deviation from randomness was assessed using the z statistic. If $|z| > 1.96$, then the null hypothesis of a random distribution must be rejected at $a = 0.05$, indicating that there is a tendency towards clustering. We also estimated warren availability in the landscape by calculating the shortest distance to a rabbit warren from any of 200 random points within the study area.

We then aimed to identify the main landscape factors that explain both warren density and size through the selection of the best-fitting, most parsimonious model using model comparison. For both models, the 13 variables were introduced as potential predictors of warren density and size (number of burrows). If preliminary univariate GAM analyses had revealed non-linear relationships, variables were transformed accordingly (**Table 1**).

Density model: For the density model, a 40 x 40 m grid was created and superimposed on all maps. Warren and variable information were extracted for each cell, and each grid cell represented a case. The total number of cells was 1690, after eliminating peripheral cells (i.e. those with less that 95% of their surface area inside the study area) and outliers and/or influential cases (Cook 1979).

The final data matrix for warren density was used to compute a series of Generalized Linear Models (GLZ), with a Gamma error distribution and a log link function. The best models supported by the data were selected using the Akaike Information Criterion (AIC), a model selection approach based on Information Theory to generate environmental models with multiple predictors (Burham & Anderson 2002). This allowed us to identify the best model based on a particular hypothesis and to rank sets of competitive models (Johnson & Omland 2004).

Since our data were influenced by spatial autocorrelation (Moran´s I of model residuals = 0.137, p = 0.005), this could lead to an underestimation of error variances and to a loss of power of the statistical models by reducing the number of degrees of freedom (Legendre 1993). To eliminate this bias, corrected AICs were calculated. This was accomplished by calculating geographically effective sample sizes (n*), given by $n^* = n/((1 + p)/(1-p))$, where p is the first-order autoregressive parameter of the residuals, approximated by the standardised Moran´s I in the first distance class. Approximated unbiased variances were obtained dividing the residual sum of squares by n*, which were then used to calculate corrected AICs (*sensu* Olalla-Tárraga et al. 2006). We compared the resulting AIC values of each model using ΔAIC, the difference between AICs of each model and the minimum AIC found. A value of $\Delta AIC > 10$ represents a poor fit relative to the best model, whereas a value of less than 2 indicates that a model is equivalent to the minimum AIC model. These ΔAIC values were also used to calculate Akaike´s weighting of each model (w_i), which can be interpreted as the probability that the model is actually the best explanatory model. The values of w_i are standardised across the candidate set of models.

Warren size model: Variables for the model for warren size were derived from 40 m buffers around each warren (area: 5026.6 m^2, approximately the mean core home range of rabbits, Kolb 1991; White *et al.* 2003;

Table 1. Mean ± s.d. of the thirteen variables included in the models and transformation applied prior to modelling according to preliminary GAM results.

Type of model		Density		Warren size	
		Mean per grid cell	**Transformation**	**Mean per 40 m buffer**	**Transformation**
Holm oak cover		11.1% ± 12.2	-	16.26% ± 9.4	-
Herb cover		69.2% ± 32.6	Square	63.72% ± 26.8	-
***Retama* cover**		0.2% ± 0.3	-	0.27% ± 0.4	-
Heterogeneity		0.2 ± 0.1	Log	0.20 ± 0.07	-
Ecotone		64.1m ± 100.6	Log	694m ± 215.6	Square
Flooded-area cover		12.6% ± 26.8	-	8.34% ± 16.2	-
Ridges cover		11.5% ± 24.9	-	14.87% ± 21.9	-
High-flat cover		4.7% ± 19.3	-	3.10% ± 14.1	-
Slope cover		41.9% ± 41.2	-	46.89% ± 36.0	-
Low-flat cover		17.4% ± 32.9	-	16.75% ± 29.8	-
Wet-low cover		13.2% ± 28.5	-	16.36% ± 25.8	-
Rock cover		5.1% ± 8.6	Log	8.49% ± 7.8	-
Ploughing	**Pl. > 15 years**	11.6% ± 29.1		6.92% ± 20.1	
	Pl. 4-15years	12.9% ± 29.4		15.42% ± 29.3	
	Pl. < 3 years	12.9% ± 29.7		8.40% ± 20.4	

Lombardi *et al.* 2007). Warrens that consisted of just one burrow (entrance) were not included in the analyses to avoid confusion with breeding stops (single burrows excavated by some females to drop their litters). Each warren and its corresponding buffer represented a case (n = 1565). Peripheral warrens and outliers were also removed in this case.

A similar procedure to that used with the density model was attempted to compute the best-fitting models for warren size. However, the model for warren size had certain limitations related to the structure of the dependent variable, number of burrows (count data), which had a Poisson distribution. Unfortunately, this type of distribution involves high levels of overdispersion which affect the final model result and also impair model comparison techniques (Crawley 1993). For this reason, a single GLZ model, including all 13 variables, was used to explain warren size. The model was computed with a Poisson distribution and a logit link. Likelihood estimates were subsequently corrected for overdispersion by altering the scaled deviance (by calculating the ratio of scaled deviance to degrees of freedom) in order to inflate standard errors and make significance tests more stringent (Crawley 1993). In this case, spatial autocorrelation of the residuals was negligible (Moran´s I of residuals = 0.015, p = 0.146), so there was no need to correct the model.

Microhabitat scale

Microhabitat characteristics (trees, shrubs, rocks, branches, etc.) found in direct association with each warren were also recorded during field surveys. At this scale, we were especially interested in the role of woody species as protection and structural support for warrens (Martins *et al.* 2002, Palomares 2003b), and the relevance of pruned holm oak branches that are often placed above warrens for protection by local game managers.

Mann-Whitney tests were used to test for differences in size between warrens with and without an associated element, and Chi^2 tests to search for significant relationships between certain elements and different warren size classes. In order to estimate rabbit preferences for certain elements, the availability of holm oaks, short scrub, *Retama* and rocks (proportion of each element with respect to the total cover of elements in each cell) was compared with the proportion of warrens associated with that element (t-tests). A Kruskal-Wallis test was used to compare the mean size of warrens associated to a particular microhabitat element.

Statistical analyses were carried out using STATISTICA 6.0 (StatSoft 2002), SAM 2.0 (Statistical Analysis in Macroecology, Rangel *et al.* 2006), and the R 2.5.1(R Development Core Team 2007).

3. Results

General results

We identified a total of 2415 rabbit warrens and 16906 burrows (warren entrances) in the study area. Total density in the sampled area (270 ha) was 8.3 warrens/ha and 59.7 burrows/ha. Fifty-three percent of the sampled grid cells (145.3 ha) had rabbit warrens, and warren density in occupied cells was 15.39 warrens/ha (range: 6.3 to 75 warrens/ha) (**Figure 2**). The smallest warrens had one entrance, and the largest 184. Mean warren size was 7.0 burrows/warren. Most rabbit warrens were small, with 61.4% having fewer than 5 burrows (**Figure 3**). The largest warrens (>10 burrows) represented 20.3% of the total warrens in the study area (n = 488). The spatial distribution of rabbit warrens in the study area was not random, since they showed a significant tendency towards clustering (R = 0.799; z = -10.75; $p < 0.05$). The mean distance from a random

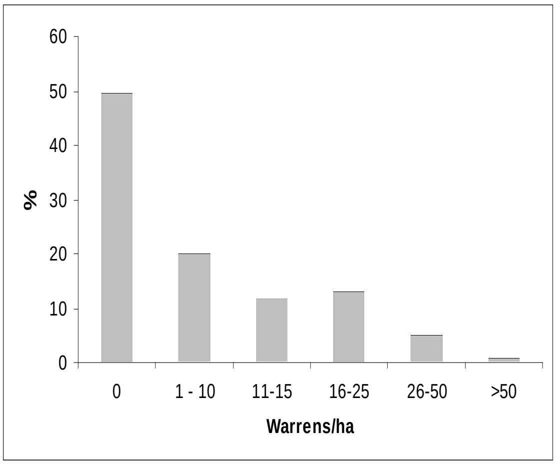

Figure 2. Percentage of sampled cells with different warren densities (warrens/ha)

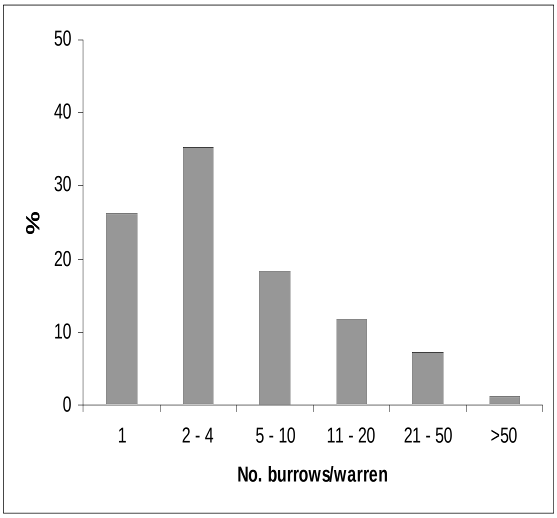

Figure 3. Percentage of rabbit warrens within each size category (no. burrows/warren)

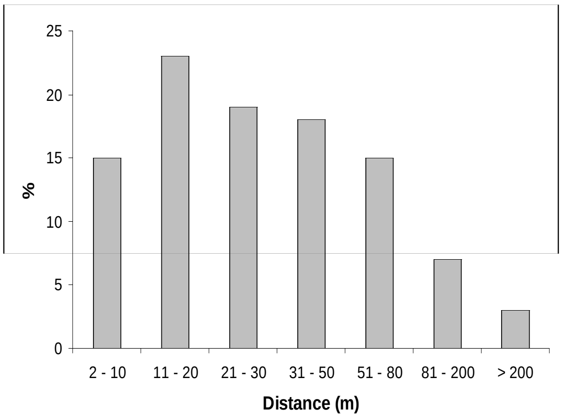

Figure 4. Percentage of random points (n=200) within different distances of a rabbit warren

point within the study area to the nearest rabbit warren (warren availability) was 43.0 ± 3.8 (s.e.) m (min: 2.1 m; max: 336.1 m) (**Figure 4**).

Warren density

Model selection, after correction for spatial autocorrelation, yielded only one model with ΔAIC<2 and the lowest w_i (AIC = 7738.89, ΔAIC = 0.00, w_i = 1) for warren density. This model included 9 explanatory variables, with a Log-likelihood of -5151.1. The Wald statistic provided the weight and statistical significance of each coefficient (estimate) in the model (**Table 2**). According to this model, the most important variables are cover of rocks, holm oaks and habitat heterogeneity as positive predictors of warren density, and cover of open pastures and flood-prone areas as negative predictors. There is also a positive effect of several geomorphology categories: high-flat areas, ridges, and slopes.

Warren size

The model for warren size initially identified 6 variables as the main predictors of warren size (cover of holm oaks, ridges and low-flat areas, habitat heterogeneity and ecotone as positive predictors; open pasture cover as a negative predictor). However, when the model was corrected for overdispersion, only open pasture cover remained as a significant negative predictor of warren size (**Table 3**).

Microhabitat elements and warren size

A total of 389 (16.2%) of warrens had no associated microhabitat element. The majority (2016; 83.8%) were associated to at least one element. Warrens with an associated element were significantly larger than those without (mean size without element: 3.5 ± 0.2 burrows; mean size with element: 8.0 ± 0.3 burrows; MannWhitney U: 267826.5, $p < 0.0001$). Large warrens were more likely to have an associated element, but single burrows also follow the general trend: a higher proportion have at least one associated element (Chi^2: 140.2; $p < 0.0001$). Holm oaks and rocks are the most relevant elements for warrens of all size classes, followed by *Retama* shrubs (**Table 5a**). When element availability was taken into account, we observed that holm oaks are less frequently associated with rabbit warrens than expected given their availability, whilst rocks and *Retama* are associated to warrens more than expected. This suggests that rabbits preferred rocks and *Retama* to holm oaks to build their warrens (**Table 5b**). Short scrub seemed to be avoided by rabbits for warren building, and there were no significant relationships between scrub and any of the warren size classes. Pruned branches were a very important element for the largest size categories, and almost all warrens with > 50 burrows had pruned branches. In general, the largest warrens of the study area were characterised by the presence of pruned branches, holm oaks, and rocks (Kruskal-Walllis test: 467.345 $p < 0.0001$, **Figure 5**).

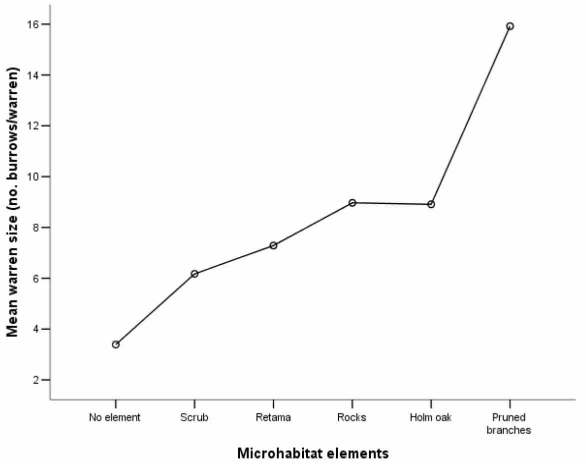

Figure 5. Mean size (no. burrows/warren) of warrens associated to a particular microhabitat element. Note that each warren considered may have more than one element.

Table 2. Variables included in the selected GLZ model for rabbit warren density, and Spearman correlations of each variable and the dependent variable (warren density). Df = degrees of freedom; S.E. = standard error; Wald = Wald statistic; p = probability

	Df	**Estimate (coefficient)**	**S.E.**	**Wald**	**p**	**Correlation**	**p**
Intercept	1	2.051	0.03	6425.290	<0.0000		
% Rock	1	0.038	0.04	130.091	< 0.0001	+0.410	< 0.01
Heterogeneity	1	0.215	0.04	28.560	<0.0001	+0.330	<0.01
% Flood-prone areas	1	-0.158	0.03	27.163	<0.0000	-0.155	<0.01
% High-flat areas	1	-0.106	0.03	15.023	<0.001	-0.074	< 0.01
% Pastures	1	0.126	0.03	13.704	<0.001	-0.210	<0.01
% Holm oak	1	0.113	0.04	8.336	< 0.01	+0.370	<0.01
% Ridges	1	-0.0849	0.03	7.673	< 0.01	+0.082	<0.01
% Slopes	1	0.061	0.03	3.854	<0.05	+0.122	<0.01
% Retamas	1	0.035	0.03	1.597	0.209	-0.020	Ns

Table 3. Variables included in the model for warren size (no. burrows/warren). Note how the significance of each variable changed when the model was corrected for overdispersion. Spearman correlations of each variable and the dependent variable (warren size) are shown. Significant predictors are highlighted in bold. Df = degrees of freedom; S.E. = standard error; Wald = Wald statistic; p = probability * = correlation significant at a = 0.05

		Without correction		**With Deviance correction**		**Correlation**
	Df	*Wald*	*p*	*Wald*	*p*	
Intercept	1	61102.89	< 0.0001	7944.71	< 0.0001	-
% Pastures	1	**55.40**	**< 0.0001**	7.203	**0.0072**	-0.002
% Holm oak	1	**25.59**	**< 0.0001**	3.327	0.068	+0.046
Ecotone	1	**23.02**	**< 0.0001**	2.993	0.084	+0.045
% Slopes	1	**15.31**	**< 0.0001**	1.991	0.158	+0.064*
% Ridges	1	**13.71**	**0.0002**	1.783	0.182	+0.032
% Wet-low	1	**5.32**	**0.021**	0.692	0.405	-0.021
% Flooded-areas	1	2.19	0.138	0.285	0.593	-0.036
% Rock	1	2.17	0.140	0.282	0.595	+0.012
% High-flat	1	1.39	0.329	0.181	0.671	-0.017
Low-flat	1	0.82	0.364	0.107	0.743	-0.066*
Heterogeneity	1	0.78	0.377	0.101	0.750	+0.022
% Retamas	1	0.73	0.392	0.758	0.758	+0.01
Ploughing	1	0.00	0.971	0.000	0.989	+0.004
Scaled deviance/Df	1551	7.69			1.0	
Loglikelihood		-8778.03			-22453.1	

Table 5. a) Number of rabbit warrens within each size category associated to the different microhabitat elements. Numbers are counts, numbers in brackets are percentages. 'Chi-square' = result of ?2 tests between the different size categories for each microhabitat element. Numbers in bold indicate a significant result at a = 0.0001. b) Overall percentage of warrens associated to different elements and the mean % availability of each element within the study area (proportion of each element with respect to the total cover of all elements).

a)

SIZE CATEGORY	**n**	**Holm Oak**	**Scrub**	**Pruned branches**	**Rocks**	***Retama***	**No element**
1 burrow	629	138 (21.9)	78 (12.4)	36 (5.7)	119 (18.9)	66 (10.5)	166 (26.4)
2-4 burrows	847	175 (20.7)	134 (15.8)	113 (13.3)	219 (25.9)	104 (12.3)	154 (18.2)
5-10 burrows	441	131 (29.7)	62 (14.1)	165 (37.4)	120 (27.2)	63 (14.3)	43 (9.75)
11-20 burrows	285	68 (23.9)	34 (11.9)	172 (60.4)	73 (25.6)	31 (10.9)	22 (7.7)
21-50 burrows	176	57 (32.4)	20 (11.4)	138 (47.5)	53 (30.1)	13 (7.4)	4 (2.3)
< 50 burrows	27	10 (37.0)	1 (3.7)	25 (92.6)	12 (44.4)	5 (18.5)	0 (0)
Chi-square		**23.76**	8.027	**704.914**	**21.91**	8.57	**109.686**

b)

	n	**Holm Oak**	**Scrub**	**Rocks**	**Retama**
% Warrens	2405	24.1%	13.7%	24.8%	11.7%
% Availability	1690	47.0%	21.8%	17.3%	3.6%
p		< 0.00001	< 0.0001	< 0.00001	< 0.00001

4. Discussion

Rabbit warrens are abundant, conspicuous structures in the studied landscape. Warren densities in the available literature range from 1.5 to 14.5 warrens/ha (Martins *et al.* 2002; Lombardi *et al.* 2003; Palomares 2003a, b; Gea-Izquierdo *et al.* 2005); and the overall density found in this study (8.27 warrens/ha) is within the highest reported, especially if we only consider occupied cells (15.4 warrens/ha). In the current study, mean warren size was 7 burrows/warren, which is towards the higher end of the wide spectrum of mean warren sizes reported in Spain (3.9 burrows/warren, Rogers & Myers 1979; 3.8-6.8 burrows/warren, Palomares 2003b; 2.3-7.5 burrows/warren, Lombardi *et al.* 2003; 4.2-6.2 burrows/warren, Gea-Izquierdo *et al.* 2005). Most studies refer to an aggregated pattern of rabbit warrens in most habitats (Martins *et al.* 2002; Lombardi *et al.* 2003; Gea- Izquierdo *et al.* 2005), and we also found that there is a tendency towards clustering, although in the study area they are widespread, and both rabbits and other taxa could readily use them as refuge (mean distance to a warren 42 m).

One of the most likely effects of such a high concentration of rabbit activities is an effect on soil properties (Eldridge & Simpson 2002, Eldridge *et al.* 2006). Although not particularly adapted for excavation with regards to morphology (Myers *et al.* 1994), rabbits may move large volumes of soil when compared with other burrowing animals, and warrens can become relatively large structures (**Table 6**). Voslamber and Veen (1985) calculated a total volume of excavated soil by rabbits of up to 70 tonnes per ha, which after a rough extrapolation suggests a potential soil turnover in our study area of up to 21000 tonnes. These effects are also likely to be persistent in time. In Australia, rabbit warrens and their effects on soils and vegetation are still observable several years after warren destruction (Eldridge *et al.* 2006). Whitford and Kay (1999) found a significant, positive relationship between the size and longevity of mammal pedturbations (r^2 = 0.845), which suggests that some of the largest warrens in our study area (e.g. warrens >30 burrows, which can occupy >100 m^2), may persist for over 100 years. There is still much to be learnt about the pedturbation capacity of rabbits, but from the available data it is clear that, in terms of density and scale, European rabbit warrens are significant landscape structures with potential effects comparable to those of well-known ecosystem engineers such as prairie dogs (**Table 6**).

Modelling showed that rabbit warren density was mostly explained by rocks, holm oak cover, and habitat heterogeneity. Cover of flood-prone areas and open pastures were also strong, but negative, predictors. Habitat heterogeneity and diversity had already been identified as an important variable for warren abundance because the resulting mosaic structure implies both access to feeding patches and nearby protective cover (Rogers & Myers 1979; Martins *et al.* 2002; Gea-Izquierdo *et al.* 2005). However, rock cover had never appeared as such a strong predictor, except in a study carried out in Australia (Myers *et al.* 1975). One possible explanation for this strong influence of rocks is that gaps and crevices created by the weathering of rocks can become a safe place for rabbits to start digging (Carvalho & Gomez 2004). This protection may be especially important in open pasture areas with no shrubs or trees (personal observation). The cover of trees and tall shrubs (holm oaks and *Retama* in the current study) is an important predictor for warren density because they provide soil stability and protective cover (Martins *et al.* 2002; Palomares 2003b; Gea-Izquierdo *et al.* 2005). Our results also confirm that rabbits clearly avoid flood-prone areas for warren building given that, especially in open areas, the flooding and subsequent collapse of warren tunnels causes high kitten mortality (Palomares 2003a). The strong negative relationship with open pasture cover (representing food availability) confirms that rabbits prefer to build warrens in places with at least some type of cover. Anti-predatory constrains are very important for the distribution of rabbit populations (Iason *et al.* 2002, Lombardi *et al.* 2003), and in the study area rabbit habitat use is relatively restricted to the vicinity of warrens, except during the drier summer months, when they have to venture further from warrens in order to have access to green food (Rueda 2006).

The inclusion of some of the geomorphology variables in the best predictive model is interesting. Rabbits concentrated their warren-building activities in slopes and ridges and avoided lowland areas. Geomorphology and the undulating topography of dehesas condition the distribution of moisture, soil fertility and productivity. The soils of slopes and ridges are usually sandy and therefore apt for warren building by rabbits (Parker *et al.* 1976, Rogers *et al.* 1979), but poor in nitrogen and organic matter (Figueroa & Davy 1991). In contrast, lowland soils are richer in nutrients and humidity (Pérez-Corona *et al.* 1998), but these areas are under a greater flooding risk under heavy rainfall. Slopes and ridges occupy about 54% of the study area, and are also the least homogeneous geomorphologic classes in terms of vegetation (e.g. slopes: areas of alternating trees, scrub and pasture patches). Therefore, rabbits are choosing heterogeneous, but less productive areas for warren building.

Ploughing variables showed significant correlations with warren density, but they were not included in the best model, and their relationship with warren size was very weak (**Table 3**). As ploughing may destroy rabbit warrens, we expected to find few warrens in periodically ploughed areas, but only found weak negative correlations with the cover of areas ploughed either very recently (<3 years), or over 15 years ago (**Appendix 1**). Ploughing has been traditionally used to stop scrub encroachment and promote pastures in dehesas (Joffre *et al.* 1988), which would increase food supply for rabbits, and promote habitat heterogeneity by breaking up large scrub patches. Ploughing also aerates soils, improves drainage and makes excavation easier, and in the study area, managed for small game hunting, tractors often avoid large rabbit warrens. Therefore, this potentially destructive human activity seems to be less detrimental than expected, and may even be beneficial for rabbits in certain areas.

With respect to the model for warren size, three characteristics of our results suggest that one or several variables that may be important to explain warren size distribution have not been considered: 1) the large overdispersion value (Crawley 1993); 2) the almost non-existent significant effects once overdispersion had been corrected; 3) and the very low correlation values between the dependent variable (warren size) and its predictors (**Table 3**). This leads us to think that, once an appropriate burrowing site has been selected by rabbits at a wider scale (density model), their ability to expand that initial burrow and turn it into a warren will probably be more dependent on microhabitat characteristics such as heterogeneity in local physical soil properties and microhabitat elements.

In fact, analyses at the microhabitat scale have revealed strong relationships between protective elements and warren size, contrary to what Gea-Izquierdo *et al.* (2005) suggested. Woody species, especially the tall *Retama* and holm oak, seem very important and encourage the building of the largest warrens, mainly because they offer shade, protection and can provide important structural support for tunnels (Martins *et al.* 2002; Palomares 2003b). Granite boulders and rocky outcrops were positively selected by rabbits and were associated, which suggests they also play a role for warren stability. Short scrub (mainly *Lavandula* bushes), however, was not used by rabbits for warren building as much as expected given its availability in the study area. One probable reason is that this type of vegetation provides less shelter and structural support than Retama shrubs and rocks. Lombardi *et al.* (2007) found that rabbit burrows in scrub were abundant, but they were small, evenly distributed and less used, and that rabbits in scrub lived in small groups at low densities.

Additionally, the input of pruned branches placed by game managers is clearly determinant for the expansion of the very largest warrens, and enables large warrens to be safely inhabited even in areas at some distance from protective woody cover (personal observation). This improves accessibility to food whilst providing protection. In humanised landscapes such as dehesas, heterogeneity and woody cover are greatly conditioned by traditional land and game management practices. In spite of this evidence, other factors such as local soil type and soil heterogeneity may also be important predictors of warren size and density (e.g.: Parer *et al.* 1987; Parker *et al.* 1976; Martins *et al.* 2002; Gea-Izquierdo *et al.* 2005), and should not be disregarded.

In summary, we have shown that rabbit warrens can reach high densities and have a widespread distribution within a dehesa. These structures can be long-lived, and have the potential to affect soil properties. Although warrens are relatively available throughout the study area, they show a tendency towards aggregation in the most heterogeneous, less productive areas of the dehesa, where holm oak and rock cover are relatively high; and away from the more productive flood-prone areas. This ensures appropriate protection and structural support for warrens, and habitat heterogeneity in these areas is ideal for rabbits, because it represents a situation where both food an refuge are readily available. Microhabitat elements related with the physical protection and support of warrens appear to be the main factors explaining warren size.

The factors that drive warren building in rabbits can also have implications for other species that may be potential warren users. For example, there is likely to be a synergic effect between advantages provided by warrens and effects of their associated microhabitat elements. An organism using a warren associated to a holm oak will benefit from double protection, as well as shade. Warrens associated to masting shrubs such as Kermes oaks (*Quercus coccifera*), abundant throughout the Mediterranean, may provide both refuge and food for certain species (e.g. a rodent using an abandoned

Table 6. Characteristics of burrows and open burrow systems created by some fossorial and semi-fossorial mammals. *Data adapted from Whitford & Kay (1999).

Burrowing animal	Soil turnover	Density	Size	Longevity (years)	Reference
European rabbit (*Oryctolagus cuniculus*)	-	8.3 warrens / ha 59.7 burrows / ha	Up to 500m^2	> 100*	Current study
	Up to 63m^3 / ha *[1]		Total tunnel length: 517m*[2]	> 5 yrs*[2]	*[1] Parer *et al.* 1987 *[2] Butler (1995) (cited in Eldridge and Simpson 2002)
	Up to 71308.0 kg / ha	40 “caves” / km^2	-	-	Voslamber & Veen (1985)
	Up to 1kg / m^2	0.02 – 0.13 / m^2	Up to 1.5m^2	-	Rutin (1992)
Prairie dogs * (*Cynomys spp*.)	200-225kg soil / colony*[3]	50-300 entrances / ha		> 15*[3]	*[3] Whicker and Detling (1988)
	1.4m^3 soil / ha*[4]	89.7 burrows / ha *[4]			*[4] White and Carlson (1984)
			5 – 250 ha*[5]		*[5] Dahlsted *et al.* (1981)
Red vizcacha rat* (*Tympanocyomys barrerae*)	-	7.3 burrow systems per ha	390.4cm^2	-	Ojeda *et al.* 1996* - Argentina
Hairy-nosed wombat* (*Lasiorhinus latifrons*)	-	0.1-03 / ha	314 - 706.5cm^2	> 50	Löffler & Margules (1980)
Banner-tail kangaroo rat* (*Dipodomys spectabilis*)	40m^2 / ha*	7-10 / ha	12.8cm^2		Reichman *et al.* (1985)
Pocket gophers (Geomyidae)	5.76 - 45.39 Kg /m^2	0.9 – 4.8 mounds / m^2	725±413.7cm^2	-	Kerley *et al.* 2004
Fringe-tailed gerbil* (*Tatera robusta*, colonial system)	2041.8 cm^2	1000 / ha		-	Senzota 1984

burrow), and management practices such as covering large warrens with pruned branches have already been identified as very relevant for the Mediterranean lizard community (Martín & López 2002; **capítulo 4**).

Furthermore, in resource-limited ecosystems such as Mediterranean dehesas, warrens located in the less productive areas have a greater potential to become a more relevant locus of nutrients and moisture for the annual plant community than in more productive areas (as shown for other burrow systems, Kinlaw 1999). It is precisely in these areas where their potential role in the amelioration of environmental stress (e.g. being used as refuge from extreme environmental temperatures and climatic events) can be most important (Crain & Bertness 2006). Warren presence is partly driven by habitat heterogeneity at the landscape scale, but warrens themselves have the potential to increase biogeochemical and physical heterogeneity at smaller scales, creating structurally more complex microhabitats within warrens (**chapter 5**), which will provide more niches (Simpson 1949; MacArthur & Wilson 1967), and increase diversity (Bazzaz 1975). The study site (a *dehesa*), is an inherently heterogeneous ecosystem, where traditional management practices have promoted a mosaic landscape, in which rabbits can reach very high densities (e.g. Rogers & Myers 1979) because they are supplied with appropriate warren building sites, protective woody cover, and grassland areas for grazing (Martins *et al.* 2002). An abundant rabbit population will increase biodiversity through various mechanisms: 1) as prey: high rabbit numbers will provide food for a wide variety of predators and boost their populations (Delibes-Mateos *et al.* 2007); 2) as herbivores: rabbits can modify habitat structure through herbivory (Gómez-Sal *et al.* 1999), disperse plant seeds in their dung (Malo *et al.* 2000; Malo *et al.* 1995), and their latrines can promote chemical fertility and plant growth (Willot *et al.* 2000), and also provide important resources for some insect species (Galante & Cartagena 1999; Verdu & Galante 2004); 3) as warren builders: recent findings show that rabbit warrens may alter floristic composition and induce plant ß-diversity (Gálvez *et al.* 2008), and burrows are used by a diverse array of other species (e.g. lizards, **capítulo 4**; badgers, Revilla & Palomares 2002; Motpellier snake: Blázquez & Villafuerte 1990 ; tortoise, Calzolai & Chelazzi 1991).

The role of ecosystem engineers in Mediterranean habitats has been poorly studied so far, but the present research shows that endemic engineers such as rabbits have the potential to modulate the availability of resources (e.g refuge) in such fluctuating environments. The potential effects induced by rabbits imply that once they choose a patch for warren building, biodiversity may be enhanced in the area (e.g. **chapter 4 & 5**). The acknowledgement of this role is useful for conservation, especially in areas where rabbits were historically abundant but have not been able to recover after the impact of the viral diseases (Fernández 2005; Delibes-Mateos *et al.* 2007), or habitat loss due to land use changes (Ward 2005). Improving rabbit populations and introducing management measures that encourage warren building (such as removing short scrub whilst leaving enough cover of tall shrubs and trees, Palomares 2003b) will promote biodiversity within the ecosystem. Further knowledge about the influence of rabbit activities on soils and different taxa within their native landscapes should be useful for the development of efficient conservation measures for these animals and their associated species.

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Appendix 1. Spearman correlations between explanatory and dependent variables (warren density and size). Variables in bold were selected for modelling. An explanation is given for discarded variables. ** Correlation significant at 0.01 level * Correlation significant at 0.05 level

VARIABLES	CORRELATIONS		Variable chosen?
	Density	Size	
% Holm oak	**0.370****	**0.046**	**Yes**
% Pasture cover	**-0.149****	**0.002**	**Yes**
% Scrub	0.065**	0.023	Highly correlated with open pasture cover (-0.776**), and correlation with warren density is poor.
% Retama	**-0.091****	**0.010**	**Yes**
% Flood-prone area	**-0.155****	**-0.036**	**Yes**
Ecotone	**0.104****	**0.045**	**Yes**
% Ridges	**0.082****	**0.032**	**Yes**
% High-Flat	**-0.074****	**-0.017**	**Yes**
% Low-Flat	**-0.025**	**-0.066***	**Yes**
% Wet-Low	**-0.056***	**0.021**	**Yes**
% Slopes	**0.122****	**0.064***	**Yes**
% Pl. < 3 years	**-0.108****	**0.024**	Included in PCA, Factor 2 (Appendix 2a,b)
% Pl. 4-15 years	**0.053***	**0.028**	Included in PCA, Factor 2 (Appendix 2a,b)
% Pl. > 15 years	**-0.127****	**0.009**	Included in PCA, Factor 2 (Appendix 2a,b)
% Rocks	**0.275****	**0.012**	**Yes**
Heterogeneity	**0.317****	**0.022**	**Yes**
Shannon´s diversity (H')	0.387**	0.023	Strong correlation with heterogeneity (+0.983) – heterogeneity was chosen because it was considered important by other authors (Carvalho & Gomes 2004; Monzón *et al.* 2004; Fernández 2005; and (Gálvez *et al.* 2008)
Pielou´s Evenness (E)	0.420**	0.014	Strong correlation with heterogeneity (+0.928) – heterogeneity chosen because considered important by other authors (Carvalho & Gomes 2004; Monzón *et al.* 2004; Fernández 2005; and (Gálvez *et al.* 2008)

Appendix 2a and b. Results of PCA on ploughing variables. In both cases, Factor 2 represents a gradient from more recently ploughed to ploughed a long time ago.

Appendix 2a. Relationship of PCA factors with the ploughing variables used for the warren density model

	Pl.<3 yrs	**Pl. 4-15 yrs**	**Pl. >15 yrs**	**Eigenvalue**	**% Variance**
Factor 1	0.364243	-0.870501	0.533354	1.174913	39.16
Factor 2	**0.806254**	**-0.093412**	**-0.703074**	**1.153086**	**38.44**
Factor 3	-0.466134	-0.483220	-0.470340	0.672002	22.40

Appendix 2b. Relationship of PCA factors with the ploughing variables used for the warren size model

	Pl.<3 yrs	**Pl. 4-15 yrs**	**Pl. >15 yrs**	**Eigenvalue**	**% Variance**
Factor 1	0.429447	-0.829242	0.557488	1.182860	39.46
Factor 2	**0.782094**	**-0.050293**	**-0.677276**	**1.072903**	**35.75**
Factor 3	-0.451557	-0.556623	-0.480108	0.744236	24.79