# Ecosystem Engineering Effects of European Rabbits in a Mediterranean Habitat

Lucía Gálvez[1,*], Antonio López-Pintor[2], José M De Miguel[2], Germán Alonso[2], Marta Rueda[1], Salvador Rebollo[1], and Antonio Gómez-Sal[1]

## Introduction

Beyond their role as primary consumers, herbivore activities can play a key part in spatial processes at the ecosystem level (e.g., McNaughton 1983; McInnes et al. 1992; De Miguel et al. 1997). Environmental factors such as geomorphology, soil and vegetation characteristics, slope, aspect etc., affect the spatial distribution of the resources they need, mainly refuge, food, and water. Therefore, a particular set of habitat characteristics influences the use of different areas for specific activities by a given herbivore species. In turn, the use of habitats by herbivores may affect such characteristics at different scales. This is the case of many sedentary herbivores which, after establishing themselves in a particular area of an ecosystem, begin their modification. Pond construction by beavers not only changes river-flow patterns and surrounding vegetation, but also nutrient cycling (Naiman et al. 1994; Pollock et al. 1995). Excavating mammals, such as prairie dogs and pocket gophers, can also have profound impacts upon soil processes and the vegetation surrounding their burrow systems (see Whitford and Kay 1999; Huntly and Reichman 1994 for thorough reviews). Species that can have significant effects on the spatial structure of the landscape and the distribution of resources, both for themselves and other organisms, are considered ecosystem engineers (Jones et al. 1994). These species can be important patch creators through their activities or structures, and these patches can be exploited by different animal and plant species, thus increasing biodiversity and potentially controlling many processes and affecting ecosystems at different scales.

The European rabbit (*Oryctolagus cuniculus* L.) belongs to this category of sedentary herbivores and is unique among lagomorphs in its social and excavatory behavior. Their burrow systems (or warrens) can reach high densities and may have a large extension (radius of more than 15 m), with effects detectable even farther away (Gillham 1955; Lange and Graham 1983). Rabbit

[1]Departamento de Ecología, Universidad de Alcalá. Edif. de Ciencias, Campus Universitario, Ctra. Madrid-Barcelona, Km. 33.600, 28871-Alcalá de Henares, Madrid, Spain; *E-mail: lucia.galvez@uah.es
[2]Departamento de Ecología, Universidad Complutense. Facultad de Ciencias Biológicas, c/ José Antonio Novais 2, Ciudad Universitaria, 28040 Madrid, Spain

P.C. Alves, N. Ferrand, and K. Hackländer (Eds.)
Lagomorph Biology: Evolution, Ecology, and Conservation: 125–139

activities include excavating, trampling, pellet deposition, browsing, etc. These activities are frequently materialized in defined structures such as burrows, associated mounds, scrapes, latrines and paths, which generate patches with different characteristics. The area surrounding warrens is subjected to high levels of such disturbance, which affects mainly soils and vegetation (Eldridge and Myers 2001). These effects follow a distinct gradient, determined by rabbit use (Gillham 1955). Latrines are clearly defined areas of pellet accumulation and soil perturbation, used as territorial beacons (Cowan 1987; Sneddon 1991). They are potentially the most important structure from the vegetation point of view, as they induce physical and chemical changes on soil properties. In Mediterranean semi-arid regions, they are important contributors to soil fertility (Willot et al. 2000) and increase plant diversity and biomass (Petterson 2001). Latrines have also been shown to facilitate plant establishment in disused quarry soils in more mesic environments (Hambler et al. 1995). This ecosystem engineer role of rabbits has received little attention in ecological studies carried out in their native habitats of the Iberian Peninsula, where the long coexistence with other animal and plant species could have conditioned the dynamics of these Mediterranean ecosystems more than previously thought. Therefore, the European rabbit can be classified as a keystone species of this ecosystem.

The main aim of this chapter is to describe rabbit engineering effects on an Iberian Mediterranean ecosystem. For this, we explored the environmental factors affecting warren location in the landscape and analyzed the effects that two structures created by rabbits, warrens and latrines, have on the herbaceous community within rabbit home ranges. We expected different preferences for warren building according to geomorphology, vegetation characteristics, and management practices. We also hypothesized that rabbit structures would promote changes in the herbaceous community around warrens, and thus be an additional source of heterogeneity in dehesa ecosystems.

## Materials and Methods

### Study Site

'Dehesas' (in Spain) or 'montados' (in Portugal) are man-made savannahs from former oak woodlands that support the highest rabbit densities in the Iberian Peninsula. The present study was carried out in central Spain on a 225-ha dehesa situated in Chapinería, south-west of Madrid (40°23′ N, 4°12′ W). The mean altitude is 670 m a.s.l., and the climate is continental Mediterranean, with 12°C and 432.6 mm of mean annual temperature and precipitation, respectively. The substrate is sandy to sandy-loamed textured, upon fractured bedrock mainly composed of granite. The vegetation is dominated by *Quercus rotundifolia* (holm oak), with other woody species such as *Lavandula stoechas* ssp. *pedunculata*, *Retama sphaerocarpa* and *Rubus* spp. Herbaceous vegetation can be divided in xerophytic pastures (on ridges, slopes and generally dry areas), and mesic pastures (on lowlands and water accumulation areas), with marked differences in productivity (low and high respectively). The management of the land is based on traditional practices typical for this agro-sylvo-pastoral-system, with periodic tree pruning to increase acorn and pasture production, rotational ploughing for cultivation and scrub encroachment control, as well as grazing by a transhumant herd of about 600 sheep. The geomorphology limits the application of these practices and promotes spatial heterogeneity in the ecosystem. The area is also specifically managed for small-game hunting (mainly rabbits), which includes cereal cultivation in some areas to be grazed by both rabbits and sheep.

## Sampling Design

### *Study of Warren Location in the Landscape*

A field survey was conducted between February and March 2002, and all warrens were identified and geo-referenced. A warren was defined as a group of burrows 2 m or less from each other. Vegetation and geomorphology layers were obtained from aerial orthophotos (1:5000) and ground confirmation. Given the scale of maps, all areas not covered by woody vegetation, rocks, paths or quarries were covered by herbaceous vegetation (patches of bare soil were not large enough to be included in the maps). Ploughing maps were obtained from aerial photographs (1:18000, 1:30000) covering the last 20 years. All maps were processed with ArcView GIS 3.2. A grid of 40 × 40 m cells was superimposed on all data layers, and sampling was carried out by randomly selecting 50% of the whole study area (550 cells, Fig. 1). From each cell the following variables were extracted: number of warrens, vegetation cover (in $m^2$) - holm oak (*Q. rotundifolia*), shrubs (*R. sphaerocarpa*), scrubs (*Lavandula stoechas* ssp. *pedunculata*), brambles (*Rubus* spp.), total herbaceous layer, and mesic pastures; cover of ploughed areas in the last 20 years (in $m^2$) according to ploughing frequency (never, 1–2, 3–4, >5 times), and time since the last ploughing event (2–7 years, 8–12, 13 or more years); cover of geomorphological classes (in $m^2$) - wet lowlands, sporadic water accumulation areas, runoff channels, low flat areas, high flat areas, slopes and ridges; cover of flood-prone areas (in $m^2$) rocks, stone heaps and stony ground. From the vegetation data, the following variables were derived: vegetation diversity (Shannon index, H') and evenness (E = H'/ln (richness) ); and habitat heterogeneity index, E(P) = H'/ln (total no. of vegetation patches) (Rescia et al. 1994).

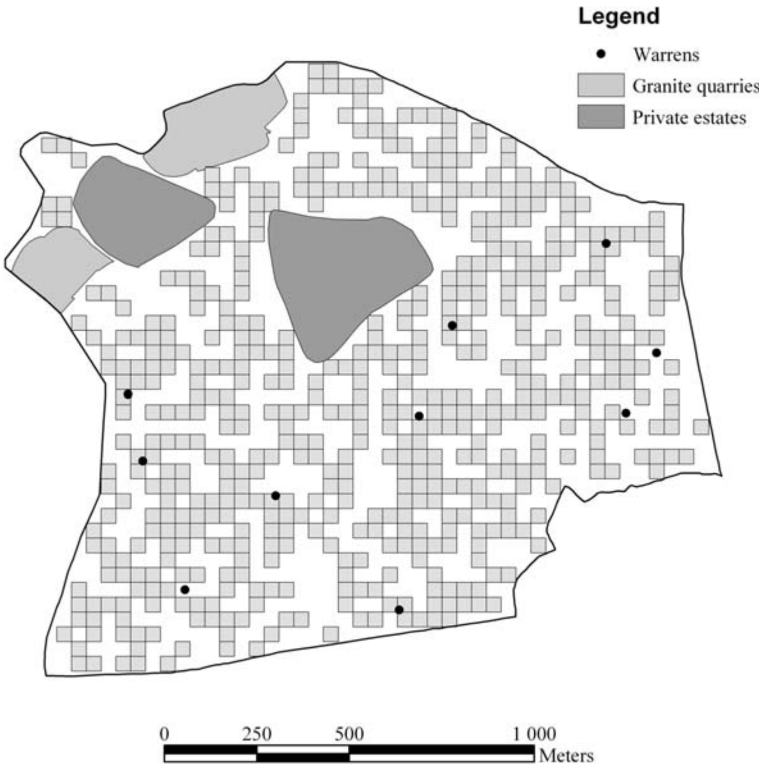



**Fig. 1** Map of study area showing the sampled plots (40 × 40 m) for the study of factors affecting warren spatial distribution, and the warrens selected for rabbit effects on the vegetation community (*black dots*). The map includes two active granite quarries with no warren presence and two small private estates for which data on warren spatial location were not available

### *Study of Plant Community Changes Due to Warrens and Latrines*

We sampled warrens and latrines to study plant community changes induced by rabbit activities inside their home ranges. For this purpose, a rabbit home range was considered as an area of imprecise outer limits surrounding a warren, and containing the highest proportion of latrines. Ten of these home range units were selected for vegetation surveys (Fig. 1), ensuring that the warrens were large (50–184 entrances). Large warrens were chosen because rabbit numbers correlate strongly with number of entrances (Cowan 1987; Palomares 2001), and a relatively high number of resident rabbits was desirable in order to observe their effects more easily. The vegetation was surveyed along four transects per warren, two following the line of maximum slope (upwards and downwards), and the other two approximately perpendicular to them. These were laid from the warren edge, outwards. Six 25 × 25 cm quadrats were laid at each transect at increasing distances from the warren:

0; 50 cm; 1.50 m; 3.50 m; 7.50 m and 15.50 m (see Fig. 2). The total number of rabbit pellets on each quadrat was used as an overall indicator of rabbit activity throughout the year (Wood 1988; Palomares 2001). This decision was based on a pellet degradation study performed in equivalent locations of the study area, which revealed that rabbit pellets could persist from a year up to 20 months (M. Rueda, unpublished data).

We investigated a total of 48 active latrines in the vicinity of eight of the warrens surveyed, at different distances from the warren (1.5 to 36 m; mean: 15.05 m) (Fig. 2). Vegetation data were collected on 10 × 10 cm quadrats, one in the central area of pellet accumulation, one in the surrounding vegetation ring (17–30 cm wide; mean: 23.29 cm) and a third one just beyond the vegetation ring. A final, "outside" quadrat was placed at approximately 1 m away from the external vegetation ring, and was considered out of the latrine's influence. Given that latrines were situated around the warrens that we had sampled, but at different distances from the warren centre, their "outside" position (see Fig. 2, latrine position no. 4) was surveyed using a 25 × 25 cm quadrat too, so that these data could be compared to the warren data. All latrine quadrats were at least 2 m away from any other latrine (range: 2–63.9 m, mean: 19.53 m) and from any of the warren transect quadrats.

In both series of quadrats, individual plant species were identified to evaluate floristic composition, and total percentage vegetation cover and mean vegetation height were measured as indicators of herbaceous community standing crop.

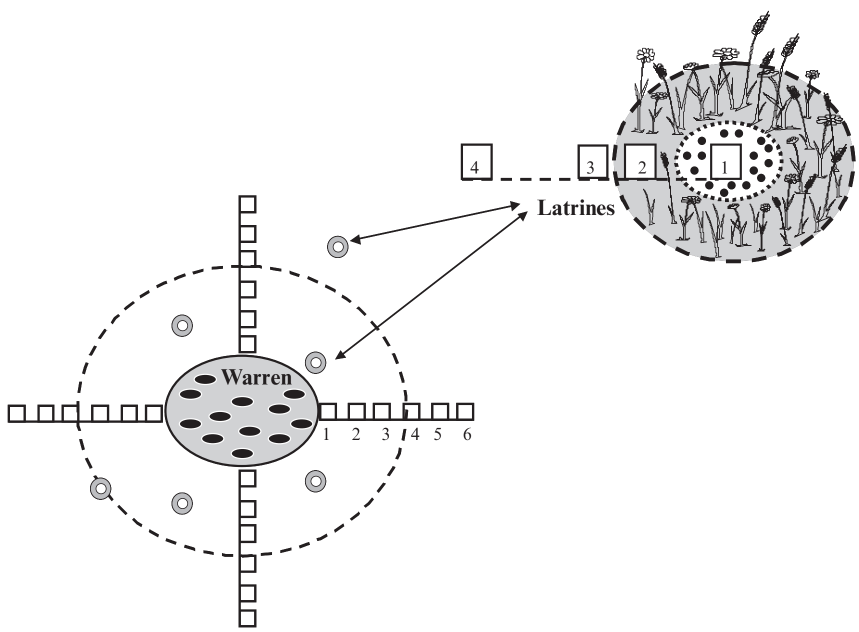



**Fig. 2** Schematic sampling scheme for individual warrens and latrines (*not to scale*)

## Data Analyses

### *Study of Warren Location in the Landscape*

Multiple regression (forward stepwise) analyses were used to determine the main environmental factors affecting the location of rabbit warrens in the landscape. Warren density was the dependent variable, and the other 27 were the potential factors to be entered into the regression model. Due to the uncertainty in the statistical tests caused by the spatial autocorrelation among data (i.e., the non independence of data, and thus overestimated degrees of freedom), the response of warren density to each variable introduced in the final regression model was further tested by partial Mantel tests (Smouse et al. 1986). These are non-parametric analyses testing the relationship of two sets of variables (warren density and each predictor variable) while keeping constant the effect of a third (geographic position of plots). In this way, they are analogous to partial correlation, although the correlation coefficient calculated tends to be smaller due to the use of distance matrices instead of raw data. The significance levels are obtained via randomization procedures (see Oden and Sokal 1992; Legendre 2000 for details).

### *Study of Plant Community Changes Due to Warrens and Latrines*

Differences in rabbit use (pellet counts) between warren transect positions were assessed using ANOVA. The herbaceous community was characterized by total vegetation cover, floristic composition, and mean vegetation height. "Floristic composition" was a synthetic variable obtained by applying a non-metric multidimensional scaling (NMS) ordination to individual species data. This is an iterative ordination technique that minimizes the stress of the k-dimensional configuration, taking into account the relationship between the dissimilarity (distance) in the original p-dimensional space and distance in the reduced k-dimensional ordination space (Clarke 1993). The distance matrix was calculated using the Sorensen index, which is more sensitive in heterogeneous data sets such as the one considered and giving less weight to outliers than Euclidean distances (Roberts 1986). For warren NMS analysis, species data from the "outside" position of latrines was added to transect data for comparison purposes. Differences in the herbaceous communities of both warrens and latrines were assessed using multivariate analysis of variance (MANOVA) performed in each case upon the three community parameters. As each home range was considered a unit, mean values per warren were used in the analyses, and warren identity was included as a block factor. In all cases, normality of data and homogeneity of variances were tested and data transformed where necessary. Statistical analyses were performed using PASSAGE 1.1 (M.S. Rosenberg 1998–2004), PCORD 4.25 (MjM Software Design 1995–1999) and SPSS 12.0 (SPSS Inc., 1989–2003).

## Results

The regression model obtained for rabbit warren locations was highly significant ($R^2 = 0.2422$ $p < 0.0001$). Table 1 shows the variables included in the final model. Warren density responded positively to holm oak, bramble and rock cover, and to vegetation heterogeneity. It responded negatively to cover of flood-prone areas, relatively elevated topographic positions, high ploughing frequency, and long intervals between ploughing episodes. In spite of the spatial autocorrelation present among the data, the partial Mantel tests confirmed the significant effect of all variables on warren density except in the case of the geomorphological ones and long ploughing intervals (Table 1).

Pellet counts confirmed a significant gradient of increasing rabbit use towards the warren ($F_{5,45} = 4.555$; $p = 0.002$; Table 2, Fig. 3a). As expected, given the different location and size of surveyed warrens, block effect (warren identity) was significant for both warren transects ($F_{36,\ 159} = 3.972$, $p < 0.001$) and latrines ($F_{21,\ 55} = 2.086$, $p = <0.0001$). Once this effect was taken into account, the MANOVA results showed highly significant differences in

**Table 1** Results for the multiple regression (forward stepwise) analysis on factors affecting warren density, and partial Mantel tests for the variables entered into the model (significance levels were obtained from a series of 1,000 randomizations)

| | Regression analysis | | | | | Mantel test | |
|---|---|---|---|---|---|---|---|
| | Beta | Partial Cor. | Semipart Cor. | t(539) | *p*-level | r | *p*-level |
| Holm oak area | 0.2632 | 0.2033 | 0.1791 | 4.820 | <0.001 | 0.2495 | <0.001 |
| Habitat heterogeneity index | 0.1213 | 0.1016 | 0.0881 | 2.372 | 0.0180 | 0.1049 | <0.001 |
| Bramble area | 0.0899 | 0.1015 | 0.0880 | 2.369 | 0.0182 | 0.1054 | 0.015 |
| Rock area | 0.1052 | 0.0953 | 0.0826 | 2.223 | 0.0266 | 0.1663 | <0.001 |
| Ploughed ≥13 years ago | −0.1093 | −0.1206 | −0.1048 | −2.822 | 0.0049 | −0.0437 | 0.1060 |
| Sporadic water accumulation area | −0.0848 | −0.0970 | −0.0840 | −2.262 | 0.0241 | −0.0345 | 0.2550 |
| Ridge area | −0.0944 | −0.1035 | −0.0897 | −2.415 | 0.0161 | −0.0198 | 0.5090 |
| Flood-prone area | −0.1039 | −0.1083 | −0.0940 | −2.529 | 0.0117 | −0.0564 | 0.042 |
| High flat area | −0.0845 | −0.0942 | −0.0816 | −2.196 | 0.0285 | −0.0359 | 0.2350 |
| High ploughing frequency | −0.0806 | −0.0900 | −0.0779 | −2.097 | 0.0364 | −0.0622 | 0.045 |

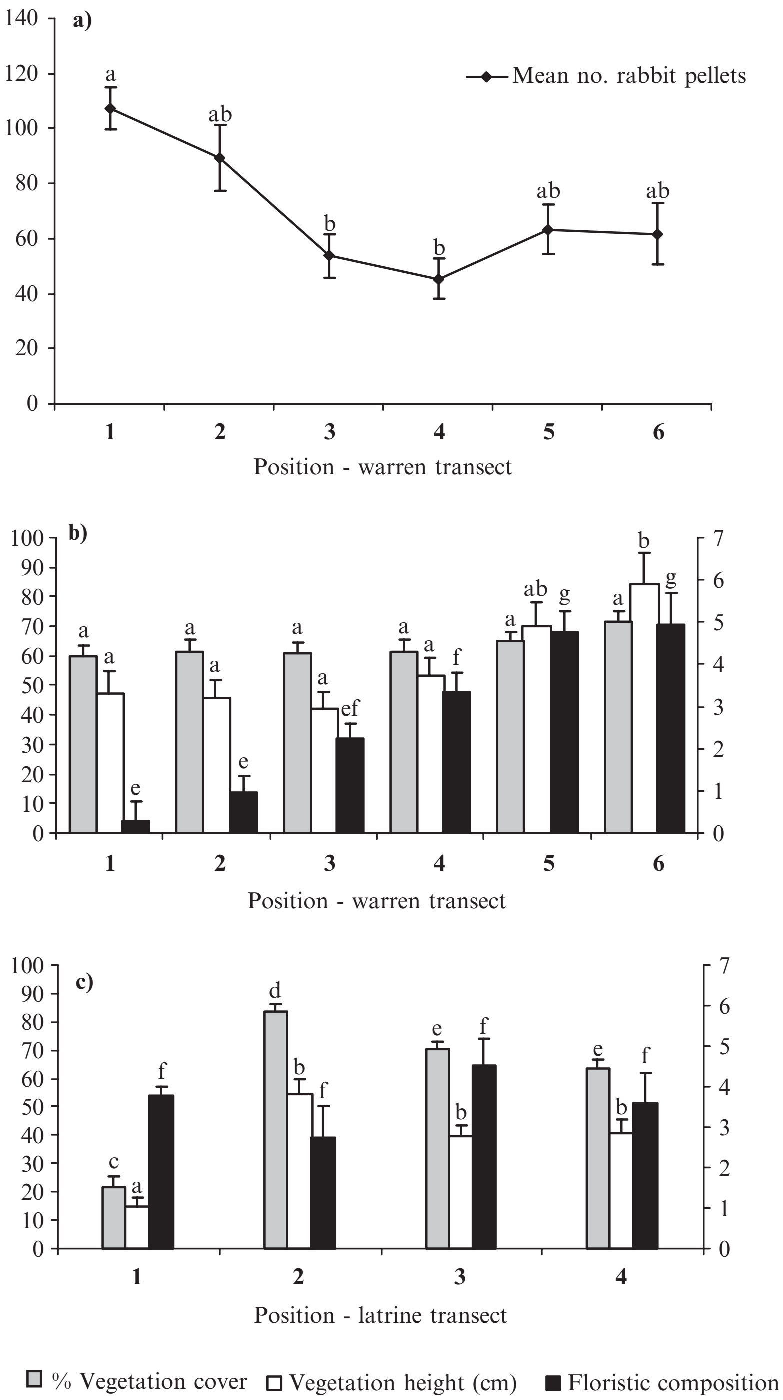
**Table 2** ANOVA results for differences in community parameters between positions for warrens and latrines. The synthetic variable "floristic composition" corresponds to the first axis of NMS ordination. (* = $p<0.05$; ** = $p<0.01$; *** = $p < 0.001$; *NS* non-significant result)

| Parameter | Warrens | Latrines |
|---|---|---|
| | *F* | *F* |
| Floristic composition | 31.321*** | 1.005 NS |
| Mean vegetation height | 7.268*** | 15.002*** |
| Vegetation cover | 1.253 NS | 79.196*** |
| Number of rabbit faecal pellets | 4.555** | - |

plant community parameters between transect positions in both cases (Wilks'Lambda, $F_{20,\ 140} = 6.869$, $p < 0.001$ and $F_{9,\ 46} = 10.315$, $p < 0.001$, respectively). This is depicted by axis I of the NMS ordination (Fig. 4), in which the arrow shows how floristic composition follows a parallel trend to rabbit use. This meant the replacement of several species (e.g., *Stellaria media* and *Urtica urens*), and most of all a change in the relative abundance of many others (e.g., *Spergularia rubra, Vulpia* spp. and *Hypochoeris glabra*). There were also significant differences in vegetation height, which followed the opposite trend: the vegetation was taller further away from the warren. Changes in herbaceous cover also followed this trend, but this result was not significant (Fig. 3b).

The central position of the latrines was an area of pellet accumulation with hardly any vegetation (only a few species had a mean cover greater than 1% in this area). Vegetation height was never above 4 cm due to constant mechanical disturbance by rabbits. This was in contrast to the surrounding vegetation ring where the herbaceous community was both significantly taller and denser compared to both the inside and outside positions of the latrine. Changes in floristic composition show a slight non-significant trend (Fig. 3c), due to a change in relative abundance of many species along the transect (e.g., *S. rubra*, *H. glabra*), with the replacement of some others (e.g., *Erodium cicutarium*, *Cerastium glutinosum*).

**Fig. 3** Effects of distance from warrens and latrines on various parameters (floristic composition data have been transformed ((NMS coordinate + 50) × 100) to enable graphical presentation). **a)** Mean (±SE) number of counted pellets at various distances from warrens (1 = near ; 6 = furthest away). **b)** Mean (±SE) vegetation height (cm), % vegetation cover and floristic composition at various distances from warrens (1 = near ; 6 = furthest away). **c)** Mean (±SE) vegetation height (cm), % vegetation cover and floristic composition at various distances from latrines (1 = central area, 2 = vegetation ring, 3 = just outside vegetation ring, 4 = 1 m away from vegetation ring). Significant differences between transect positions were investigated using Tukey's post hoc test. *Bars* with equal letters are not significantly different


a)
Mean no. rabbit pellets
Position - warren transect
b)
Position - warren transect
c)
Position - latrine transect
% Vegetation cover
Vegetation height (cm)
Floristic composition

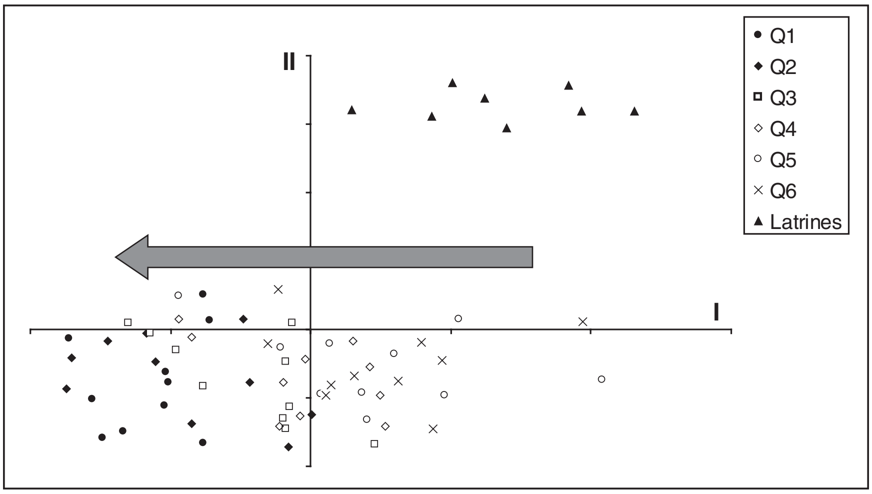



**Fig. 4** Results of NMS performed upon species abundance data for each warren transect position and the outer position of latrines. ● Q1 = position 1; ◆ Q2 = position 2; □ Q3 = position 3; ◊ Q4 = position 4; ○ Q5 = position 5; × Q6 = position 6; ▲ Latrines = outer position of latrines. The *arrow* indicates the gradient captured by the first axis, which also reflects rabbit use measured as number of rabbit faecal pellets found in each quadrat

An additional result from NMS ordination for the warren influence area showed that floristic composition was very different between latrine and warren quadrats at any of the warren transect positions, despite the fact that the surveyed latrines were situated at different distances from the warren. Figure 4 shows further results of NMS ordination, where axis I represents differences in floristic composition between warren transect positions, and axis II represents differences between warren positions and the outside position of latrine transects, showing that floristic composition is still under the latrine's influence despite these quadrats being 1 m away. This effect is reinforced by the fact that latrine distance to the warren did not have an effect on herbaceous community parameters (floristic composition: $r = -0.004$, $p = 0.978$; vegetation height: $r = -0.285$, $p = 0.052$; vegetation cover: $r = -0.090$, $p = 0.648$).

## Discussion

Results showed that certain habitats within the dehesa landscape were preferred or rejected by rabbits for warren building. Wet lowland areas seem to be avoided by rabbits for warren construction, as they are flood-prone due to their topographic position and excess clay. Parer and Libke (1985) reported that flooding is negative for the survival of pups and young rabbits, although it does not seem to affect adult individuals. This selective mortality and the associated flooding and collapsing of warrens would have important consequences for local rabbit populations (Palomares 2003a).

Most warrens were concentrated in areas of high woody vegetation cover and habitat heterogeneity. Many authors have already highlighted the importance of both trees and shrubs as providers of refuge for rabbits to reduce predation (Moreno et al. 1996; Lombardi et al. 2003; Palomares 2003b), and also as a possible structural support for their burrow systems in areas of unstable soils (Palomares 2003b). Woody species (especially trees and shrubs) in arid and semi-arid environments promote nutrient enrichment and amelioration of microenvironmental conditions under their canopies (Archer et al. 1988; Vetaas 1992; Callaway 1995; Callaway and Pugnaire 1999). However, this potentially higher productivity can be counteracted by an excess of shade when the canopy is too dense, which reduces herb density. For rabbits, both cover and food are important. Hence, it would be necessary to have separated complementary zones, i.e., a closed area for refuge and an open area for grazing, or else to have them interspersed. The literature provides examples of both cases for the Iberian Peninsula (Moreno and Villafuerte 1995; Lombardi et al. 2003). In the current study, rabbits preferred the most interspersed situation: the positive response of warren density to both holm oak cover and the heterogeneity index implies that rabbits prefer the most fragmented parts of the landscape.

Traditional management practices are essential for the maintenance of dehesa structure. Among them, ploughing is used to prevent shrub encroachment, and generally involves cereal cultivation both as the initial step in the pasture generation process and as fodder for herbivores (Spiers 1981; Joffre et al. 1988). In those dehesa ecosystems with the additional aim of game exploitation, rabbit grazing in these crop fields is explicitly considered. In our study site, besides mowing of productive zones and tree pruning, ploughing is an important factor regarding warren location. Excessively high ploughing frequencies negatively affect warren location, probably because of the changes induced in the herbaceous community by frequent disturbance, and the peril of warren destruction in the process.

Environmental factors operating at landscape or ecosystem scale regarding refuge and pasture availability depend on both geomorphological and management characteristics. These factors condition warren location, whereas rabbit engineering activities have effects at a lower scale. Within each warren home range, rabbits introduce further heterogeneity in the ecosystem through their different activities, affecting mainly, but not only, the herbaceous community. Results showed significantly greater rabbit activity in the vicinity of warrens than further away. This resulted in lower vegetation height due to constant trampling and herbivory, but no differences in vegetation cover between positions near the warren and those further away. Floristic composition varied with distance from warrens, which implies that some species disappeared or decreased in abundance near warrens, probably because they succumbed to rabbit herbivory and disturbance. Other species were favored by the warren's influence. Changes in floristic composition were coupled with differences in plant growth forms. Near the warren dwarf, prostrate, creeping and rosette growth forms were observed, which explains why vegetation height is lower and how cover is maintained despite intense rabbit activity in this area. This is consistent with Gillham's (1955) records of a higher proportion of such plant growth forms found in the vicinity of rabbit warrens in the Pembrokeshire islands.

The herbaceous community associated with latrines followed a slightly different pattern. Mechanical disturbance seems to be the main factor operating in latrines, since the main significant differences are observed in the central area, which is subjected to trampling and scratching by rabbits. Extra nitrogen from feces and urine may be responsible for an increase in vegetation cover and height in the surrounding vegetation ring (Floate 1981), but do not appear to have dramatic effects on floristic composition at a first glance, given the nitrophilous nature of some of the recorded species. However, ordination results for floristic composition suggest that leached nutrients could exert their influence beyond the distance (1 m) considered in this study, since the area around latrines is clearly different in floristic composition from the other surveyed positions within the rabbit's home range. This suggests that latrines may be providing new opportunities for plant germination and establishment. In fact, other studies about the effects of latrines on Mediterranean soil properties have concluded that they are an important locus of organic matter and enhance soil chemical fertility and plant growth in semi-arid Mediterranean ecosystems, thus promoting diversity and a greater stability of the system (Willot et al. 2000; Petterson 2001).

## Conclusions

This chapter demonstrates that warrens and latrines support a distinct annual plant community. The general processes involved in the shaping of these communities, soil disturbance and pellet accumulation, are common to all mammalian herbivores, and have a deep impact on the vegetation (Harper 1977), irrespective of local plant species assembly and biogeographical zone. Although some of those effects can be species-specific, the final result is a change in some, if not all, the community parameters analyzed in this study (floristic composition, total vegetation cover, and mean vegetation height). These engineering effects act as bottom-up forces that may influence community structure and the behavior of other species (Bangert and Slobodchikoff 2000). This role is twofold: for herbaceous species, which take advantage of the spaces created by rabbit disturbance and herbivory or nutrient enrichment; and potentially for other species that can use these different plant assemblages and strata as resources themselves (e.g., insects). Latrines have already been typified as an important niche for endemic dung beetles (Verdu and Galante 2004) and warrens can be used as a temporary refuge or even be taken over by other species, for example reptiles (Blazquez and Villafuerte 1990) and other mammals (Villafuerte, pers. comm.). In several places around the world, European rabbit plasticity and colonizing ability has lead them to reach pest status. However, in the resource-limited ecosystems of the Mediterranean basin, rabbits are prey for more than 20 predators, and in some cases they comprise more than 40% of the consumed biomass (Delibes and Hiraldo 1981). Therefore, rabbits are a keystone species and, as our results show, have the potential to increase biodiversity at different scales.

*Acknowledgements:* We would like to thank the management of the Dehesa Santo Ángel de la Guarda, Chapinería, for allowing us to work at the study site. We also thank Montse Soria, Gonzalo García, Eduardo Velázquez, Diego Gamo, David Polanco, Nancy Nápoles, Isabel Lorente, Daniel Cabello and Jose Ignacio Gómez Crespo for their help with field work. This work is part of the projects REN2000-0783/GLO and REN2003-05553/GLO, Ministerio de Ciencia y Tecnología (MCyT). Marta Rueda is supported by a FPI grant from the MCyT and Lucía Gálvez by a FPI grant from the Comunidad Autónoma de Madrid.

## References

Archer S, Scifres C, Bassham CR, Maggio R (1988) Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecol Monogr 58:111–127

Bangert RK, Slobodchikoff CN (2000) The Gunnison's prairie dog structures a high desert grassland landscape as a keystone engineer. J Arid Environ 46:357–369

Blázquez MC, Villafuerte R (1990) Nesting of the Montpellier snake (*Malpolon monspessulanus*) inside rabbit warrens at Doñana National Park (SW Spain), phenology and a probable case of communal nesting. J Zool Lond 222:692–693

Callaway RM (1995) Positive interactions among plants. Bot Rev 61:306–349

Callaway RM, Pugnaire FI (1999) Facilitation in plant communities. In: Pugnaire FI, Valladares F (eds) Handbook of functional plant ecology. Marcel Dekker, New York, pp 623–648

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Austral J Ecol 18:117–143

Cowan DP (1987) Aspects of the social organisation of the European wild rabbit (*Oryctolagus cuniculus*). Ethology 75:197–210

Delibes M, Hiraldo F (1981) The rabbit as prey in the Iberian Mediterranean ecosystem. In: Myers K, Maclnnes CD (eds) Proceedings of the world lagomorph conference, August 1979, Guelph, Ontario. Guelph, Guelph University Press. pp 614–622

De Miguel JM, Rodríguez MA, Gómez-Sal A (1997) Determination of animal behavior-environment relationships by correspondence analysis. J Range Manage 50:85–93

Eldridge DJ, Myers CA (2001) The impact of warrens of the European Rabbit (*Oryctolagus cuniculus*) on soil and ecological processes in a semi-arid Australian woodland. J Arid Environ 47:325–337

Floate MJS (1981) Effects of grazing by large herbivores on nitrogen cycling in agricultural ecosystems. In: Clark FE, Rosswall T (eds) Terrestrial nitrogen cycles. Swedish Natural Science Research Council, Stockholm, pp 585–601

Gillham ME (1955) Ecology of the Pembrokeshire islands. III. The effect of grazing on the vegetation. J Ecol 43:172–206

Hambler DJ, Dixon JM, Hale WHG (1995) Ten years in rehabilitation of spoil: appearance, plant colonists and the dominant herbivore. Environ Conserv 22:323–334

Harper JL (1977) Population biology of plants. Academic Press, San Diego

Huntly N, Reichman OJ (1994) Effects of subterranean mammalian herbivores on vegetation. J Mamm 75:852–859

Joffre R, Vacher J, de los Llanos C, Long G (1988) The dehesa: an agrosilvopastoral system of the Mediterranean region with special reference to the Sierra Morena area of Spain. Agroforest Syst 6:71–96

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Lange RT, Graham CR (1983) Rabbits and the failure of regeneration in Australian arid zone Acacia. Austr J Ecol 8:377–381

Legendre P (2000) Comparison of permutation methods for the partial correlation and partial Mantel tests. J Statist Comput Simul 67:37–73

Lombardi L, Fernandez N, Moreno S, Villafuerte R (2003) Habitat-related differences in rabbit (*Oryctolagus cuniculus*) abundance, distribution, and activity. J Mamm 84:26–36

McInnes PF, Naiman RJ, Pastor J, Cohen Y (1992) Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology 73:2059–2075

McNaughton SJ (1983) Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. Ecol Monogr 53:291–320

Moreno S, Villafuerte R (1995) Traditional management of scrubland for the conservation of rabbits *Oryctolagus cuniculus* and their predators in Doñana National Park. Biol Conserv 73:81–85

Moreno S, Villafuerte R, Delibes M (1996) Cover is safe during the day but dangerous at night: the use of vegetation by European wild rabbits. Can J Zool 74:1656–1660

Naiman RJ, Pinay G, Johnston CA, Pastor J (1994) Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. Ecology 75:905–921

Oden NL, Sokal RR (1992) An investigation of three-matrix permutation tests. J Class 9:275–290

Palomares F (2001) Comparison of three methods to estimate rabbit abundance in a Mediterranean environment. Wildl Soc Bull 29:578–585

Palomares F (2003a) The negative impact of heavy rains on the abundance of a Mediterranean population of European rabbits. Mammal Biol 68:224–234

Palomares F (2003b) Warren building by European rabbits (*Oryctolagus cuniculus*) in relation to cover availability in a sandy area. J Zool Lond. 259:63–67

Parer I, Libke JA (1985) Distribution of rabbit, *Oryctolagus cuniculus*, warrens in relation to soil type. Austr Wildl Res 12:387–405

Petterson DA (2001) The effects of the wild rabbit (*Oryctolagus cuniculus*) on soils and vegetation in semi-arid, south-eastern Spain. PhD. Dissertation, University of Leeds, Leeds, UK

Pollock MM, Naiman RJ, Erickson HE, Johnston CA, Pastor J, Pinay G (1995) Beaver as engineers: influences on biotic and abiotic characteristics of drainage basins. In: Jones CG, Lawton JH (eds) Linking species and ecosystems. Chapman & Hall, New York, pp 117–126

Rescia AJ, Schmitz MF, Martín de Agar P, de Pablo CL, Atauri JA, Pineda FD (1994) Influence of landscape complexity and land management on woody plant diversity in northern Spain. J Vegetation Sci 5:505–516

Roberts DW (1986) Ordination on the basis of fuzzy set theory. Vegetation 66:123–131

Smouse PE, Long JC, Sokal RR (1986) Multiple regression and correlation extension of the Mantel test of matrix correspondence. Syst Zool 35:627–632

Sneddon IA (1991) Latrine use by the European rabbit (*Oryctolagus cuniculus*). J Mamm 72:769–775

Spiers B (1981) Vegetation survey of semi-natural grazing lands (dehesas) near Mérida, southwest Spain, as a basis for land use planning. ITC Technical Report no. 6, Enschede, The Netherlands

Verdu JR, Galante E (2004) Behavioural and morphological adaptations for a low-quality resource in semi-arid environments, dung beetles (Coleoptera, Scarabaeoidea) associated with the European rabbit (*Oryctolagus cuniculus* L.) J Nat Hist 38:705–715

Vetaas OR (1992) Micro-site effects of trees and shrubs in dry savannas. J Vegetation Sci 3:337–344

Whitford WG, Kay FR (1999) Biopedturbation by mammals in deserts: a review. J Arid Environ 41:203–230

Willot SJ, Miller AJ, Incoll LD, Compton SG (2000) The contribution of rabbits (*Oryctolagus cuniculus*) to soil fertility in semi-arid Spain. Biol Fert Soils 31:379–384

Wood DH (1988) Estimating rabbit density by counting dung pellets. Austr Wildl Res 15:665–671