

Warren building by European rabbits (*Oryctolagus cuniculus*) in relation to cover availability in a sandy area

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Abstract

Warrens of the wild European rabbit *Oryctolagus cuniculus* are of concern in the Iberian Peninsula as a way to recover rabbit populations. However, there are no studies on the selection of sites where rabbits build their warrens. Between 1995 and 1997, in addition to warren size (number of entrances), the vegetation characteristics and the occurrence of tree roots in the ground surface occupied by warren entrances in Mediterranean scrubland and pastureland habitats were recorded in a sandy area of the Doñana National Park. Pastureland warrens were about twice as large as warrens in Mediterranean scrubland, and 1.8–1.4 times larger in the first study year than in the other 2 years. Warrens in pastureland were built more between tree roots (13.3–17.8%) than those built in Mediterranean scrubland (0.7–1.8%). In Mediterranean scrubland, most of the ground surface occupied by warren entrances was under tall shrubs (79.7–87.9%), with some under short shrubs (4.5–7.4%). In pastureland, these figures were 2.0–3.8% for tall shrubs, and 17.2–19.8% for short shrubs. Warrens were built between tree roots significantly less than expected in the Mediterranean scrubland, and slightly more than expected in the pastureland. Whereas warren surface was occupied by short shrubs significantly less than expected in the Mediterranean scrubland, the opposite pattern occurred in the pastureland; however, in both habitats tall shrubs were significantly preferred. These results suggest that rabbits may seek protection against collapsing warrens by selecting sites with some supporting structures such as the roots of trees or shrubs. Scrubland vegetation (preferably tall shrubs) should be favoured for medium- and long-term habitat management of areas aimed at supporting large rabbit populations. Furthermore, in sandy areas, some kind of stable ground support and external protection should be provided when creating artificial warrens for rabbits.

Key words: cover selection, open and scrubland habitats, *Oryctolagus cuniculus*, warren building, warren size

INTRODUCTION

Underground dens or warrens are commonly used by European rabbits *Oryctolagus cuniculus* for breeding and for protection from predators and weather (Parer & Libke, 1985; Villafuerte, 1994). These warrens may be structurally complex and have from a few to >100 entrances (Kolb, 1985; Parer, Fullagar & Malafant, 1987). Warrens are particularly important for rabbit presence and abundance in open habitats, where being underground is the only place for protection when the grass is short (Myers & Parker, 1965; Palomares & Delibes, 1997). In closed habitats, rabbits may survive by living between scrubland and using seasonally isolated burrows for breeding (Gibb & Fitzgerald, 1998), but in scrubland areas where rabbits reach high densities they also build warrens that are mainly used during the breeding season (Wheeler, King & Robinson, 1981; Kolb, 1991, 1994; Palomares, 2001a).

This study investigated the selection of sites where rabbits build their warrens in two clearly different habitats

(Mediterranean scrubland and pastureland) for 3 years (the first year was the last one of a long dry period, and the other 2 years were characterized by higher than average rainfall). In these habitats, rabbits are subjected to different predation pressures and the effect of heavy rains (Moreno, Villafuerte & Delibes, 1996; Palomares & Delibes, 1997). Therefore, different responses were expected in the selection of sites where rabbits build their warrens.

When scrubland is available, foraging rabbits prefer to stay close to protection (Moreno *et al.*, 1996), and during resting, rabbits also prefer the protection of vegetation to warrens (Kolb, 1994). Therefore, it might be expected that rabbits would positively select sites with scrubland to build their warrens in both types of habitats. On the other hand, rabbit reproduction is negatively affected by heavy rains because young rabbits are killed by flooding, blocking or collapsing of warrens, the effect being particularly intense in open habitats. Therefore, it might also be expected that rabbits would select sites with scrubland vegetation to

build their warrens, this selection being stronger in open than in closed habitats. Furthermore, a change in warren site selection towards sites with more protection from rain (particularly in the open habitats) would be expected after successive years with a higher than average rainfall. This study looks at whether warrens were built among tree roots (which might prevent the collapse of warrens), and beneath the protection of short and tall shrubs. Rabbits are more abundant in areas with tall shrubs (Palomares *et al.*, 2001), so a different selection pattern might be expected between short and tall shrubs for warren building.

METHODS

Study area

The study was carried out in the north of Doñana National Park, in an area called Coto del Rey (south-western Spain; 37°9'N, 6°26'W) between 1995 and 1997. The Doñana National Park is a flat, sandy area containing 3 main biotopes: scrubland, dunes, and marsh (Valverde, 1958). The climate is Mediterranean sub-humid, with mild, wet winters and hot, dry summers, and average annual rainfall is between 500 and 600 mm. However, rainfall during the first year of study was low (253 mm) and a continuation of a longer dry period that started in 1990–91 with rainfall closeto or less than average. The other 2 years of study were characterized by heavy rainfall, which in several months exceeded 200 mm (annual totals of 1032 mm and 885 mm, respectively).

Coto del Rey is characterized by a mixture of relatively well-conserved areas of Mediterranean scrubland and ash stands where *Pistacia lentiscus* shrubs predominate, and cleared areas for cattle grazing with isolated trees (*Quercus suber* and *Olea europaea*); marsh extends to the south of the study area. The terrain is flat and sandy with ground heights ranging in the study area between 1 and 6.4 m a.s.l. More information on the study area can be found in Palomares *et al.* (2001).

Warren surveys

Warren size (number of entrances) and the vegetation characteristics of the sites where warrens were found were surveyed in 2 clearly different habitats of the study area (Mediterranean scrubland and pastureland). Surveys were carried out in April 1995 in a part of the pastureland habitat and in summer 1995, 1996 and 1997. Warren surveys consisted of recording the number of entrances and the vegetation characteristics in the area occupied by warren entrances. Active and inactive entrances were counted for each warren. Collapsed entrances were frequently observed during the last 2 years of study, but they were not counted. In addition to the number of entrances, a record was also made of whether the warrens were built between tree roots, and the percentage of cover by short and tall shrubs in the

area occupied by the warren entrances. This area was obtained after connecting the most external entrances of each warren by straight lines. It was not possible to be certain that all entrances considered as belonging to the same warren were actually interconnected. However, groups of entrances were usually spatially isolated from each other, and when ferrets have been used to catch rabbits in these warrens they can appear at any entrance of the supposed warren (J. Calzada, pers. comm.). Warrens were considered as built among tree roots if any tree was inside the area occupied by warrens. The shrub species formed 2 clearly defined layers according to their growth potential. So, the tall shrub layer included species such as *P. lentiscus*, which reaches between 2.5 and 4 m, whereas other species such as *Halimium halimifolium* only reaches 1.5 m. For warren counting, teams of 3–5 persons slowly walked small sections of area to survey for warrens everywhere. In the pastureland, the same 342-ha study plot was surveyed each year. In the Mediterranean scrubland, a 126-ha study plot was surveyed in 1995, but in 1996 and 1997 only the same 23 ha situated within the 126 ha was sampled as during the previous year. Because warren density may change in relation to distance to the marsh border (Palomares *et al.*, 2001), the plots surveyed in both habitats included a range of distances from the marsh.

To check for any selection of vegetation characteristics measured in warrens, a survey of the characteristics of these variables was carried out in 100 random points for each habitat in summer 1997. Random points were generated within the limits of plots surveyed using the FoxPro database program (Microsoft Corporation). For each of these points, the presence or absence of tree roots, and the percentage of short and tall shrub cover on a circle of 5 and 9.5 m diameter centred in the random points for Mediterranean scrubland and pastureland, respectively, was recorded. Each of these diameters was the mean value of the average longer and shorter axes measured for 284 and 57 warrens in each habitat, respectively, in August 1994 (Palomares, 2001a).

Data analyses

The effect of habitat, year or its interaction on the number of warren entrances, cover by short shrubs, and cover by tall shrubs was tested with analysis of variance and a type III sum of squares using procedure generalized linear models (GLM) for unbalanced design in a SAS software package (SAS Institute, 1990a). Data could not be adequately transformed to meet the parametric analysis of variance assumptions of normality and homoscedasticity, therefore data were ranked using procedure RANK in SAS (SAS Institute, 1990b), before performing the GLM procedure. To test for differences in tree root presence in warrens resulting from habitat, year or its interaction, a contingency table was constructed and frequencies were analysed by procedure CATMOD in SAS (SAS Institute, 1990c) for categorical data analysis. In all analyses, only $P \leq 0.05$ was accepted as significant.

Table 1. Number of entrances of rabbit *Oryctolagus cuniculus* warrens for Mediterranean scrubland and pastureland habitats 1995, 1996 and 1997. *n*, number of warrens surveyed

Habitat	Mediterranean scrubland			Pastureland		
	1995	1996	1997	1995	1996	1997
<i>n</i>	859	138	163	472	316	226
Mean \pm SE	6.8 \pm 0.314	3.8 \pm 0.252	3.8 \pm 0.221	11.7 \pm 0.760	8.1 \pm 0.645	8.2 \pm 1.052
Range	1–126	1–18	1–17	1–218	1–116	1–122

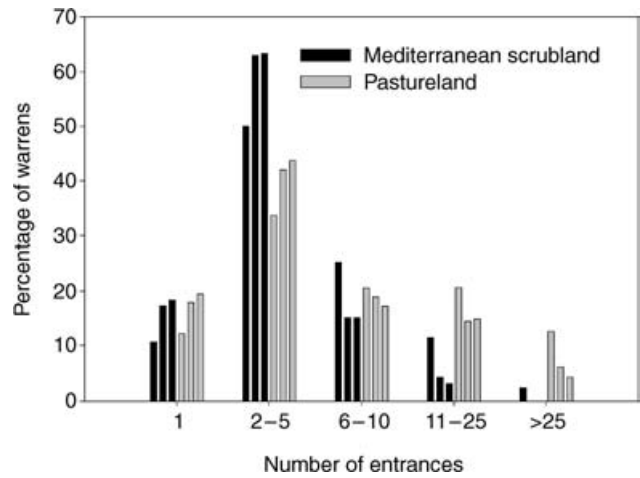
RESULTS

There were significant differences in warren size between habitats ($F = 39.5$, d.f. = 1, $P < 0.001$) and for years within habitats ($F = 43.9$, d.f. = 2, $P < 0.001$). There was not a statistically significant interaction between habitat and year ($P = 0.652$). Warrens in the pastureland were about twice as large as warrens in the Mediterranean scrubland (Table 1). Warrens in the first year of study were 1.8 and 1.4 times larger than those in 1996 or 1997 for Mediterranean scrubland and pastureland, respectively (Table 1). There were no differences in warren size between the last 2 years of study in any habitat ($P < 0.05$; Table 1).

Grouping warrens in categories of size, the pattern was similar in both habitats, with small warrens (<6 entrances) and larger warrens (≥ 6 entrances) increasing and diminishing, respectively, after the first year of study (Fig. 1).

Few warrens were found between tree roots in the Mediterranean scrubland (0.7–1.8%); however, the percentage increased to 13.3–17.8% for the pastureland (Table 2). Differences between habitats were highly significant ($\chi^2 = 120.1$, d.f. = 1, $P < 0.001$), but not between years ($\chi^2 = 3.76$, d.f. = 2, $P = 0.152$). The interaction between habitat and year was not significant ($\chi^2 = 2.89$, d.f. = 2, $P = 0.2353$).

Most of the warren surface in the Mediterranean scrubland habitat was covered by tall shrubs (79.7–87.9%), and only between 4.5% and 7.4% by short shrubs; however, the pattern was different in the pastureland habitat with

**Fig. 1.** Frequency distribution of rabbit *Oryctolagus cuniculus* warren sizes (number of entrances) in Mediterranean scrubland and pastureland habitats in Doñana National Park during 1995, 1996 and 1997; bars in this order for each habitat and warren size interval.

17.2–19.8% of the warren surface occupied by short shrubs and only between 2.0% and 3.8% occupied by tall shrubs (Table 2). Again, differences between habitats were highly significant ($F = 200.2$, d.f. = 1, $P < 0.001$ and $F = 3051.5$, d.f. = 1, $P < 0.001$, for short and tall shrubs, respectively). However, only for tall shrubs, differences were significant between years ($F = 6.31$, d.f. = 2, $P = 0.002$), and there was also a significant

Table 2. Frequency of occurrence of tree roots and mean percentages (\pm SE) of cover by short and tall shrubs in the observed surfaces occupied by *Oryctolagus cuniculus* warren entrances and random similar surfaces for Mediterranean scrubland and pastureland habitats in 3 years of study. Significant differences between random points and observed warrens for each variable were tested by χ^2 test for tree roots, and constructing 95% confidence intervals around the random mean and comparison with the observed mean for short and tall shrub covers. NS, not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

	Mediterranean scrubland				Pastureland			
	Random	1995	1996	1997	Random	1995	1996	1997
<i>n</i>	100	859	138	163	100	473	316	226
Warrens with tree roots (%)	11	1.5***	0.7**	1.8**	10	17.8 NS	13.6 NS	13.3 NS
Short shrub cover (%)	17.7 ^a 12.4–23.0	7.4 \pm 1.5*	5.7 \pm 3.0*	4.5 \pm 2.4*	6.2 ^a 2.7–9.7	17.2 \pm 2.7*	19.8 \pm 3.6*	19.3 \pm 4.3*
Tall shrubs cover (%)	34.3 ^a 26.4–42.2	79.7 \pm 2.4*	81.9 \pm 5.8*	87.9 \pm 4.5*	0.5 ^a 0.0–1.2	3.8 \pm 1.5*	2.0 \pm 1.3*	2.4 \pm 1.7*

^a This is the mean and 95% confidence interval.

interaction between habitat and year ($F = 11.7$, d.f. = 2, $P < 0.001$). The interaction was because cover by tall shrubs tended to increase as expected along years in the Mediterranean scrubland, and to decrease in the pastureland (Table 2).

Analysis of site selection revealed further interesting results. First, warrens were built between tree roots significantly less than expected in the Mediterranean scrubland, whereas in the pastureland they were built between tree roots more than expected, although the trend was not significant (Table 2). In both habitat types, the availability of tree roots was similar (10% and 11%). Second, whereas the warren surface occupied by short shrubs was significantly less than expected in the Mediterranean scrubland, an opposite pattern was found in the pastureland, where the average ground cover by short shrubs was 6.2% for random points, and for warrens it was between 17.2 and 19.8% (Table 2). However, in both habitat types, the warren surface occupied by tall shrubs was between 2.5 and 4.0–5.6 times higher than random for Mediterranean scrubland and pastureland, respectively (Table 2).

DISCUSSION

Warren size was clearly different in each habitat studied, which may be an indirect consequence of the vegetation characteristics of each habitat in relation to the avoidance of predation (for a discussion, see Palomares & Delibes, 1997; Palomares, 2001a; Palomares *et al.*, 2001). However, differences in the size of warrens between years resulted from the negative effect of rain, by both directly destroying warrens and indirectly decreasing rabbit numbers and therefore the possibilities for re-opening warrens. Warren and entrance densities (per ha) decreased from 1.5 to 0.7 and from 18.2 to 6.1, respectively, for the pastureland habitat, and from 7.6 to 7.0 and from 38.1 to 26.6, respectively, for the Mediterranean scrubland habitat, after the 2 years of higher than average rainfall. Rabbit density also decreased by four to five times after the first year of heavy rainfall. The decline of rabbit numbers may also explain the observed change in warren size (i.e. to smaller warrens) during the 2 years of heavy rains.

The results of warren site selection revealed clear differences between habitats. However, there was no difference between years, suggesting that there was no selection by rabbits to re-open or use the warrens most protected from rain (see below). Warrens were built more between tree roots in the pastureland than in the Mediterranean scrubland, which suggested that the rabbits could look for protection against collapsing warrens by selecting sites with some supporting structure such as the roots of trees. This is in agreement with the fact that this pattern was not observed in the Mediterranean scrubland where rabbits did not build warrens between tree roots, but between scrubland vegetation, and particularly tall shrubs, which might have the same function with the additional advantage of providing protection against predation (Moreno *et al.*, 1996).

Another difference was also found in each habitat type. Whereas short shrub vegetation was negatively selected in the Mediterranean scrubland by rabbits to build their warrens, this was positively selected in the pastureland. In both habitats, however, tall shrubs were positively selected. These differences reflect the different local responses of the rabbits to environmental conditions, but also bring insights on rabbit preferences for warren building. First, rabbits prefer to build warrens between any type of scrubland rather than in open areas. This could be related both to warren stability in the loose and unstable ground of the study area, and to increased avoidance of predation risk because of the cover provided by scrubland on the surface of the warren and because the shrub roots impede the access of digging predators (Reichman & Smith, 1990). Second, rabbits prefer to build warrens between tall rather than short shrubs. This could be related to the same factors mentioned previously, i.e. the roots of tall shrubs must provide better stability to the underground warren system, and the greater cover of tall shrubs above ground increases the possibility of successfully avoiding predators.

During the past decades, rabbit populations are declining in the Iberian Peninsula where European rabbits originated (López-Martínez, 1989; Branco, Ferrand & Monnerot, 2000). In this area, rabbits are of double concern because they are important for human hunters (Rogers, Arthur & Soriguer, 1994), and they are an irreplaceable prey for many endangered predator species (Delibes & Hiraldo, 1981). Therefore, efforts are being made to recover or maintain rabbit numbers, some of which are focused directly on warrens (Gortázar *et al.*, 2000; Sanz-Zuasti & Pablos, 2000). The results of this study may be useful to maintain or recover rabbit populations. First, rabbits prefer scrubland vegetation (preferably tall shrubs) to build warrens, therefore this type of vegetation should be favoured for medium and large habitat management of areas aimed at having large rabbit populations. This is particularly important because many of the management activities proposed for rabbit recovery include removing scrubland vegetation to favour potential food for rabbits (Moreno & Villafuerte, 1995). Even though the benefits of this practice are clear, care should be taken in selecting the type of shrubs to be removed, trying to leave tall shrubs untouched, at least if they are similar to those found in Coto del Rey. Data obtained in different sites of the Doñana area show an acceptable positive correlation between an index of rabbit abundance and the percentage of cover of tall scrubs, whereas the relationship was negative with short shrubs (Palomares, 2001b). Therefore, short shrubs should be the ones removed during habitat improvement for rabbits. Second, in sandy areas similar to those in the area studied here, stable ground support should be provided when creating artificial warrens for rabbits. This support should replace the role of tree roots or the shrubs in natural areas. Third, in addition to underground support, external protection should also be provided in areas where artificial warrens are going to be built for rabbits.

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