

European rabbits as ecosystem engineers: warrens increase lizard density and diversity

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Abstract Mammals that build extensive open burrow systems are often classified as ecosystem engineers, since they have the potential to modulate the availability of resources for themselves and other organisms. Lizards may benefit from the heterogeneity created by these structures, especially if coupled with an increased offer of sites for refuge and thermoregulation. However, information about these engineering effects by burrowing animals is scarce. We investigated the influence of European rabbit burrows on several parameters of a Mediterranean lizard community (abundance, density, diversity and body condition) in three different habitats (open pastures, holm oak and scrub patches). We found that lizards were positively associated with burrows, and that burrows determined lizard presence at otherwise unfavourable habitats. Moreover, community parameters such as density and species richness were higher in sites with burrows. Burrows influenced lizard species in different ways, and were also relevant for other Mediterranean vertebrates, as revealed by questionnaires to experts. We also explored the possible resources provided by burrows for lizards. Warrens offer relatively abundant prey and appropriate retreat sites for refuge and thermoregulation. Warrens may have further implications within the ecosystem, acting as stepping stones, allowing lizards to reach otherwise inaccessible habitat patches. This study shows that European rabbit warrens have a positive influence on lizard density and diversity, and confirms the role of rabbits as ecosystem engineers. This reinforces the need for appropriate conservation measures for rabbits, especially given their threatened status in the Iberian Peninsula. Furthermore, our study highlights that taking into account the influence of engineering activities increases our awareness of species interactions, and may translate into more adequate conservation measures for the preservation of biodiversity.

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Introduction

Open burrow systems have been recognised as an important component of many ecosystems, influencing geomorphology, plant communities and faunal diversity, and improving resources for many taxa (Kinlaw 1999; Whitford and Kay 1999). Burrowing activities aerate soils, homogenise soil horizons, and may increase fertility and plant productivity (Markwell and Daugherty 2002). They promote the redistribution of resources and increase allochthonous nutrient inputs that can dramatically affect food web dynamics and resource availability (Jefferies 2000). Burrowing vertebrates often have an array of commensals that benefit from their fossorial activities. They may affect the spatial distribution of invertebrates (Hawkins and Nicoletto 1992; Bangert and Slobodchikoff 2006), promote bird diversity (Lai and Smith 2003), influence grassland community composition (Whicker and Detling 1998), and benefit small mammals, reptiles and amphibians (Lomolino and Smith 2003). A common characteristic of open burrow systems is that they are often long-lived, constituting patches of relatively reliable resources. Above all, extensive burrow systems represent an important source of heterogeneity in many ecosystems, and therefore enhance biodiversity (Christensen 1997). For these reasons, several mammals that build extensive burrow systems are often classified as ecosystem engineers, since they have the potential to modulate the availability of resources for themselves and other organisms through direct and indirect interactions, with important implications for community ecology and the maintenance of biodiversity (Jones et al. 1994).

Reptiles are especially sensitive to habitat heterogeneity (Pianka 1966), so they are likely to benefit from structural elements such as burrows (Kretzer and Cully 2001). Lizard habitat choice is determined by their ectothermic condition, which implies a great dependence on climatic variables and a high vulnerability to predation under certain conditions. Burrow availability may be especially relevant in arid and semi-arid environments, where they may serve as shelter from extreme temperatures (van Heerden and Dauth 1987). Burrows also have higher humidity values than above-ground (Kay and Whitford 1978), which can be important for lizard egg development (Castilla and Swallow 1995; Ji and Braña 1999). Lizards are usually active foragers (McBrayer and Reilly 2002), and extensive burrow systems such as prairie dog towns may be advantageous foraging grounds due to the often high abundance of arthropod commensals (Davis and Theimer 2003).

Unfortunately, there is still a vacuum of knowledge about commensal relationships between burrowing ecosystem engineers and the lizard community in several ecosystems around the world. In Southern Europe, the European rabbit (*Oryctolagus cuniculus*) is a native fossorial species that can create extensive burrow systems called warrens. Rabbits have been widely studied as a keystone species in Mediterranean food webs (e.g. Villafuerte et al. 1997; Delibes-Mateos et al. 2007), and are very relevant in the Iberian Peninsula, where they have important bottom-up consequences for endangered, charismatic species such as the Iberian lynx (*Lynx pardinus*) and the Imperial eagle (*Aquila adalberti*) (e.g. Calvete et al. 1997; Moreno et al. 2004). Rabbits have suffered a massive decline in the last decades (Virgós et al. 2007), qualifying as a threatened species, and being Red Listed in Portugal. Therefore, this reinforces the importance of studying their

role as ecosystem engineers, since their top–down effects have seldom been studied (but see Gálvez et al. 2008). So far, rabbit warren use by reptiles in the Mediterranean has been reported for a snake (*Malpolon monspessulanus*; Blazquez and Villafuerte 1990) and a tortoise (*Testudo Hermani*; Calzolari and Chelazzi 1991). Warrens are formed by several burrows or entrances, and can become very conspicuous (occupying an area of up to 850 m², personal observation) and abundant (over 10 warrens/ha; Revilla et al. 2001; Gea-Izquierdo et al. 2005) in Mediterranean landscapes. Therefore, it is likely that they can act as a source of heterogeneity and resources for the Mediterranean lizard community, and thus influence community parameters such as density and diversity.

In this study, we explored the role of European rabbits as ecosystem engineers by investigating the effect of rabbit burrows on the lizard community in a Mediterranean ecosystem. In these areas, lizards show a preference for scrub cover and rocky outcrops, whereas grasslands or cultivated land constitute unfavourable habitats (Martín and López 2002). We hypothesised that if rabbit burrows represent a source of heterogeneity and/or resources for lizards, burrow availability will influence habitat choice and thus be reflected in lizard density and diversity, and this trend would be enhanced at the most unfavourable habitats. We also explored the possible resources provided by burrows and whether they had an influence on lizard body condition. With this study we aim to improve the knowledge about the ecological role of burrowing vertebrates in their native habitats. Having extensive information about their effects on lizard communities may translate into more adequate conservation measures for the preservation of biodiversity in Southern Europe.

Materials and methods

Study area

The present study was carried out in a 330 ha area near Madrid, central Spain (40°23' N, 4°12' W). The climate is continental-Mediterranean. Mean altitude is 670 m, and mean temperature and precipitation are 12°C and 432.6 mm, respectively (Ministerio de Agricultura 1989) but with strong interannual variations. The study area can be classified as a “dehesa”. Dehesas are man-made savannah-like landscapes characterised by a mosaic of cleared holm oak woodlands with an annual grass understorey. In the study area the substrate is sandy and lays upon fractured granite bedrock, and the dominant tree species is the holm oak (*Quercus ilex* L. subsp. *rotundifolia* (Lam.)). The area is managed for small game hunting and maintains traditional practices such as periodic ploughing to control scrub encroachment, as well as mowing of the most productive areas. The main herbivores are a dense rabbit (*Oryctolagus cuniculus*) population (8.3 warrens/ha) and a transhumant herd of about 600 sheep.

Four lacertid lizard species are abundant at the study area: *Psammodromus algirus*, *Psammodromus hispanicus*, *Acanthodactylus erythrurus* and *Podarcis hispanica*. *P. algirus* is a medium-sized (adult snout-vent length 60–90 mm, mass 6–16 g) insectivorous lizard that inhabits shrub and woodland habitats in the Iberian Peninsula, south-eastern France and north-west Africa (Díaz and Carrascal 1991; Carretero et al. 2002a). *P. hispanicus* is a small (adult snout-vent length 38–41 mm, mass 1.3–1.5 g) insectivorous lizard that prefers dry, relatively open habitats and sandy substrates with alternating dense scrub vegetation and bare soil. It is widely but sparsely distributed in the Iberian Peninsula, and is also present in North-western Africa (Bauwens et al. 1995; Carretero et al. 2002b).

A. erythrurus is a medium-sized (adult snout-vent length 69–82 mm, mass 8–9 g) mainly myrmecophagous (ant-eating) lizard that prefers open sandy areas with sparsely distributed vegetation, and is present in the Iberian Peninsula and Northern Africa (Salvador 1982; Pérez-Mellado 1998). *Po. hispanica* is a medium-sized (adult snout-vent length 52–57 mm, mass 3–4 g) insectivorous lizard usually associated with rocky outcrops and stone walls, and widely distributed in the Iberian Peninsula, southern France and North-western Africa (Bauwens et al. 1995; Sousa and Pérez-Mellado 2002).

We identified three main habitat types within the study area (Fig. 1): “scrub patches”, “holm oak patches” and “open pasture patches”. Scrub patches (mean size: $7140.30 \pm 7890.83 \text{ m}^2$) are areas of high scrub cover (min: 70%), mainly *Lavandula stoechas*, which are usually found on ridges and slopes. Holm oak patches (mean size: $170.40 \pm 112.33 \text{ m}^2$) are individuals or small groups of holm oak trees, often associated with small rocky outcrops, where basal shoots form a layer of scrubby undergrowth of 20–50% cover and 15–50 cm high, with large amounts of holm oak leaf litter. Open pasture patches (mean size: $166.34 \pm 319.68 \text{ m}^2$) correspond to sparse herbaceous pastures and cultivated areas that fill up the matrix between holm oak and scrub patches. They are characterised by a short and highly diverse annual herbaceous community (approx. 50% herbaceous cover).

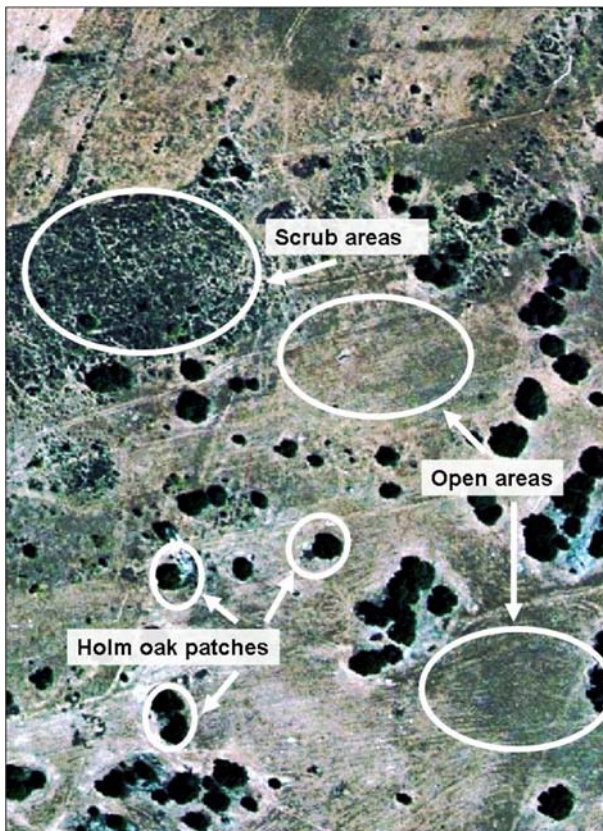


Fig. 1 Aerial photograph showing a portion of the study area and the relative positions of each habitat type

Lizard surveys and captures

In July–August 2004, a total of 91 sampling sites with and without rabbit burrows were selected among the different habitat types, according to availability within the landscape (Table 1). Rabbit burrows were counted at each sampling site. An average of 55.92 burrows were found in scrub areas (mean density = 0.013 ± 0.034 burrows/m²), 3.9 in holm oak areas (mean density = 0.014 ± 0.035 burrows/m²) and 54 burrows in open pasture patches (warrens) (mean density = 0.44 ± 0.69 burrows/m²). The structural characteristics of each site (woody vegetation cover, rocks, bare ground and vegetation height) were recorded, and sites were mapped on an aerial photograph to calculate site area using a GIS. Preliminary tests were carried out to check differences between sites with and without burrows within each habitat type in surface area, vegetation parameters (woody and herbaceous vegetation height and cover) and general habitat characteristics (rock and bare ground cover). No differences were found (all $P > 0.05$) for most variables, with the exception of vegetation height in open areas, which was higher when burrows were present ($P < 0.001$).

Lizard surveys were carried out at each sampling site. Scrub patches were sampled using 5 m wide line transects (between 2 and 6 transects, depending on patch size) that were walked in search for lizards following the method described in Díaz and Carrascal (1991). This procedure could not be used for holm oak patches and open pastures due to their small size, so they were carefully inspected for 7–10 min. We always tried to survey 40 m²/min, ensuring an equivalent sampling effort in all cases. All observed individuals were counted, noting species, sex, age (adult/subadult/juvenile) and approximate snout-vent length (SVL) whenever possible. Counts took place on two different days at each site,

Table 1 Summary of general data from lizard surveys in 91 sampling sites. Data are shown for each habitat category

	Sites with burrows				Sites without burrows			
	Open	Holm oak	Scrub	Total	Open	Holm oak	Scrub	Total
No. sampling sites	19	13	14	46	17	22	6	45
No. sites where lizards were found	16	8	11	35	0	7	4	11
Total no. lizards	36	10	46	92	0	10	20	30
Males	7	1	10	18	0	1	2	3
Females	13	6	13	32	0	–	3	3
Undefined gender	16	3	23	42	–	9	15	24
Adults	24	10	31	65	0	6	14	20
Subadults	7	–	11	18	0	2	6	8
Juveniles	2	–	4	6	0	1	0	1
Undefined age	3	–	–	3	–	1	–	1
<i>P. algirus</i>	1	7	7	15	0	5	1	6
<i>A. erythrurus</i>	20	2	16	38	0	0	10	10
<i>P. hispanicus</i>	11	0	22	33	0	0	8	8
<i>Po. hispanica</i>	4	1	1	6	0	4	0	4
Total spp. richness	4	3	4	4	0	2	3	3
Mean evenness	0.25	0	0.49	0.24	0	0	0.42	0.06

Note that we were unable to specify the species of two individuals

with an average of 13 days between surveys, and the highest number of individuals of each species seen on a particular day was used for calculating lizard abundance and density.

In addition, some individuals ($n = 26$) were captured by noosing, measured, weighed and any signs of parasites and predation (tail regeneration) annotated. Lizard snout-vent length, total length and body weight were used as measures of body condition. Females were palpated in order to assess whether they were gravid, and the number of eggs. All captured specimens were marked (red nail-varnish) to avoid recapture during the study period.

Abundance and density of lizards were used to characterise lizard presence at warrens. Use of burrows by vertebrates in general was explored using questionnaires sent to 31 Spanish experts (13 herpetologists and 18 mammalogists). Questionnaires mainly asked about observed evidence of vertebrates using rabbit burrows.

Resources provided by burrows

Prey, refuge and microclimatic conditions provided by burrows were evaluated in open pasture areas, the most potentially unfavourable habitat for lizards in dehesas (Martín and López 2002), and therefore the habitat type where we expected to find the strongest potential positive role of warrens for rabbits. For this purpose, we selected 10 open areas without burrows and 10 nearby warrens, all with at least 10 burrow entrances.

Relative prey (arthropod) abundance was estimated by randomly placing 20×20 cm quadrats inside warren patches (open pasture areas with burrows, all >10 burrows, mean: 58 burrows) and paired pasture patches without burrows. For one minute, all arthropods sighted inside the quadrat were counted and identified up to order (Díaz and Carrascal 1991). This procedure was repeated four times at each patch. This census technique assumes that the relative abundance of prey is being measured from the point of view of these lizards, which are often active ground foragers and use a variety of techniques, including active searching and ambushing. It also assumes that all insects are selected as actual prey.

The role of burrows as refuge was assessed through direct observations of lizard use, from the moment the individual was perceived to the moment it disappeared out of our visual field, noting if burrows were used. We also used correlations of lizard numbers with burrow abundance at each warren. Holm oak branches that game-keepers place over rabbit warrens as part of the management practices have already been identified as potentially important refuges for lizards by Martín and López (2002), so the cover of these branches above rabbit warrens was also recorded.

In summer, temperature and % relative humidity (RH) were measured inside and outside rabbit burrows using a thermo-hygrometer (HI 9065-Hanna Instruments). We took 18 pairs of measurements at 6 warrens (all >10 burrows, mean: 26.3 burrows) which were, on average, 100 m away from each other. Measurements were taken at different times of day (dawn: 6:00–7:00; morning (A.M.): 8:00–10:00; noon: 12:00–13:30; afternoon (P.M.): 16:30–17:30, all GMT times), in order to compare daily fluctuations inside and outside rabbit burrows.

Data analyses

Lizard density (lizards/ha) was used for inter-habitat comparisons, as patch size differed between habitats ($P < 0.05$). Lizard abundance was used for intra-habitat comparisons, as

total surveyed area in patches with and without burrows did not differ within each habitat type (all $P > 0.05$). Lizard diversity parameters considered in each sampled patch were species richness, and evenness (Pielou's evenness index, Pielou 1966).

Two-way ANOVAs with presence of burrows and habitat type as factors were used to explore lizard density, diversity and body condition. Type III sum of squares was used because the design was unbalanced, since we did not have an equal number of sampling sites with and without burrows and for all habitat types. Chi-square tests were used for population structure data (proportion of males, females, adults and juveniles) within and between patches with and without burrows. Relationships between the number of rabbit burrows and lizard abundance in the whole study area, body condition parameters and abundance of individuals with regenerated tails were tested using Pearson's correlations.

Correlations were also used to test for relationships between lizard abundance and number of rabbit burrows at warrens, and Partial correlations were used to control for the cover of holm oak branches placed on rabbit warrens. Mann–Whitney U -tests were used to test for differences in prey availability on and off rabbit warrens, and T -tests were used to compare temperature and humidity values inside and outside burrows. All statistical analyses were carried out using SPSS 13.0 (SPSS Inc., 1989–2003).

Results

Lizard community parameters

Lizards were found in 46 out of 91 sites surveyed. Presence of lizards was significantly linked to presence of rabbit burrows ($\chi^2 = 8.25$, $P = 0.004$) and lizards were only found in open pasture areas if rabbit burrows were present (Table 1). A total of four species of lizards were observed in the study area. The maximum number of lizard species was only found when rabbit burrows were present, for all habitats (Table 1). Moreover, total lizard abundance in the whole study area increased with number of rabbit burrows ($r = 0.584$, $P < 0.001$), and so did individual species abundances (*P. hispanicus*: $r = 0.564$, $P < 0.001$; *A. erythrurus*: $r = 0.456$, $P < 0.001$; *Po. hispanica*: $r = 0.210$, $P < 0.01$) except for *P. algirus* ($r = -0.083$, $P > 0.05$).

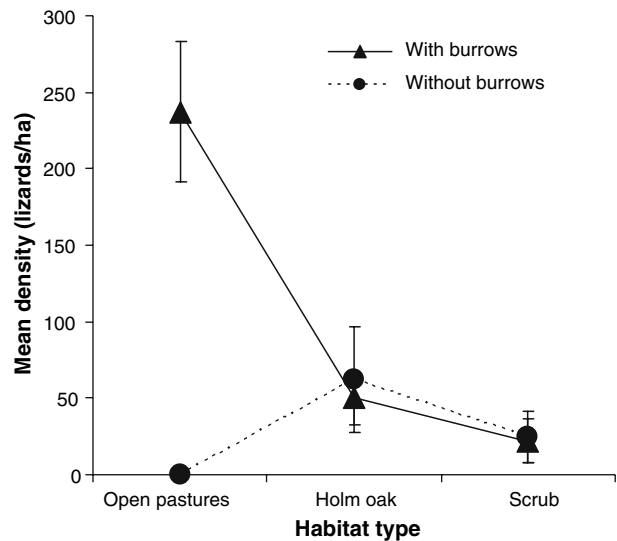
Lizard density was influenced by habitat type and burrow presence and their interaction (habitat \times burrow presence) (Table 2). Density was highest in open areas with burrows and lowest in scrub areas both with and without burrows (Fig. 2), and was positively correlated with number of burrows ($r = 0.513$, $P < 0.001$). Density of *A. erythrurus* was influenced by burrow presence, while *P. hispanicus* density showed a significant effect of habitat type (Fig. 3, Table 2). Density of both species increased with number of burrows (*A. erythrurus*: $r = 0.21$, $P < 0.05$; *P. hispanicus*: $r = 0.20$, $P < 0.05$). Density of *P. algirus* and *Po. hispanica* was not influenced by burrow presence or habitat type (Fig. 3, Table 2).

There were no significant differences in the proportion of males and females (χ^2 : 0.448, $P = 0.503$) or adults and juveniles (χ^2 : 1.429, $P = 0.232$) between areas with and without rabbit burrows (Table 1). Areas without burrows had equal numbers of males and females, and 68.9% of lizards were adults, 27.6% were subadults and 3.4% juveniles (Table 1), while areas with burrows had more females than males (61.8% and 38.2%, respectively; χ^2 : = 3.920, $P = 0.048$), and 73.44% of the individuals were adults, 20.31% subadults and 6.25% juveniles (Table 1).

Table 2 Results of two-way ANOVAs testing the effects of type of habitat and rabbit burrow presence on lizard densities, diversity parameters and snout-vent length (SVL)

	Habitat <i>F</i> (df = 2)	Burrow presence <i>F</i> (df = 1)	Interaction habitat × burrow presence <i>F</i> (df = 2)
Total lizard density	13.73***	8.32**	5.34**
Density <i>P. algirus</i>	1.13ns	0.02ns	0.25ns
Density <i>P. hispanicus</i>	8.27**	2.7ns	11.75***
Density <i>A. erythrurus</i>	0.48ns	5.43*	10.41*
Density <i>Po. hispanica</i>	0.80ns	0.31ns	1.51ns
Species richness	10.79***	18.99***	5.78**
Evenness	14.00***	2.47ns	1.69ns
Total lizard SVL	1.578ns	6.979**	3.979*

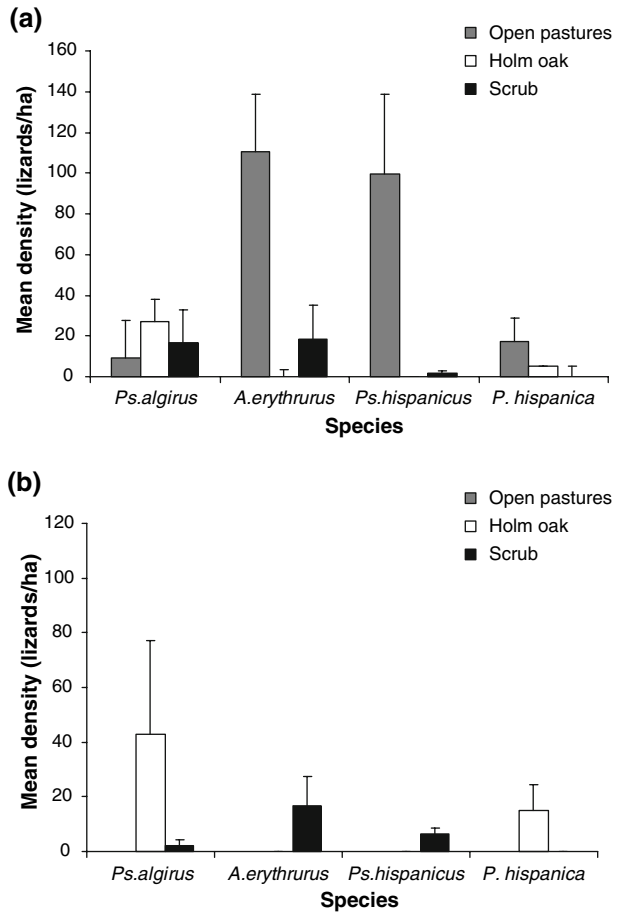
* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$, ns = not significant

Fig. 2 Mean (\pm SE) lizard density per habitat, in sites with and without burrows

Lizard adult snout-vent-length (SVL) was mainly influenced by burrow presence (burrow presence: $F = 6.979$, $P = 0.009$; habitat type: $F = 1.578$, $P = 0.211$; habitat × burrow presence: $F = 3.979$, $P = 0.049$). In general, lizards were larger in sites with burrows than in those without (Mean \pm SE = 5.20 ± 0.30 and 4.47 ± 0.21 , respectively). Correlations between body condition parameters and number of rabbit burrows were all non-significant (all $P > 0.05$), except for *P. algirus* weight in holm oak patches (weight: $r = 0.973$, $P = 0.013$) and *A. erythrurus* captured in open areas with burrows (SVL: $r = 0.845$, $P = 0.017$; total length: $r = 0.778$, $P = 0.034$; weight: $r = 0.845$, $P = 0.017$).

Out of 26 captured lizards, 13 individuals showed regenerated tails. There was no significant relationship between number of burrows and number of individuals with regenerated tails ($r = 0.182$, $P = 0.319$). Of 16 captured females, five were gravid (three *A. erythrurus* and two *P. algirus*), with an average of 2.2 eggs. All gravid females were captured in sites with rabbit burrows.

Fig. 3 Mean lizard densities (\pm SE) for individual species in (a) sites with burrows within each habitat, and (b) sites without burrows within each habitat



Lizard species richness was significantly influenced by presence of burrows and habitat type (Table 2). Mean species richness was higher in areas with burrows (Fig. 4). Evenness was only significantly influenced by habitat type (Table 2), and scrub areas with burrows showed the highest values (Table 1). There was a positive correlation between species richness ($r = 0.59, P < 0.001$) and evenness ($r = 0.44, P < 0.001$) with the number of rabbit burrows.

General use of burrows by Mediterranean vertebrates

Nineteen (61%) consulted experts responded to our questionnaire, 7 herpetologists and 12 mammologists. Reptiles and amphibians were the most frequent groups observed using rabbit burrows (Table 3). A total of 13 (68%) experts had observed lizards using rabbit burrows, mainly *Psammodromus algirus*, *Acanthodactylus erythrurus* and *Lacerta lepida*. Other groups observed inside rabbit burrows were rodents (5 experts, 26.3%), birds (4 experts, 21.1%), and carnivores (5 experts, 26.3%), including Iberian lynx kittens (*Lynx pardinus*; Jacinto Román, personal communication, Table 4).

Fig. 4 Mean species richness (\pm SE), per habitat, in sites with and without burrows

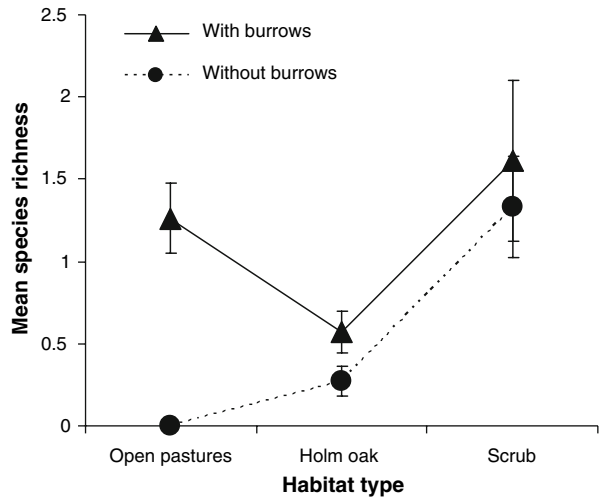


Table 3 Taxa observed by field experts inside rabbit burrows as reported in response to questionnaires

	Number of experts that have observed this species inside a rabbit burrow	% with respect to the total number of experts (19)
Reptiles and amphibians		
<i>Psammotromus algirus</i>	2	10.5
<i>Acanthodactylus erythrurus</i>	2	10.5
<i>Lacerta lepida</i>	5	26.3
Snakes (<i>Colubridae</i> , <i>Viperidae</i>)	11	57.9
<i>Bufo</i> spp.	5	26.3
Carnivores		
<i>Mustela putorius</i>	1	5.3
<i>Herpestes ichneumon</i>	4	21.1
<i>Meles meles</i>	2	10.5
<i>Vulpes vulpes</i>	3	15.8
<i>Lynx pardinus</i>	1	5.3
Rodents		
<i>Microtus</i> spp.	1	5.3
<i>Rattus</i> sp.	3	15.8
<i>Apodemus</i> sp.	3	15.8
Birds		
<i>Falco tinnunculus</i>	1	5.3
<i>Athene noctua</i>	4	21.1

Note that one expert may have sighted more than one species inside rabbit burrows

Resources provided by burrows

In open pasture areas with burrows (warrens), there was an overall positive and significant correlation of lizard abundance and number of rabbit burrows ($r = 0.557$, $P = 0.007$). A

Table 4 Mean temperature (°C) and relative humidity (%) inside and outside rabbit burrows

	Inside burrows	Outside burrows	T-test	P
Temperature (°C)				
Dawn	14.44	13.39	1.128	0.278
A.M.	24.25	25.21	-1.075	0.310
Noon	31.33	34.43	-3.129	0.005
P.M.	27.38	28.61	-2.598	0.016
T range	16.90	20.53	-2.596	0.041
Relative humidity (%)				
Dawn	72.25	68.07	1.716	0.108
A.M.	54.82	41.68	7.696	0.000
Noon	43.90	24.74	7.621	0.000
P.M.	47.31	26.47	5.925	0.000
T Range	29.14	43.40	-6.141	0.001

Significant ($P < 0.05$) results are indicated in bold

partial correlation controlling for the cover of holm oak branches above warrens confirmed this positive relationship ($r = 0.502$, $P = 0.017$). For individual species, correlations were especially significant in the case of *P. hispanicus* and *Po. hispanica* (*P. algirus*: $r = -0.217$, $P > 0.05$; *P. hispanicus*: $r = 0.492$, $P < 0.001$; *A. erythrurus*: $r = 0.352$, $P < 0.05$; *Po. hispanica*: $r = 0.732$, $P < 0.001$). Twenty-four lizards were observed using rabbit burrows as refuge to escape from researchers.

Arthropod abundance, richness and evenness did not differ significantly between areas with and without burrows (means \pm SE: 0.90 ± 0.19 and 1.02 ± 0.26 , respectively, $P = 0.684$). Formicidae was the most abundant family at both rabbit warrens and open pastures without burrows (60% and 50%, respectively), followed by Diptera (27% and 22%, respectively).

August temperatures measured inside and outside burrows did not differ significantly at dawn, but remained lower (in some cases up to 7°C lower) than outside throughout the day (Table 4). Total fluctuations in temperature inside burrows were significantly lower than outside (Table 4). Relative humidity was higher inside than outside burrows (Table 4). Even at noon, when outside humidity can drop to 11% under full sun conditions, burrows remain relatively moist (inside burrows at noon: min = 32.1%, max = 69.3%), and humidity values fluctuate significantly less than outside throughout the day (Table 4).

Discussion

To the best of our knowledge, this is the first study that attempts to describe the relationship between a burrowing mammal and the lizard community in Mediterranean ecosystems. Results show that there is a positive relationship between rabbit burrows and lizard presence; that resources provided by burrows are the base of this relation; and that rabbit warrens encourage lizard use of otherwise unsuitable habitat. As a consequence, lizard diversity increases in areas with burrows, including the most favourable habitats (holm oak and scrub patches, Table 1).

Lizard community parameters

Presence of lizards was positively related to rabbit burrows, and the main effects of burrow presence on abundance and density were found in open pasture areas, where no lizards were found unless rabbit burrows were present. Habitat choice by lizards in managed ecosystems such as dehesas is probably influenced by the intensity of management decisions (Martín and López 2002). The degree of human intervention on vegetation structure (ploughing, mowing, scrub clearance), and grazing intensity, will all determine the availability of adequate microhabitats for lizards in a certain patch. Often, the range of operative temperatures for lizards can be very narrow (Adolph 1990), and structural heterogeneity within a habitat may be crucial to cope with variations in thermal conditions, especially under fluctuating Mediterranean climate conditions.

Our results on lizard habitat use in a dehesa agree with previous studies (Pollo and Pérez-Mellado 1991; Martín and López 2002) except for the use of open pasture areas. These authors had reported little or null use of open pasture areas by the lizard community, most likely due to the lack of sites for thermoregulation and/or appropriate retreat sites in the face of predators (Pollo and Pérez-Mellado 1991). In the present study, all species considered were present at least once in open areas with burrows (warrens), and no lizards were found in open areas unless rabbit burrows were available. Therefore rabbit warrens are encouraging individuals of all species to colonise patches that would otherwise be inaccessible for them.

Rabbit burrow availability seemed most relevant for *A. erythrurus* and *P. hispanicus*. The very high densities of these two lizard species at warren patches were surprising, since previous studies in dehesa ecosystems have identified their preference for patches with reduced grazing pressure and where shrub encroachment has occurred (Martín and López 2002). Results for *P. algirus* agree with other authors in their preference for holm oak patches (Díaz and Carrascal 1991; Martín and López 2002), and their low abundance in scrub. However, in the present study we observed a marked, almost significant, increase in the density of this species in scrub areas if rabbit burrows were present (Fig. 3a). *Po. hispanica* was the least abundant species in the study area, and was often only found in patches with high rock cover (personal observation), which concurs with previous information about habitat preferences of this species (Sousa and Pérez-Mellado 2002). Although *Po. hispanica* density did not differ between patches with and without rabbit burrows, in areas where burrows were present there was a significant relationship between them and the abundance of this species.

Sites with burrows had slightly higher proportions of females and juveniles than sites without, and all captured gravid females were found in sites with rabbit burrows. The home range of gravid females tends to be relatively small (Perry and Garland 2002), so patches with rabbit burrows may be providing optimal microsites for gravid females. Also, given the more stable microclimatic conditions inside rabbit burrows, they could constitute appropriate egg-laying sites.

Larger lizards were usually found in areas with rabbit burrows, with heavier *P. algirus* individuals in their preferred holm oak patches. Additionally, *A. erythrurus* captured at larger warrens (i.e. with more burrows) were larger and heavier, suggesting a positive effect of burrow availability on the body condition of this species. No specific trends were found for *P. hispanicus* and *Po. hispanica*.

Open burrow systems are a major resource for many species, being an important source of local biodiversity (Kinlaw 1999; Whitford and Kay 1999). For instance, very different species assemblages are found on and off prairie dog colonies (Kretzer and Cully 2001;

Shiple and Reading 2006), and kangaroo rat mounds promote lizard diversity (Hawkins and Nicoletto 1992). The present study considered a community with four species, and identified significant effects of burrow presence on diversity parameters. Lizard species richness was significantly higher in areas with rabbit burrows in all habitats, and there is a trend of increased evenness of the lizard community with increasing number of rabbit burrows. Burrows therefore induce habitat partitioning in this ecosystem, especially since they are differentially used by certain species (*A. erythrurus* and *P. hispanicus*) and seem less important for other species (*Po. hispanica*).

General use of burrows by Mediterranean vertebrates

So far, we have shown that rabbit burrow presence and abundance can significantly influence a Mediterranean lizard community. Questionnaire responses from experts have supported our results. *P. algirus* and *A. erythrurus* have been observed using rabbit burrows by other scientists, and a larger lizard, *Lacerta lepida*, is also often reported. In fact, the most common taxonomic groups found using rabbit burrows are reptiles and amphibians, which is in agreement with detailed studies of prairie dog towns (*Cynomys ludovicianus*, Kretzer and Cully 2001) and pocket gopher colonies (*Thomomys* spp., Reichman and Seabloom 2002). Several birds and carnivores were also reported (Table 4). Particularly important is the association of rabbits with badgers (*Meles meles*) in Mediterranean environments. In a study of badger sett distribution in Doñana, south-western Spain, setts were found intimately linked to rabbit warrens, where over 80% of sampled badger setts originated from existing rabbit burrows (Revilla et al. 2001). Rabbit warrens have also been observed as refuge for endangered species such as Iberian Lynx (*Lynx pardinus*, CITES Appendix I) in southern Spain (Jacinto Román, personal communication), and the Hermann's tortoise (*Testudo hermanni*, CITES Appendix II) in Tuscany, Italy. This tortoise uses available rabbit burrows very often, mainly to spend the night, and also for short daytime rests (Calzolari and Chelazzi 1991).

Resources provided by warrens

Our results suggest that rabbit burrows increase the availability of several resources for the lizard community in the least favourable habitat. First, there was a positive correlation of lizard abundance with number of burrows. Second, we have presented direct evidence of lizards actively using rabbit burrows as refuge. Martín and López (2002) suggested that the traditional game-keeping practice of placing holm oak branches above warrens may provide shade and protection for lizards. However, partial correlations controlling for cover of branches showed that the relationship of lizard abundance with burrows remains strong, which suggests that burrows per se are an important resource for lizards.

We did not find a more abundant or diverse arthropod community linked to rabbit warrens compared with open areas without burrows, contrary to trends observed in other colonial systems such as those of prairie dogs (Bangert and Slobodchikoff 2006), and fairy-prions (Markwell and Daugherty 2002). There are problems inherent to any method of measuring prey availability, as stated by Wiens (1984). The limitations of our method, such as the fact that it measures relative rather than absolute abundances, could be part of the reason for this different trend. In dehesas, open pastures often harbour the highest prey abundances (Martín and Salvador 1995), whilst in disturbed and intensively grazed areas such as rabbit warrens one may expect to find lower abundances (Kruess and Tschantke

2002). However, mean arthropod abundances in this study (0.96 ± 0.12 arthropods per minute of search) were within the range recorded by Iraeta et al. (2006) at a “better” (1.71 ± 0.23) versus a “worse” (0.62 ± 0.23) site for *P. algirus*. Data are comparable because these authors used the same insect census technique as in the present study. This implies that at rabbit warrens lizards may be benefiting from a combination of factors: they have access to high prey abundances at both the warren and adjacent pastures, whilst reducing predation risk due to the high availability of safe retreat sites (burrows).

In addition, results have shown that lizards may also use rabbit burrows as thermally suitable retreat sites. Temperatures inside burrows at dawn were higher than those outside, and temperatures fluctuate less inside rabbit burrows, which suggests that they are more thermally stable. This implies that a lizard inside a rabbit burrow would be able to maximise the total time spent with a temperature closer to its preferred temperature, increasing energy gain or minimising metabolic costs (Huey et al. 1989). In the morning, a thermally optimal refuge is also important because lizards need a secure, insulated place to attain optimal temperature with no disturbance (Martín and Salvador 1995). Later in the morning, temperatures start rising inside burrows, but they always remain cooler than outside. Therefore, burrows are potential sites for thermoregulation during the day, and could be especially useful under the extreme heat conditions of the Mediterranean summer, when air temperatures can exceed 39°C and ground temperatures 47°C during midday. At this time, temperatures inside rabbit burrows can be up to 8.6°C cooler than outside (personal observation).

Relative humidity follows a similar trend to temperature, and burrow moisture never falls under 30%, whilst outside it can drop below 15% during the hottest daytime hours. Although lizards have tough, scaly bodies resistant to desiccation, their soft-shelled eggs are likely to suffer from hydric stress. Inside rabbit burrows, moisture is maintained throughout the day, so they are a potentially appropriate egg-laying sites.

Ectotherms are conditioned by a trade-off between thermal benefits, social advantages and predator avoidance (Downes and Shine 1998). Choice of retreat sites by lizards also implies energy budget and growth considerations (Bennet 1980), but, often, lizards have no choice but to prioritise refuge opportunities over thermoregulation constraints (Downes and Shine 1998; Amo et al. 2004). Rabbit burrows offer several advantages as retreat sites: they are thermally stable, can be used as refuge from predators and offer abundant prey.

Conservation of the lizard community: warrens as stepping stones

Dehesas have been shaped by human activities for centuries. Traditional management results in a mosaic distribution of resources which promotes high rabbit abundances (Blanco 1998), since they benefit from the protective cover of scrub and holm oak forest remnants, and food in the pasture areas (Rogers and Myers 1979). Contrary to expectations in such a humanised landscape, the herpetological fauna of Mediterranean dehesas is no less diverse than the equivalent climax holm oak forest woodlands that would exist without human management (Pérez-Mellado 1992).

However, the abandonment of traditional practices and uncontrolled land use changes may lead to the local extinction and/or isolation of populations of some species (e.g. *P. algirus*, Carretero et al. 2002a; Díaz et al. 2000). Other species, such as *A. erythrurus*, are likely to be affected by indiscriminate afforestation, which would increase cover and reduce insolation below their preferred threshold (Hódar 2002).

The abandonment of traditional land-use practices can be detrimental for both rabbits and lizards (Moreno and Villafuerte 1995; Martín and López 2002), especially if it results

in patch isolation, affecting connectivity between lizard subpopulations. The high lizard densities found in warrens situated in unsuitable open areas suggest that rabbit warrens could be acting as stepping stones, linking patches of favourable habitat and aiding/promoting lizard dispersal. Warrens could be mitigating the effects of land fragmentation and abandonment in two ways: (1) they may be useful “stopover sites” for dispersing juveniles which may enable them to cross the otherwise impermeable pasture matrix and reach new suitable patches; (2) they may constitute optimal habitat patches, thus becoming part of the home range of lizards.

This positive role of rabbits in Iberian ecosystems through ecosystem engineering adds up to their bottom-up relevance in Mediterranean food webs. Rabbit decline has been dramatic in the last decades due to disease, habitat fragmentation, land use changes and overhunting. There is a need to update the conservation classification of European rabbits in Mediterranean ecosystems since their status in the Iberian Peninsula meets the criteria of the “Vulnerable” IUCN category (Virgós et al. 2007). The only Mediterranean country where they have been included in a national Red List is Portugal. This update should spur more conservation efforts which will benefit species living in rabbit-dependent ecosystems, such as the lizards considered here.

In conclusion, our findings emphasize the need to study the ecological role of engineering activities by fossorial vertebrates. These animals are abundant in many ecosystems and their activities create new structures that modulate the availability of resources and/or alter environmental conditions for other taxa. In this study we found a positive effect of European rabbit warrens on density and diversity of reptiles. These positive effects were more intense in environments otherwise unfavourable for all species considered. Taking into account the influence of engineering activities increases our awareness of species interactions, and may translate into more adequate conservation measures for the preservation of biodiversity.

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