## Capítulo 4

# El conejo europeo como ingeniero de ecosistemas: los vivares aumentan la densidad y diversidad de lagartijas

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Lucía Gálvez Bravo, Josabel Belliure & Salvador Rebollo (*Under review in Biodiversity and Conservation*). European rabbits as ecosystem engineers: warrens increase lizard density and diversity.


### Resumen

El término "ingeniero de ecosistemas" es a menudo empleado para definir a aquellos mamíferos que construyen grandes colonias o "sistemas de madrigueras". Estos tienen la capacidad de modular la disponibilidad de los recursos, tanto para ellos mismos como para otros organismos. Las lagartijas pueden beneficiarse de la heterogeneidad creada por estas estructuras, especialmente si además se incluye un aumento de la oferta de lugares donde refugiarse y termorregular. Sin embargo, existe poca información sobre estos efectos ingenieros de los animales excavadores. En el presente capítulo se investigó la influencia de las madrigueras de conejo sobre varios parámetros de una comunidad mediterránea de lagartijas (abundancia, densidad, diversidad y condición corporal) en tres hábitats diferentes (pastizales abiertos, parches de encinas y parches de matorral). También se exploraron los posibles recursos que aportan las madrigueras para las lagartijas. Se encontró que las lagartijas estaban positivamente asociadas a las madrigueras, y que la presencia de madrigueras era condición esencial para la presencia de lagartijas en los hábitats más desfavorables. De hecho, parámetros de la comunidad como densidad y riqueza de especies fueron mayores en lugares con madrigueras de conejo. Las madrigueras pueden ser resultar muy relevantes para las lagartijas, y los resultados de encuestas enviadas a diversos expertos confirmaron que también pueden ser importantes para otros vertebrados. Los vivares constituyen zonas de una relativa abundancia de presas, y lugares apropiados para refugiarse y termorregular. Además, pueden tener implicaciones que van más allá, actuando como "estriberones" (corredores discontinuos), permitiendo que las lagartijas lleguen a parches de hábitat que de otro modo serían inaccesibles. Los resultados presentados demuestran que los vivares del conejo europeo ejercen una influencia positiva sobre la densidad y diversidad de lagartijas, y confirman el papel de los conejos como ingenieros de ecosistemas. Además, se resalta que tener en cuenta la influencia de las actividades de animales ingenieros aumenta el conocimiento de las interacciones entre especies, lo que puede luego traducirse en medidas más adecuadas para la preservación de la biodiversidad.

# 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 also explored the possible resources provided by burrows for lizards. 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.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. 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.

*Keywords*: burrows; dehesa; Mediterranean, *Oryctolagus cuniculus*; stepping stones

## 1. 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 & Kay 1999). Burrowing activities aerate soils, homogenise soil horizons, and may increase fertility and plant productivity (Markwell & Daugherty 2002). They promote the redistribution of resources and increase allochtonous 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 & Nicoletto 1992; Bangert & Slobodchikoff 2006), promote bird diversity (Lai & Smith 2003), influence grassland community composition (Whicker & Detling 1998), and benefit small mammals, reptiles and amphibians (Lomolino & 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 & 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 & Dauth 1987). Burrows also have higher humidity values than above-ground (Kay & Whitford 1978), which can be important for lizard egg development (Castilla & Swallow 1995; Ji & Braña 1999). Lizards are usually active foragers (McBrayer & 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 & 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). Great efforts have been made in recent years for rabbit conservation as the main prey of 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). Therefore, rabbit bottom-up relationships have received great attention, but their role as ecosystem engineers and 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*; Blázquez & Villafuerte 1990) and a tortoise (*Testudo Hermani*; Calzolai & Chelazzi 1991). Rabbit warrens, however, can be conspicuous (occupying an area of up to 850 $m^2$, 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 in show a preference for scrub cover and rocky outcrops, whereas grasslands or cultivated land constitute unfavourable habitats (Martín & 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.

## 2. Materials and methods

*Study area*

The present study was carried out in a 330 ha dehesa near Madrid, central Spain (40º 23´ N, 4º 12´ W). The climate is continental-Mediterranean. Mean altitude is 670m, and mean temperature and precipitation are 12ºC and 432.6 mm respectively (Ministerio de Agricultura 1989) but with strong interannual variations. 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 (7.6 warrens/ha) and a trashumant herd of about 600 sheep.

Four lacertid lizard species are abundant in the study area: *Psammodromus algirus*, *Psammodromus hispanicus*, *Acanthodactylus erythrurus* and *Podarcis hispanica*. *Ps.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 & Carrascal 1991; Carretero *et al.* 2002a ). *Ps. 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 (Pérez-Mellado 1998). *P. hispanica* is a medium-sized (adult snout-vent length 52-57mm, 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 & Pérez-Mellado 2002).

We identified three main habitat types within the study area: "scrub patches", "holm oak patches" and "open pasture patches". Scrub patches are areas of high scrub cover (min: 70%), mainly *Lavandula stoechas*, which are usually found on ridges and slopes. Holm oak patches are individuals or small groups of holm oak trees, often associated with small rocky outcrops, where basal resprouts 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 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).

*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 (**Table 1**). Rabbit burrows were counted at each sampling site. An average of 55.92 burrows were found in scrub areas, 3.9 in holm oak areas and 54 burrows in open pasture patches (warrens). The structural characteristics of each site (woody vegetation cover, rocks, bare ground and vegetation height) were recorded, and 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 (no differences, all $p>0.05$) and structural variables (no differences except for open pastures, which showed larger structural values in patches with than without burrows: $p<0.05$; $p > 0.05$ for the other habitats).

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 Diaz & 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 minutes, representing an equivalent sampling effort to surveys in scrub patches. All observed individuals were counted, annotating species, sex, age (adult / subadult / juvenile) and approximate snout-vent length (SVL) whenever possible. Counts took place on two different days at each site, 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. All captured specimens were

**Table 1.** Summary of general data from lizard surveys in 91 sampling sites. Data are shown for each habitat category. Note that we were unable to specify the species of two individuals.

| | **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 were 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 |
| *P.algirus* | 1 | 7 | 7 | 15 | 0 | 5 | 1 | 6 |
| *A.erythrurus* | 20 | 2 | 16 | 38 | 0 | 0 | 10 | 10 |
| *P.hispanicus* | 11 | 0 | 22 | 33 | 0 | 0 | 8 | 8 |
| *Po. hispanica* | 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 |

marked (red nail-varnish) to avoid recapture during the study period.

*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 & López 2002). Relative prey (arthropod) abundance was estimated by tossing 20 × 20 cm quadrats inside warren patches (open pastures 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 (Diaz & Carrascal 1991). This procedure was repeated 4 times at each patch. The role of burrows as refuge was assessed through direct observations of lizard use and 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 & López (2002), so the cover of these branches above rabbit warrens was also recorded.

Temperature and % relative humidity (RH) were measured inside and outside rabbit burrows (18 pairs of measurements at 6 warrens), using a thermo-hygrometer (HI9065-Hanna Instruments). 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*

Abundance and density of lizards were used to characterise presence of lizards at warrens, and use of burrows by vertebrates in general was explored using questionnaires sent to 31 Spanish experts (13 herpetologists and 18 mammalogists).

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. 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).

## 3. 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 burrows absolutely determined the presence of lizards in the case of open pasture areas (**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 (*Ps.hispanicus*: $r = 0.564$, $p < 0.001$; *A. erythrurus*: $r = 0.456$, $p < 0.001$; *P. hispanica*: $r = 0.210$, $p < 0.01$) except for *Ps. algirus* ($r = -0.083$, $p > 0.05$).

Lizard density was influenced by habitat type and burrow presence and their interaction (habitat × burrow presence) (**Table 2**). Density was highest in open areas with burrows and lowest in scrub areas both with and without burrows (**Figure 1**), and was positively correlated with number of burrows ($r = 0.513$, $p<0.001$). Density of *A.erythrurus* was influenced by burrow presence, while *Ps. hispanicus* density showed a significant effect of habitat type (**Figure 2, Table 2**). Density of both species increased with number of burrows (*A. erythrurus*: $r = 0.21$, $p < 0.05$; *Ps.hispanicus*: $r = 0.20$, $p < 0.05$). Density of *Ps. algirus* and *P.hispanica* was not influenced by burrow presence or habitat type (**Figure 2, Table 2**).

There were no significant differences in the proportion of males and females ($Chi^2$: 0.448, p = 0.503) or adults and juveniles ($Chi^2$ : 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; $Chi^2$ : = 3.920, p = 0.048), and 73.44% of the individuals were adults, 20.31% subadults and 6.25% juveniles (**Table 1**).

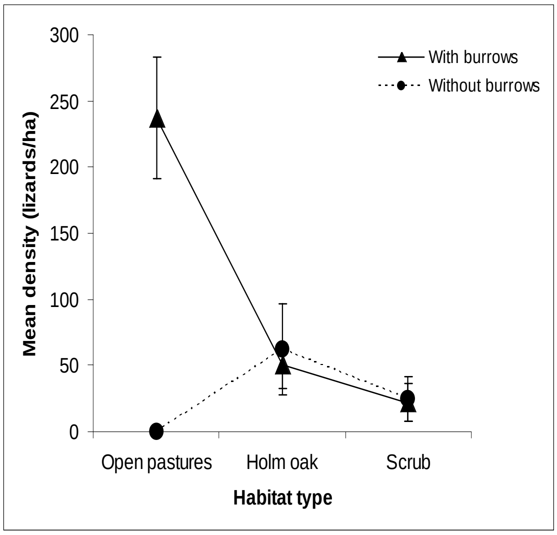


**Figure 1.** Mean (± S.E.) lizard density per habitat, in sites with and without burrows

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 ± s.e. = 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: $r = 0.778$, 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 *Ps. algirus*), with an average of 2.2 eggs. All gravid females were captured in sites with rabbit burrows.

Lizard species richness was significantly influenced by presence of burrows and habitat type (**Table 2**). Mean species richness was higher in areas with burrows (**Figure 3**). 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.

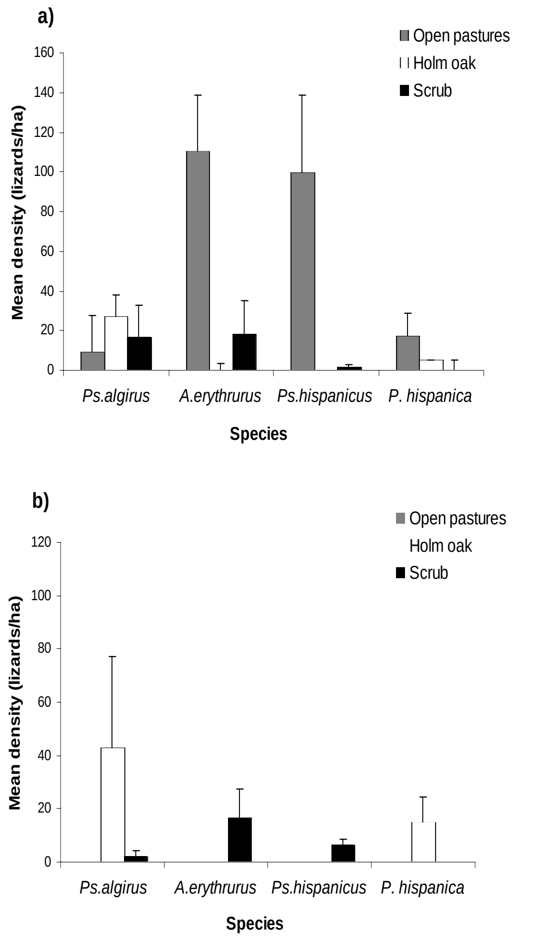


**Figure 2.** Mean lizard densities (+S.E.) for individual species in a) sites with burrows within each habitat, and b) sites without burrows within each habitat

*General use of burrows by Mediterranean vertebrates*

Nineteen (61%) consulted experts responded to our questionnaire. 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 3**).

*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 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 *Ps.hispanicus* and *P. hispanica* (*Ps. algirus*: $r = -0.217$, $p > 0.05$; Ps.hispanicus: $r = 0.492$, $p < 0.001$; *A. erythrurus*: $r = 0.352$, $p < 0.05$; *P. 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

**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). * = = 0.05; ** = p = 0.01; *** = p = 0.001, ns = not significant

| | **Habitat** | **Burrow presence** | **Interaction Habitat × Burrow presence** |
|---|---|---|---|
| | F (df = 2) | F (df = 1) | F (df = 2) |
| Total lizard density | **13.73*** ** | **8.32** ** | **5.34** ** |
| Density *P. algirus* | 1.13ns | 0.02ns | 0.25ns |
| Density *P. hispanicus* | **8.27** ** | 2.7ns | **11.75*** ** |
| Density *A. erythrurus* | 0.48ns | **5.43* ** | **10.41* ** |
| Density *Po. hispanica* | 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* ** |

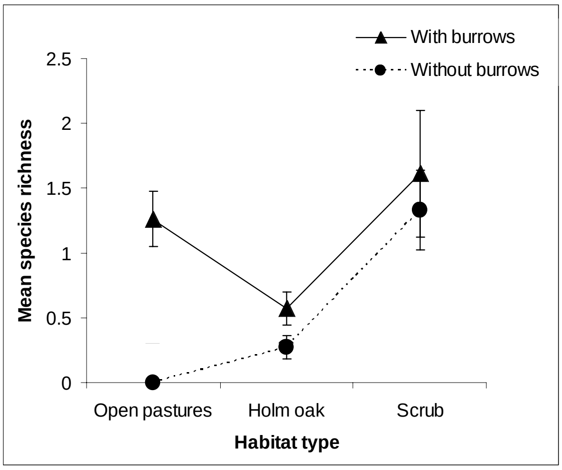


**Figure 3.** Mean species richness (± S.E.), per habitat, in sites with and without burrows

and without burrows (means ± 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).

Temperatures inside and outside burrows did not differ significantly at dawn, but remained lower (in some cases up to 7ºC 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 that outside throughout the day (**Table 4**).

## 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 humanized ecosystems such as dehesas is probably influenced by the intensity of management decisions (Martín & 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, specially under fluctuant Mediterranean climate conditions.

Our results on lizard habitat use in a dehesa agree with previous studies (Pollo & Pérez-Mellado 1991; Martín & 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 & 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. In general, there was a positive association of

**Table 3.** Taxa observed by field experts inside rabbit burrows as reported in response to questionnaires. Note that one expert may have sighted more than one species inside rabbit burrows.

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

lizard abundance and density with the number of rabbit burrows found at each sampling site, which suggests that burrow availability is allowing the coexistence of more individuals at a given habitat patch.

Rabbit burrow availability seemed most relevant for *A. erythrurus* and *Ps. 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 & López 2002). Results for *Ps. algirus* agree with other authors in their preference for holm oak patches (Díaz & Carrascal 1991, Martín & 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 (**Figure 2a**). *P. 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 & Pérez-Mellado 2002). Although *P.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 & Garland 2002), so patches with rabbit burrows may be providing optimal microsites for gravid females. Moreover, this could also be encouraging juveniles, since dispersal tends to be lower in high quality habitats, which in turn usually have higher lizard densities (Boudjemadi *et al.* 1999).

Larger lizards were usually found in areas with rabbit burrows, with heavier *Ps. 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 *Ps. hispanicus* and *P. hispanica*.

**Table 4.** Mean temperature (ºC) and Relative Humidity (%) inside and outside rabbit burrows. Significant (p< 0.05) results are indicated in bold.

| | Inside burrows | Outside burrows | T-test | *p* |
|---|---|---|---|---|
| **Temperature (ºC)** | | | | |
| 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** |
| Tº 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** |
| Tº Range | 29.14 | 43.40 | -6.141 | **0.001** |

Open burrow systems are a major resource for many species, being an important source of local biodiversity (Kinlaw 1999; Whitford & Kay 1999). For instance, very different species assemblages are found on and off prairie dog colonies (Kretzer & Cully 2001; Shipley & Reading 2006), and kangaroo rat mounds promote lizard diversity (Hawkins & 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. This, together with the observation that rabbit warrens in open areas support high lizard densities, suggests that burrows allow more individuals to coexist in the whole study area, especially in the case of *Ps.hispanicus* and *A.erythrurus*. Burrows therefore induce habitat partitioning in this ecosystem, especially since they are differentially used by certain species (*A. erythrurus* and *Ps. hispanicus*) and seem less important for other species (*P. hispanica*).

*General use of burrows by Mediterranean vertebrates*

So far, we have proved that rabbit burrow presence and abundance significantly influence a Mediterranean lizard community. Questionnaire responses from experts have ratified our results. *Ps. 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 & Cully 2001) and pocket gopher colonies (*Thomomys* spp., Reichman & Seabloom 2002). Surprisingly, 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 (Calzolai & 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 & 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.

Contrary to trends observed in other colonial systems such as those of prairie dogs (Bangert & Slobodchikoff 2006), and fairy-prions (Markwell & Daugherty 2002), we did not find a more abundant or diverse arthropod community linked to rabbit warrens compared with open areas without burrows. In dehesas, open pastures often harbour the highest prey abundances (Martín & Salvador 1995), whilst in disturbed and intensively grazed areas such as rabbit warrens one may expect to find lower abundances (Kruess & Tscharntke 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 *Ps. algirus*. 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). Further research into the arthropod community of rabbit warrens is therefore desirable, especially with respect to the Family Formicidae, the main prey items of *A. erythrurus*.

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, isolated place to attain optimal temperature with no disturbance (Martin & 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 39ºC and ground temperatures 47ºC during midday. At this time, temperatures inside rabbit burrows can be up to 8.6ºC cooler than outside (personal observation). Burrows thus provide lizards with appropriate sites to cope with extremely high temperatures during daytime (van Heerden & Dauth 1987; Kay & Whitford 1978), and allow lizards to extend the period of "elevated" body heat because they retain the day's warmth at night, when temperatures plummet (King 1980).

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 & 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 constrains (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. Relatively warm temperatures inside burrows during the coldest hours facilitate processes such as digestion and gonadal maturation, and opportunities to monitor and defend territories (Congdon *et al.* 1979).

*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, since they benefit from the protective cover of scrub and holm oak forest remnants, and food in the pasture areas (Rogers & 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. *Ps. 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 & Villafuerte 1995, Martín & López 2002), especially if it results in patch isolation, affecting connectivity between lizard subpopulations. This may have important implications for lizard communities, from effects on intraspecific interactions and reduced fitness of some individuals due to competition for resources (Lecomte & Clobert 1996), to local extinctions. 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 tampering 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. Also, the high densities and positive effects on lizard body condition observed at warrens could have implications for juvenile dispersal. These cues could be both attracting dispersers and encouraging juveniles to stay, according to the "public information hypothesis" (Doligez *et al.* 2002). Genetic studies that confirmed parental relationships of lizards found within a particular warren, or in nearby scrub and holm oak patches would help elucidate the exact role of warrens in the population dynamics of lizard species

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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## References

Adolph, S.C. (1990) Influence of behavioural thermoregulation on microhabitat use by two Sceloporus lizards. Ecology 71: 315-327.

Amo, L., López, P., & Martín, J. (2004) Trade-offs in the choice of refuges by common wall lizards: do thermal costs affect preferences for predator-free refuges? Canadian Journal of Zoology 82: 897-901.

Bangert, R.K. & Slobodchikoff, C.N. (2006) Conservation of prairie dog ecosystem engineering may support arthropod beta and gamma diversity. Journal of Arid Environments 67: 100-115.

Bauwens, D., Garland, T., Jr., Castilla, A.M., & Van Damme, R. (1995) Evolution of sprint speed in lacertid lizards: morphological, physiological and behavioral covariation. Evolution 49: 848-863.

Bennet, N.C. (1980) The thermal dependence of lizard behaviour. Animal Behaviour 28: 752-762.

Blázquez, M.C. & Villafuerte, R. (1990) Nesting of the Montpellier snake (Malpolon monspessulanus) inside rabbit warrens ate Doñana National Park (SW Spain): phenology and a probable case of communal nesting. Journal of Zoology 222: 692-693.

Boudjemadi, K., Lecomte, J., & Clobert, J. (1999) Influence of connectivity on demography and dispersal in two contrasting habitats: an experimental approach. Journal of Animal Ecology 68: 1207-1224.

Calvete, C., Villafuerte, R., Lucientes, J., & Osácar, J.J. (1997) Effectiveness of traditional wild rabbit restocking in Spain. Journal of Zoology 241: 271-277.

Calzolai, R. & Chelazzi, G. (1991) Habitat use in a central Italy population of Testudo hermanni Gmelin (Reptilia: Testudinae). Ethology, Ecology and Evolution 3: 153-166.

Carretero, M.A., Montori, A., Llorente, G.A., & Santos, X. (2002a). Psammodromus algirus In Atlas y Libro Rojo de los Anfibios y Reptiles de España (eds J.M. Pleguezuelos, R. Márquez & M. Liziana), pp. 259-261. Dirección General de Conservación de la Naturaleza, Madrid.

Carretero, M.A., Santos, T., Montori, A., & Llorente, G.A. (2002b). Psammodromus hispanicus. In Atlas y Libro Rojo de los Anfibios y Reptiles de España (eds J.M. Pleguezuelos, R. Márquez & M. Liziana), pp. 262-264. Dirección General de Conservación de la Naturaleza, Madrid.

Castilla, A.M. & Swallow, J.G. (1995) Artificial egg-laying sites for lizards: a conservation strategy. Biological Conservation 72: 387-391.

Congdon, J.D., Ballinger, R.E., & Nagy, K.A. (1979) Energetics, temperature and water relations in winter aggregated Sceloporus jarrovi (Sauria: Iguanidae). Ecology 60: 30-35.

Christensen, N.L. (1997). Manageing for heterogeneity and complexity on dynamic landscapes. In The Ecological Basis for Conservation: Heterogeneity, Ecosystems, and Biodiversity (eds S.T.A. Pickett, R.S. Ostfeld, M. Shachak & G.E. Likens). Chapman and Hall, New York.

Davis, J.R. & Theimer, T.C. (2003) Increased lesser earless lizard (Holbrookia maculata) abundance on gunnison´s prairie dog colonies and short term responses to artificial prairie dog burrows. American Midland Naturalist 150: 282-290.

Delibes-Mateos, M. (2006) Relaciones entre los cambios poblacionales del conejo, la gestión cinegética, el hábitat y los depredadores: implicaciones para la conservación, Universidad de Castilla-La Mancha, CSIC, Ciudad Real.

Díaz, J.A., Carbonell, R., Virgós, E., Santos, T., & Tellería, J.L. (2000) Effects of forest fragmentation on the distribution of the lizard Psammodromus algirus. Animal Conservation 3: 235-240.

Diaz, J.A. & Carrascal, L.M. (1991) Regional distribution of a mediterranean lizard: influence of habitat cues and prey abundance. Journal of Biogeography 18: 291-297.

Doligez, B., Danchin, E., & Clobert, J. (2002) Public information and breeding habitat selection in a wild bird population. Science 297: 1168-1170.

Downes, S. & Shine, R. (1998) Heat, safety or solitude? Using habitat selection experiments to identify a lizard´s priorities. Animal Behaviour 55: 1387-1396.

Gálvez, L., López-Pintor, A., De Miguel, J.M., Alonso, G., Rueda, M., Rebollo, S., & Gómez-Sal, A. (2008). Ecosystem engineering effects of European rabbits in a Mediterranean habitat. In Lagomorph Biology. Evolution, Ecology and Conservation (eds P.C. Alves, N. Ferrand & K. Hackländer), pp. 125-140. Springer-Verlag. Heidelberg-Berlin

Gea-Izquierdo, G., Muñoz-Igualada, J., & San Miguel-Ayanz, A. (2005) Rabbit warren distribution in relation to pasture communities in Mediterranean habitats: consequences for management of rabbit populations. Wildlife Research 32: 723-731.

Hawkins, L.K. & Nicoletto, P.F. (1992) Kangaroo rat burrows structure the spatial organization of ground-dwelling animals in a semiarid grassland. Journal of Arid Environments 23: 199-208.

Hódar, J.A. (2002). Acanthodactylus erythrurus. In Atlas y Libro Rojo de los Anfibios y Reptiles de España (eds J.M. Pleguezuelos, R. Márquez & M. Liziana), pp. 244-246, Madrid.

Huey, R.B., Peterson, C.R., Arnold, S.J., & Porter, W.P. (1989) Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. Ecology 70: 931-944.

Iraeta, P., Monasterio, C., Salvador, A., & Díaz, J.A. (2006) Mediterranean hatchling lizards grow faster at higher altitude: a reciprocal transplant experiment. Functional Ecology 20: 865-872.

Jefferies, R.L. (2000) Allochthonous inputs: integrating population changes and food web dynamics. Trends in Ecology and Evolution 15: 19-22.

Ji, X. & Braña, F. (1999) The influence of thermal and hydric environments on embryonic use of energy and nutrients, and hatchling traits, in the wall lizards (Podarcis muralis). Comparative Biochemistry and Physiology. Part A: Molecular and Integrative Physiology 124: 205-213.

Jones, C.G., Lawton, J.H., & Shachak, M. (1994) Organisms as ecosystem engineers. Oikos 69: 373-386.

Kay, F.R. & Whitford, W.G. (1978) The burrow environment of the banner-tailed kangaroo rat, Dipodomys spectabilis, in South-central New Mexico. American Midland Naturalist 99: 270-279.

King, D. (1980) The Thermal Biology of Free-Living Sand Goannas (Varanus gouldii) in Southern Australia Copeia 4: 755-767.

Kinlaw, A. (1999) A review of burrowing by semi-fossorial vertebrates in arid environments. Journal of Arid Environments 41: 127-145.

Kretzer, J.E. & Cully, J.F. (2001) Effects of black-tailed prairie dogs on reptiles and amphibians in Kansas shortgrass prairie. Southwestern Naturalist 46: 171-177.

Kruess, A. & Tscharntke, T. (2002) Contrasting responses of plant and insect diversity to variation in grazing intensity. Biological Conservation 106: 293-302.

Lai, C.H. & Smith, A.T. (2003) Keystone status of plateau pikas (Ochotona curzoniae): effect of control on biodiversity of native birds Biodiversity and Conservation 12: 1901-1912

Lecomte, J. & Clobert, J. (1996) Dispersal and connectivity in populations of the common lizard Lacerta vivipara: an experimental approach. Acta Oecologica 17: 585-598.

Lomolino, M.V. & Smith, G.A. (2003) Terrestrial vertebrate communities at black-tailed prairie dog (Cynomys ludovicianus) towns. Biological Conservation 115: 89-100.

Markwell, T.J. & Daugherty, C.H. (2002) Invertebrate and lizard abndance is greater on seabird-inhabited islands than on seabird-free islands in the Marlborough Sounds, New Zealand. Ecoscience 9: 293-299.

Martín, J. & López, P. (2002) The effect of Mediterranean dehesa management on lizard distribution and conservation. Biological Conservation 108: 213-219.

Martín, J. & Salvador, A. (1995) Microhabitat selection by thr iberian rock lizard Lacerta monticola: effects on density and spatial distribution of individuals. Biological Conservation 79: 303-307.

McBrayer, L.D. & Reilly, S.M. (2002) Prey processing in lizards: behavioral variation in sit-and-wait and widely foraging taxa. Canadian Journal of Zoology 80: 882-892.

Ministerio de Agricultura, P.y.A. (1989). Caracterización agroclimática de la provincia de Madrid, Madrid.

Moreno, S. & Villafuerte, R. (1995) Traditional management of scrubland for the conservation of rabbits Oryctolagus cuniculus and their predators in Doñana National Park, Spain. Biological Conservation 73: 81-85.

Moreno, S., Villafuerte, R., Cabezas, S., & Lombardi, L. (2004) Wild rabbit restocking for predator conservation in Spain. Biological Conservation 118: 183-193.

Pérez-Mellado, V. (1998) *Acanthodactylus erythrurus* (Schinz, 1834) En: Reptiles. Salvador, A. (Coord.) Fauna Ibérica vol. 10. Museo Nacional de Ciencias Naturales, Madrid.

Perry, G. & Garland, T.J. (2002) Lizard home ranges revisited: effects of sex, body size, diet, habitat and phylogeny. Ecology 83: 1870-1885.

Pianka, E.R. (1966) Convexity, desert lizards, and spatial heterogeneity. Ecology 47: 1055-1059.

Pielou, E.C. (1966) The measurement of diversity in different types of biological collections. Journal of Theoretical Biology 13: 131-144.

Pollo, C.J. & Pérez-Mellado, V. (1991) An analysis of a Mediterranean assemblage of three small lacertid lizards in Central Spain. Acta Oecologica 12: 655-671.

Reichman, O.J. & Seabloom, E.W. (2002) The role of pocket gophers as subterranean ecosystem engineers. Trends in Ecology and Evolution 17: 44 - 49.

Revilla, E., Palomares, F., & Fernández, N. (2001) Characteristics, location and selection of diurnal resting dens by Eurasian badgers (Meles meles) in a low density area. Journal of Zoology 255: 291-299.

Rogers, P.M. & Myers, K. (1979) Ecology of the European wild rabbit Oryctolagus cuniculus (L.) in Mediterranean habitats. I. Distribution in the landscape of the coto Doñana, S. Spain Journal of Applied Ecology 16: 691-703.

Shipley, B.K. & Reading, R.P. (2006) A comparison of the herpetofauna and small mammal diversity on black-tailed prairie dog (*Cynomys ludovicianus*) colonies and non-colonized grasslands in Colorado. Journal of Arid Environments 66:27-41.

Sousa, P. & Pérez-Mellado, V. (2002). Podarcis hispanica. In Atlas y Libro Rojo de los Anfibios y Reptiles de España (eds J.M. Pleguezuelos, R. Márquez & M. Liziana), pp. 244-246, Madrid.

van Heerden, J. & Dauth, J. (1987) Aspects of adaptation to an arid environments in free-living ground squirrels Xerus inauris. Journal of Arid Environments 13: 83-89.

Villafuerte, R., Lazo, A., & Moreno, S. (1997) Influence of food abundance and quality on rabbit fluctuations: conservation and management implications in Doñana National park (SW Spain). Revue d´ écologie -La Terre et la Vie 52: 345-356.

Whicker, A.D. & Detling, J.K. (1998) Ecological Consequences of Prairie Dog Disturbances. BioScience 38: 778-785.

Whitford, W.G. & Kay, F.R. (1999) Biopedturbation by mammals in deserts : a review. Journal of Arid Environments 41: 203-230.

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