

Habitat use and spatial behaviour in the European rabbit in three Mediterranean environments

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KEYWORDS

Doñana National Park;
Food quality;
Habitat selection;
Home range size;
Mediterranean ecosystems;
Oryctolagus cuniculus;
Predation risk; Prey behaviour; Resource availability

Summary

The abundance and behaviour of mammalian prey species such as the European rabbit (*Oryctolagus cuniculus*) are known to be regulated by the availability of both food for maintenance and reproduction and shelter for protection against predators and harsh weather. However, the effect of vegetation structure and temporal variations in food availability on habitat selection and spatial behaviour are still poorly understood. The present study investigated the relationship between rabbit spatial ecology and vegetation structure and food quality and quantity in three neighbouring areas in SW Spain that differed in the distribution and amount of refuge sites and food patches. In all, 35 rabbits were radiotracked in the three study areas and home range and core area sizes in different seasons and at different times of the day estimated. Spatial behaviour was then compared with parameters of vegetation cover and food quantity and quality. Lastly, rabbit habitat selection at two levels was studied: home range selection and selection within home ranges. Home range size varied from one study area and season to another, but was not dependent on either sex or the availability or quality of food. We suggest that differences in home range size between study areas respond to differences in vegetation cover, with smaller home ranges in areas with higher proportion of sheltering vegetation. It was found that habitat selection patterns varied between the three areas in terms of the need for rabbits to exploit to a maximum the scarcest resource in each situation, thereby optimising access to both feeding and refuge patches. This pattern was manifest at the home range level of habitat selection but not at the level of selection within home ranges. Findings were consistent with the high behavioural plasticity of the

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European rabbit in its native habitats and provide useful information for habitat management.

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Zusammenfassung

Die Abundanz und das Verhalten von Säugern, die wie das Europäische Kaninchen (*Oryctolagus cuniculus*) die Beute von Räubern werden können, werden bekanntermaßen durch die Verfügbarkeit von Nahrung für Lebenserhalt und Reproduktion sowie Unterschlupf zum Schutz vor Räubern und widrigem Wetter gesteuert. Der Einfluss von Vegetationsstruktur und zeitlichen Schwankungen der Nahrungsverfügbarkeit auf die Habitatwahl und das Raumnutzungsverhalten ist indessen immer noch unzureichend geklärt. Die vorliegende Studie untersuchte die Beziehung zwischen der Raumnutzung durch Kaninchen und der Vegetationsstruktur und der Nahrungsqualität und -menge in drei benachbarten Gebieten SW-Spaniens, die sich hinsichtlich der Verteilung und Menge von Zufluchtsorten und Nahrungsplätzen unterschieden. Insgesamt wurden in den drei Gebieten 35 Kaninchen mit Sendern ausgerüstet, und die Größen der Heimbereiche und ihrer Kerngebiete wurden zu verschiedenen Jahres- und Tageszeiten ermittelt. Das Raumnutzungsverhalten wurde dann mit den Parametern zur Vegetationsbedeckung sowie Nahrungsmenge und -qualität verglichen. Schließlich wurde die Habitatwahl der Kaninchen auf zwei Ebenen untersucht: Wahl des Heimbereiches und Wahl innerhalb des Heimbereiches. Die Größe des Heimbereichs variierte von einem Untersuchungsgebiet zum anderen und von einer Jahreszeit zur anderen, hing aber nicht vom Geschlecht der Tiere oder von der Nahrungsverfügbarkeit oder -qualität ab. Wir schlagen vor, dass die Unterschiede in der Heimbereichsgröße zwischen den Untersuchungsgebieten den Unterschieden in der Vegetationsbedeckung entsprechen, wobei die kleineren Heimbereiche in Gebieten mit einem höheren Anteil Deckung bietender Vegetation auftraten. Wir fanden, dass die Muster der Habitatwahl zwischen den Gebieten insofern variierten, als die Kaninchen die jeweils seltenste Ressource maximal ausbeuten mussten, wobei der Zugang zu Nahrungs- und Zufluchtsplätzen optimiert wurde. Dieses Muster war offenkundig für die Ebene der Habitatwahl, nicht aber auf der Ebene der Aufenthaltswahl innerhalb des Heimbereiches. Die Befunde stimmen mit der hohen Plastizität des Verhaltens des Europäischen Kaninchen überein und bieten nützliche Informationen für das Habitatmanagement.

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Introduction

Habitat selection is a decision taken by animals to satisfy vital requirements concerning food, shelter and reproduction (Bond, Burger, Leopold, Jones, & Godwin, 2002). Specific requirements are influenced by inherent characteristics of species such as life history traits, individual characteristics such as sex and age and by extrinsic environmental factors such as competition, predation pressure and seasonal food supply. For prey species, predation pressure represents one of the most important extrinsic factors influencing the spatial behaviour of individuals and habitat selection (Bos & Carthew, 2003; Kotler, 1997; Lima & Dill, 1990). During the last decade, ecologists have devoted great efforts to understanding the forces behind the selection of certain habitat types and the implications for predator avoidance. It has been noted that some

prey species benefit from adopting different habitat selection decisions in different environments in order to decrease vulnerability to predators (Lima, 1998).

Several studies have shown the ecological flexibility of the European rabbit (*Oryctolagus cuniculus*), a key prey species in Mediterranean ecosystems, and its ability to adapt behaviourally to predator pressure and food availability (Jaksic & Soriguer, 1981; Lombardi, Fernández, Moreno, & Villafuerte, 2003; Moreno, Villafuerte, & Delibes, 1996; Stott, 2003). Indeed, different aspects of rabbit biology such as activity rhythms, spatial and social behaviour and reproductive parameters are known to vary in accordance with the predation pressure that rabbit populations have to withstand. However, many of these studies have been performed in areas in which the European rabbit is an alien species and have focused on implications for

rabbit control and eradication (e.g. Moseby, De Jong, Munro, & Pieck, 2005; White et al., 2003). Other studies have focused on the effects of habitat structure on rabbit abundance, prompted by a concern for the species' decline in its native distribution area in light of the irruption of epidemic diseases (Fernández, 2005; Rogers & Myers, 1979). Paradoxically, neither rabbit spatial behaviour nor habitat selection has been sufficiently studied in Iberian Mediterranean ecosystems, where the species is native and of key importance in the conservation of numerous vertebrate predators. In these ecosystems rabbits constitute one of the most important trophic links for converting plant to animal biomass and are consumed by almost 30 predator species (Delibes & Hiraldo, 1981); just how rabbit habitat-use and spatial behaviour react to spatial and temporal variations in resource availability in different habitats is still unresolved. Addressing this question is crucial for a better understanding – and thus conservation – of vertebrate communities in Mediterranean ecosystems.

We investigated space use and habitat selection by European rabbits in their native range in a protected area in the south-west Iberian Peninsula. Our main goal was to examine how rabbits made use of three different areas, all in close proximity and all differing in vegetation cover, food availability and quality. Specifically, we aimed to test whether the use of space and habitat in the European rabbit was related to differences between areas in (1) cover of pasture patches providing food, (2) seasonal variability in food availability and quality and (3) shrub cover providing protection against predators. First of all, we analysed the home range size of rabbits with respect to sex, area, season and time of day (day or night), and then explored whether or not home range size was related to seasonal changes in food availability and quality. Previous studies have shown this relationship in some lagomorph species (Boutin, 1984; Hulbert, Iason, Elston, & Racey, 1996). Similarly, we expected that rabbits would increase their home ranges in areas and seasons in which food availability and quality decreased. Secondly, we tested for sexual differences in home range size that may arise from different land tenure and reproductive behaviour between males and females. The theory predicts larger home ranges for males in many mammal species and particularly in the European rabbit (Gibb, 1993), a fact which has been related to reproductive tactics aimed at maximising access to females (Cowan, 1987). Lastly, we analysed habitat selection both at home range level and within home ranges (i.e. the

second and third levels of selection, as per Johnson, 1980). We expected to find that patterns in habitat selection differed between the study areas in accordance with the optimal strategies for exploiting those vegetation patches providing the best access to the limiting resources present in each environment, i.e. pastures for food and dense vegetation for sheltering from predators.

Material and methods

Study area and the rabbit population

This study was performed in the north of the Doñana National Park (SW Spain; 3719° N, 6126° W). The climate is Mediterranean sub-humid with mild rainy winters and hot dry summers; rainfall is concentrated from mid-autumn to mid-spring (500–600 mm per year). The terrain is flat, at sea level and predominantly sandy.

The three study areas were separated from each other by about 2 km (Fig. 1) and differed in their vegetation composition and structure:

1. The scrubland is dominated by Mediterranean bush (*Pistacia lentiscus* L.) and scrub formations

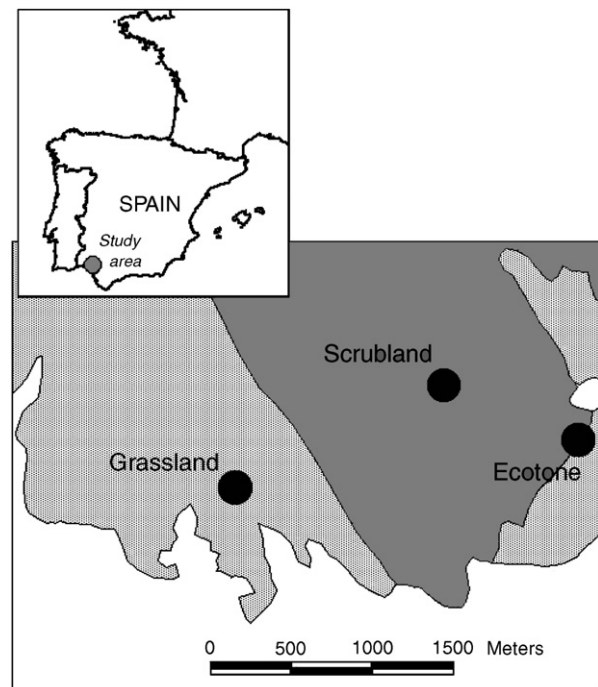


Figure 1. Location of the three study areas (circles) in the Doñana National Park, south-west Spain. The dark grey area represents scrub-dominated habitats, the light-coloured areas are grassland and white areas are marshland.

(*Halimium* spp., *Cistus* spp., *Ulex* spp., *Stauracanthus ginestoides*). Grass covers around 54% of the surface area, the remainder being largely occupied by bushes and scrub (43%) that provide abundant shelter for rabbits.

2. The grassland in open areas is dominated by short herbaceous vegetation (mainly Compositae and Gramineae) with scattered trees (*Quercus suber* and *Olea europaea*). Bush and scrub cover is only 10.5% of the area, while grass covers 88%.
3. The ecotone is the edge biotope lying between the Mediterranean scrubland and non-flooded pastures adjacent to the marshes. Bush and scrub cover is 22.5% and grass cover is 75%.

Rabbits live at different densities in these areas and are more abundant in the ecotone than in the other two areas (Lombardi et al., 2003). Predation pressure is high in the three study areas and a large number of carnivore and raptor predators such as Iberian Lynx (*Lynx pardinus*), Red Fox (*Vulpes vulpes*), Egyptian Mongoose (*Herpestes ichneumon*), Black Kite (*Milvus migrans*) and Bonelli's Eagle (*Hieraaetus fasciatus*), among others, all feed on rabbits. These predator species are found in all three study areas, although their hunting effectiveness varies according to the vegetation structure: raptors are more effective in open areas, while carnivores are better suited to habitats with more cover (Murray, Boutin, O' Donoghue, & Nams, 1995).

We defined the boundaries of the study areas as the minimum convex polygon encompassing all rabbit radiolocations in each area (see radiotracking procedures below). The resulting sizes were: scrubland 13.3 ha, ecotone 7.5 ha and grassland 20.6 ha (calculated from 1491, 1085 and 1045 independent rabbit radiolocations, respectively).

Estimate of food availability and quality

Pasture samples were collected in 1997 at the beginning of each season from ten plots of ca. 0.12 m² randomly distributed in each study area. The pasture was cut at ground level and samples were dried in a hot-air oven at 50 °C to constant weight and were then weighed. Food quality was estimated by measuring the protein content in the vegetation samples. The average percentage of the total dry weight due to raw proteins (PC) was measured using the Kjeldahl procedure, in which the protein content is calculated by multiplying the nitrogen content of each homogenised sample by a

factor of 6.25 to reflect the mean nitrogen content in the proteins (Holmes, 1980).

In a previous study, Lombardi et al. (2003) estimated the biomass available per hectare (BA) in the three study areas by measuring in the sample plots the amount of dry matter in the pasture layer and then correcting for the pasture cover in each area. In the present study, we additionally estimated the total protein availability in the herbaceous layer (PA, in kg/ha) by multiplying BA by PC. We used PA as an estimator of food availability based on its quality (Wallage-Drees, 1983) and hence derived information on the habitat quality needed to satisfy rabbits' nutritional requirements.

We tested the differences in protein availability between areas and seasons using repeated-measures ANOVA, introducing the season as the within-subject factor and the area as the between-subject factor. PA data were log transformed. Protein content (PC) was analysed using two-ways ANOVA. Analyses were performed using the GLM and GENMOD procedures in the SAS Statistical package (SAS Institute Inc., 1990).

Capture of animals and radiotracking

Rabbits were captured and radiotracked between April 1997 and June 1998. Rabbits were flushed out of their warrens by muzzled ferrets (*Mustela furo*) and then captured in nets. All animals were sexed by their external genitalia and weighed to determine their ages (Soriguer, 1981). Each rabbit was ear-marked with individually identifiable numbered metal tags and fitted with a radiotracking collar of ca. 20 g equipped with a posture activity sensor (Biotrack, Wareham, Dorset, United Kingdom).

Rabbits were radiotracked during four intensive periods of 30 days each, corresponding to the four different seasons of the year. All rabbits were located 2–3 times a day during these periods. In addition, they were routinely located three times a week in between these four intensive periods. Locations were performed by triangulating pairs of fixed stations. The location error estimated from experimental trials was ± 10 m. For the home range analyses we selected radiofixes separated by at least 6 h, in order to avoid any autocorrelation between consecutive locations (Lombardi et al., 2003). Plotting the size of home ranges vs. number of locations, we found that 15 locations were enough for obtaining a stable estimate of the size of a rabbit's home range.

Use of the space by the European rabbit

We analysed the home range size of 35 adult individuals with sufficient radiolocations (N between 30 and 60): 10 from the scrubland (3 males and 7 females), 14 from the ecotone (5 and 9, respectively) and 11 from the grassland (7 and 4). Home ranges were estimated using 90% fixed Kernel isolines (KI90), which were calculated with least-squares cross-validation and adjusted to extreme locations (Worton, 1989). Similarly, we estimated the 50% kernel isoline (KI50) to define core areas of high use intensity within home ranges. Home range and core area sizes were estimated for the full radiotracking period and for each season. We additionally calculated separate Kernel isolines for rabbit locations by day, i.e. between sunrise and sunset (N = 35 individuals), and at night, i.e. between sunset and sunrise (N = 19).

We first analysed the variability in home range size (KI90) and core areas (KI50) with respect to sex, area and season. Preliminary analyses indicated that first-order interactions were not significant and therefore were not further considered. Secondly, we tested to see if home range and core area size were correlated with changes in grass biomass availability (BM), protein content (PC) and/or protein availability (PA). Analyses were performed with generalised linear mixed models (GLMM—McCullagh & Nelder, 1989) using the GLIMMIX macro for SAS v. 8.02 (Littell, Milliken, Stroup, & Wolfinger, 1996; SAS Institute Inc., 1990). We fitted individual rabbit as random term in all models because some individuals were monitored during different seasons during the study period. We chose the error function that minimised deviance corrected by over-dispersion (in all cases it was the Poisson distribution and the log-link). The statistical significance of fixed effects was tested using Type III tests.

Habitat selection

We generated a detailed vegetation map of the three study areas from geo-referenced black-and-white aerial photographs at a scale of 1:2000. We differentiated four dominant vegetation types within grid cells of 20 m: (1) scrub (SC) dominated by *Halimium halimifolium*, *Ulex* spp. and *Stauracanthus ginestoides*; (2) bushes (BS) mostly dominated by *Pistacia lentiscus*; (3) pastures (PS) with grass and soils with low vegetation cover and (4) flooded areas (FL), mostly seasonal ponds with hydrophilic vegetation. The digital map was built and analysed using ArcInfo GIS v. 8.2 (ESRI, Inc., Redlands, CA, USA).

We then analysed habitat use with respect to availability for 35 rabbits at two different levels of selection: home range selection (second level of selection sensu Johnson, 1980) and habitat selection within home ranges (third level of selection). For the analyses of the home range selection, habitat availability was defined as the proportion of cover of each vegetation type within each study area, while habitat use was estimated as the proportion of each vegetation type within the KI90 home range. In the analyses of habitat selection within the home ranges, availability was defined as the proportion of cover within each home range and habitat use was defined as the proportion of independent radiolocations within each habitat type. Flooded patches were very poorly represented within home ranges and therefore we included them with pastures in the same vegetation class in the third-level habitat selection. In addition, we distinguished between daylight and night-time periods in the third-level selection analysis.

We employed compositional analysis (Aebischer, Robertson, & Kenward, 1993) to test habitat selection. To assess statistical significance we used Wilk's lambda (λ) transformed with the formula $-\ln \lambda$ (where N is the number of animals or radiolocations) and compared with probability values under the χ^2 distributions with $H-1$ degrees of freedom (where H is the number of habitat types considered). Habitat use was non-random if $P < 0.05$.

The order of habitat preference was obtained from the residual matrix following Aebischer et al. (1993) and its statistical significance was calculated by comparing the mean value and the standard deviation with a t-distribution (with $n-1$ degrees of freedom, where n was the number of territories or individuals used in the analysis). Compositional analysis was performed using the R v. 2.01 free statistical package (R Development Core Team, Vienna, Austria). For comparative purposes we also computed the Jacob's (1974) index for habitat preference (see Electronic Appendix A)

Results

Food availability and quality

The protein content of grasses differed between study areas ($F_{1,2} = 7.59$, d.f. = 2, 101; $P < 0.001$) and seasons ($F_{1,3} = 10.99$, d.f. = 3, 101; $P < 0.001$), but interaction was not significant ($F_{1,6} = 1.28$, d.f. = 6, 101; $P = 0.27$). Protein content tended to be higher

in the ecotone, decreasing in summer and reaching maximum values in winter in all three areas (Fig. 2A).

We also found differences in total protein availability between areas ($F_{19:01}$, d.f. 2, 81; $P=0.001$) and seasons ($F_{9:34}$, d.f. 3, 81; $P=0.001$) and interaction was significant ($F_{2:40}$, d.f. 6, 81; $P=0.035$). PA was highest in the grassland (110.64 kg/ha \pm 11.4 SE), intermediate in the ecotone (58.64 \pm 6.2 kg/ha) and notably lowest in the scrubland (26.67 \pm 2.6 kg/ha). The highest seasonal values of PA in the ecotone and grassland were found during the spring, while in the scrubland the highest value occurred in autumn. PA was at its lowest during the winter in all areas. The total protein availability in the grassland was higher than in the other areas in all seasons, although this value declined rapidly from spring to winter (Fig. 2B).

Space use

We found significant differences in rabbit home range and core area size between study areas and

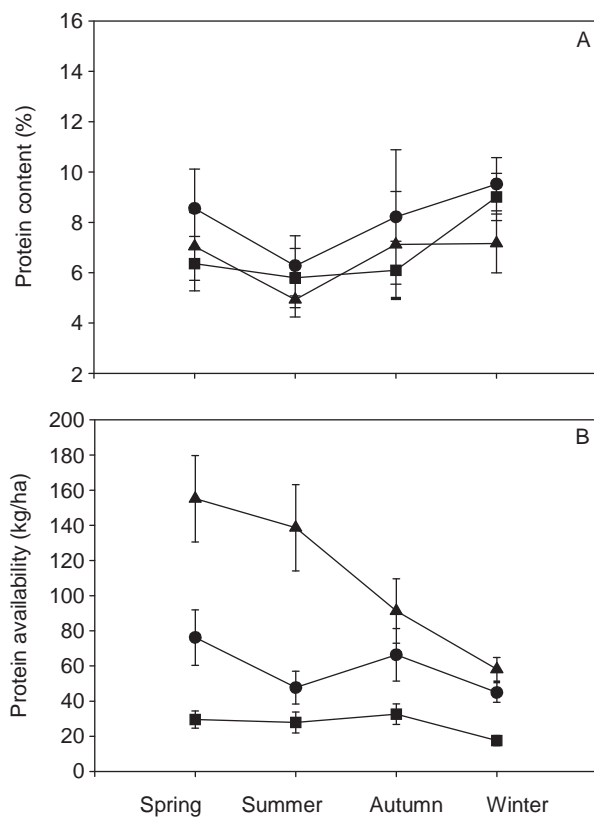


Figure 2. Average values (\pm standard error) of (A) protein content and (B) total pasture protein availability in the three study areas in Doñana. Squares: scrubland; circles: ecotone; triangles: grassland. Vertical lines indicate the standard error.

seasons, but not between sexes (Table 1). Home ranges and core areas were on average larger in the grassland and smaller in the ecotone; while larger areas and ranges were found in the spring (Fig. 3A; see Electronic Appendix A: Table 1). A second model relating home range size to food availability and quality indicated that differences in home range size were not significantly related to food availability and quality (Table 2); indeed, core area size was correlated with the total protein availability in the herbaceous layer (Table 2).

We found significant differences in the amount of area used by day and at night ($w^2_{11:46}$; $P=0.001$). Larger areas were used at night (mean 1.24 ha \pm 0.17 SE; N_{19} vs. 0.83 \pm 0.1 ha; N_{30}). The area of origin and interaction between time of day and area were also significant (all $w^2_{13:01}$; all $P=0.001$). Rabbits in the grassland and in the ecotone used larger areas at night, while in the scrubland they used slightly larger areas by day (Fig. 3B).

Home range habitat selection

Rabbits used the available habitats non-randomly in the three areas: scrubland ($-N \ln I_{11:471}$, d.f. 3, $P=0.001$), ecotone ($-N \ln I_{38:590}$, d.f. 3, $P=0.001$) and grassland ($-N \ln I_{96:364}$, d.f. 2, $P=0.001$). The compositional preference analysis indicated that pasture patches were most preferred in the scrubland and significantly different from bush patches (Table 3). In the ecotone, bush patches were preferred and flooded patches were avoided, while in grassland, where bushes were absent, scrub was the preferred habitat type and flooded patches were also avoided

Table 1. Generalised linear mixed models for home range size (KI90) and size of core areas (KI50) of European rabbits with respect to sex, area and season

Model effect	d.f.	w^2	P
HOME RANGE-KI90			
Sex	1	0.01	0.946
Area	2	10.53	0.015
Season	3	6.40	0.041
Individual: $Z_{2:13}$; P_{14} 0.017			
CORE AREAS-KI50			
Sex	1	0.01	0.925
Area	2	12.41	0.002
Season	3	23.62	0.001
Individual: $Z_{2:55}$; P_{14} 0.005			

Individual rabbits δN_{35} were included as a random term in the models. P-values ≤ 0.05 are shown in bold.

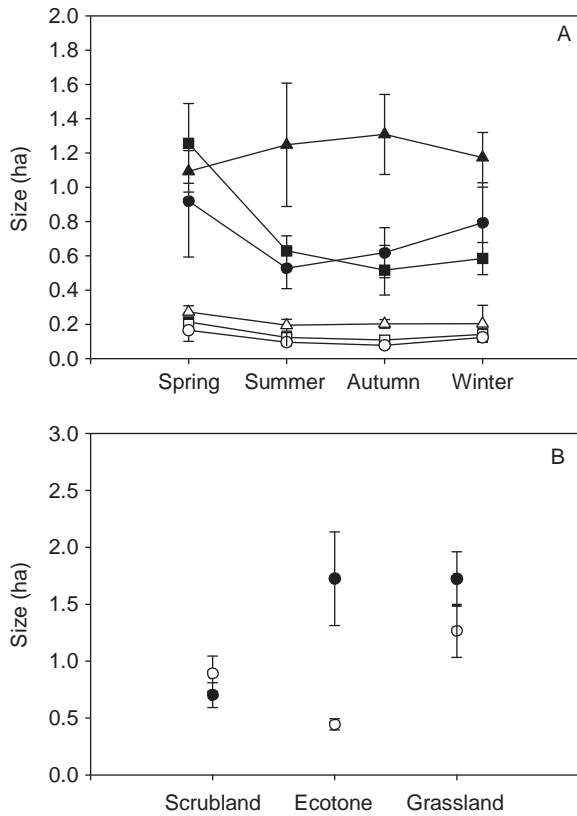


Figure 3. (A) Mean home range size (solid symbols) and core area size (open symbols) of European rabbits during four seasons at the three study areas. Squares: scrubland; circles: ecotone; triangles: grassland. (B) Area used by European rabbits in three habitat types by day (open symbols) and at night (solid symbols), measured with Kernel 90 isolines. Bars indicate the standard error.

Table 2. Generalised linear mixed models for home range size (KI90) and size of core areas (KI50) of European rabbits with respect to protein content (PC), biomass availability (BA) and total pasture protein availability (PA $\frac{1}{4}$ PC*BA) in the herbaceous layer

Model effect	d.f.	w ²	P
HOME RANGE—KI90			
PC	1	0.58	0.447
BA	1	0.01	0.907
PA	1	0.03	0.852
Individual: Z $\frac{1}{4}$ 1.84; P $\frac{1}{4}$ 0.033			
CORE AREAS—KI50			
PC	1	0.07	0.792
BA	1	1.34	0.247
PA	1	3.91	0.048
Individual: Z $\frac{1}{4}$ 2.28; P $\frac{1}{4}$ 0.011			

Individual rabbits $\delta N \frac{1}{4} 35\delta$ were included as a random term in the models. P-values ≤ 0.05 are shown in bold.

Table 3. Compositional preference order for home range selection and habitat selection within home ranges (SC $\frac{1}{4}$ scrub patches, BS $\frac{1}{4}$ bush patches, PS $\frac{1}{4}$ pasture patches, FL $\frac{1}{4}$ flooded patches)

Scale of analysis	Compositional preference order ^a
Home range selection	
Scrubland	PS 4 SC 4 BS//PS 4 BS
Ecotone	BS 4 SC 4 PS 4 FL
Grassland	SC 4 PS 4 FL
Habitat selection within home ranges	
Scrubland	
Day	PS 4 SC 4 BS
Night	SC 4 BS 4 PS
Ecotone	
Day	PS 4 BS 4 SC
Night	PS 4 BS 4 SC
Grassland	
Day	SC 4 PS
Night	SC 4 PS

^a **4** Indicates significant differences between groups (P ≤ 0.05).

(Table 3; see also Electronic Appendix A: Tables 2 and 3).

Habitat selection within home ranges

Habitat use within the home ranges did not significantly deviate from a random pattern in the scrubland by day ($-\text{N ln } \mathbf{1} \frac{1}{4} 0.311$, d.f. $\frac{1}{4}$ 2, P ≤ 0.05) and at night ($-\text{N ln } \mathbf{1} \frac{1}{4} 0.935$, d.f. $\frac{1}{4}$ 2, P ≤ 0.05 ; Table 3). However, we observed a non-random pattern of habitat use in the ecotone by day ($-\text{N ln } \mathbf{1} \frac{1}{4} 7.948$, d.f. $\frac{1}{4}$ 2, P ≤ 0.05), but not at night ($-\text{N ln } \mathbf{1} \frac{1}{4} 2.367$, d.f. $\frac{1}{4}$ 2, P ≤ 0.05). These differences are a product of the preference for patches of pasture and bushes over patches of scrub (Table 3). A similar pattern was found in the grassland (day: $-\text{N ln } \mathbf{1} \frac{1}{4} 13.545$, d.f. $\frac{1}{4}$ 1, P ≤ 0.05 ; night: $-\text{N ln } \mathbf{1} \frac{1}{4} 0.705$, d.f. $\frac{1}{4}$ 1, P ≤ 0.05). Here, scrub patches were preferred during daylight hours (Table 3; see also Electronic Appendix A: Tables 2 and 3).

Discussion

Our study indicates that differences in rabbit home range size are not attributable to variations in food availability between study areas and seasons. Other factors, probably related to the availability of refuges and predator avoidance, seem to be the cause for differences in spatial behaviour. Moreover, habitat selection analyses

suggest that rabbits are able to compensate for limitations in food and refuge availability in different environments by adapting habitat selection decisions at home range level.

Habitat correlates of home range size

We found no relationship between home range size and parameters of food quantity and quality in the European rabbit. Moreover, home range size was, on average, larger in spring, when the availability of high-quality food was greater, and in grassland, where pasture cover was highest. Therefore, our study does not support the idea that food availability is the prime factor regulating spatial behaviour in the European rabbit. On a more general level, food does not seem to be at present the chief factor regulating rabbit populations in Mediterranean environments. For example, the studied habitats supported much higher rabbit densities in the past under similar conditions of vegetation structure and food availability (Moreno & Villafuerte, 1995). However, rabbit densities have slumped over the last few decades as a consequence of the arrival of two infectious diseases, Myxomatosis and Rabbit Haemorrhagic Disease (Villafuerte, Calvete, Gortázar, & Moreno, 1994) and it has been suggested that the prevalence of these diseases interferes in the relationship between rabbit abundance and habitat structure (Fernández, 2005). Decreasing rabbit density certainly involves reduced competition for food in general and is probably the reason why in our study rabbits did not change their home ranges when the food supply fluctuated.

On the other hand, other factors such as the risk of predation and refuge availability seem to have a significant effect on rabbit spatial behaviour in Mediterranean habitats that contain a large number of predators. Rabbits were exposed to a rich variety of vertebrate predator species in the three study areas, some of which live at high densities. For example, up to 28 pairs of Black Kite and three pairs of Red Foxes per km² have been recorded in this area (Fedriani, Palomares, & Delibes, 1999; Forero, Donázar, & Hiraldo, 2002). We believe that under such predation pressure differences in home range size and core areas between the three habitats were a response to the availability of shelter providing predator avoidance and were only indirectly related to pasture availability.

For example, rabbits showed the largest home range and core area sizes in the grassland, despite the fact that biomass and total protein availability overall were greatest in these areas. However, in

these open areas refuges against predators are scarce and consist of just a few large burrows, while aboveground protective vegetation is scant (Lombardi et al., 2003; Palomares & Delibes, 1997). Under these conditions, locally high rabbit densities around burrows may reduce food availability in their vicinity and increase local competition, therefore forcing rabbits to move greater distances to forage. Indeed, rabbits in the grassland are often observed to forage far away from burrows at night (unpubl. data). In the ecotone, where grass biomass and total protein availability were intermediate between grassland and scrubland, rabbits had the smallest home ranges and core areas. The structure of the ecotone allows rabbits to optimise their spatial behaviour and to be able to easily access feeding and refuge patches. Burrows are congregated here along the border of the scrubland with pastures adjacent to the marsh. Therefore, rabbits have immediate access to both high-quality food in the pastures and to shelter in the scrubland, which is provided both by scrub vegetation cover and numerous burrows (Lombardi et al., 2003). This favours smaller home range size. Nevertheless, as in the grassland we also detected a greater use of space at night associated with foraging intrusions into the pasture areas.

In the scrubland, rabbit home ranges were intermediate in size. We expected that the lower biomass values and protein availability in the grass layer would lead rabbits to feed over larger areas, thereby compensating for the lack of food and its low quality (Hulbert et al., 1996). This prediction was shown to be false and food quantity and quality were poor predictors of home range size. Compared to the grassland, the scrubland provided the opposite conditions for rabbits: scrub provides abundant shelter and burrows are small, evenly distributed and less well-used (Lombardi et al., 2003). Rabbits here live in small groups and at low densities. We suggest that this implies lower local competition for food and that the existence of refuges was not a limiting factor: home ranges were thus smaller. Unlike the other two habitat types, rabbits in the scrubland used larger areas by day than at night. This might reflect the wide availability of refuge sites for resting and also the higher diurnal rabbit activity observed in this area, which seems to be related to predator avoidance (Lombardi et al., 2003; Moreno et al., 1996).

Lastly, we found no differences in home range size between the sexes. This contrasts with findings from previous studies, in which males tended to have larger home ranges (Cowan, 1987; Gibb, 1993). However, we found larger core areas in spring compared to winter, above all for male

rabbits, probably because of their increased mobility during periods of peak sexual activity and attempts to find mates.

Habitat selection

Our results support the idea that rabbits are highly flexible when selecting home ranges and show that selection decisions depend on the dominant vegetation structure in each particular area. Vegetation patches providing refuges were used in higher proportion than their availability by rabbits living in the ecotone and the grassland, although pastures – here, not a limiting factor – were used proportionally to their availability. On the contrary, pastures were the preferred habitat type in the scrubland, where this resource is scarcer.

We also found that flooded habitat patches were systematically avoided. These patches have the potential to provide good forage during the dry season, when pasture production is limited in other areas and rabbits can benefit from the proximity of ponds and lagoons where the water table is higher and green pastures survive longer. Indeed, [Fernández \(2005\)](#) found that rabbit abundance is higher in the vicinity of flooded areas. However, establishing home ranges within these areas can also be hazardous because heavy rains often cause high rabbit mortality ([Palomares, 2003](#)).

Rabbits did not show any clear habitat selection pattern within home ranges, above all in the scrubland where all vegetation types were used in proportion to their availability during both periods of the day. In the ecotone we only found a significant preference for bushes and pastures over scrub patches during resting periods. This can be explained by the distribution of burrows along the edge of the line between bushes and pastures, where rabbits spend most of the day (unpubl. data). In the grassland rabbits preferred scrub patches to pastures by day in accordance with their need for refuge habitat during resting periods.

Management implications

The European rabbit is a key prey species in the Mediterranean environments of the Iberian Peninsula and particularly in the Doñana National Park, which purely in terms of faunal richness is one of the most important protected areas in Europe. Some seriously threatened predator species such as the Spanish Imperial Eagle and the Iberian rely heavily on rabbit abundance for survival. One important conservation goal in this area is the

development of active vegetation management aimed at aiding the recovery of rabbit abundance, since it seems that other measures such as general area protection are not sufficiently effective for favouring rabbits and their predators ([Fernández, 2005](#)). The present study provides insights into how resource availability affects spatial behaviour and habitat selection in wild rabbits and can be used as a tool in local habitat management aimed at restoring rabbit populations in Mediterranean environments. As we have shown, the main limiting factor on rabbit populations in the three different environments seems not to be food, but refuge availability, which apparently influences both rabbit spatial behaviour and home-range habitat selection. These results reflect well anti-predator behaviour in environments where rabbits have to withstand high predation pressures, such as in the Doñana National Park ([Delibes & Hiraldo, 1981](#)). Therefore, a good combination of patches of scrub and pasture is vital for improving rabbit habitat and, as suggested by results from our three study areas, for regulating home range size. This agrees with [Gibb's \(1993\)](#) suggestion that food biomass per unit area is a poor (inverse) indicator of range size in rabbits and that it is more likely to be a combination of pastures for feeding and reproduction and shelter from predators and from weather harshness that decisively influences home range size. The importance of both vegetation types is also reflected at larger spatial scales and influences population abundance ([Fernández, 2005](#); [Fernández, Delibes, Palomares, & Mladenoff, 2003](#)). Therefore, vegetation management should aim to increase refuge availability and optimise access to scrubland and pastureland patches by generating networks of ecotones between these vegetation types within small spatial management units of around 1 ha. This will provide rabbits with the resources they need at the spatial scale of their home ranges.

Acknowledgements

This research was funded by the Spanish Dirección General de Investigación Científica y Técnica (project PB94-0480). L. Lombardi was funded by a grant from the University of Rome La Sapienza and N. Fernández by a FPI Research Grant from the Spanish Council for Scientific Research and a Marie Curie Host Fellowship provided by the European Commission (HPMD-CT-2001-00109). We are grateful to Alfonso Fernández and Gloria Portales for their help with the fieldwork. We would also like to

thank E. Angulo and two anonymous referees for their valuable comments and suggestions.

Appendix A. Supplementary Materials

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.baae.2006.09.004](https://doi.org/10.1016/j.baae.2006.09.004).

References

- Aebischer, N. J., Robertson, P. A., & Kenward, R. E. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology*, 74, 1313–1325.
- Bond, B. T., Burger, L. W., Jr., Leopold, B. D., Jones, J. C., & Godwin, K. D. (2002). Habitat use by cottontail rabbits across multiple spatial scales in Mississippi. *Journal of Wildlife Management*, 66, 1171–1178.
- Bos, D. G., & Carthew, S. M. (2003). The influence of behaviour and season on habitat selection by a small mammal. *Ecography*, 26, 810–820.
- Boutin, S. (1984). Effect of late winter food addition on numbers and movements of snowshoe hares. *Oecologia*, 62, 393–400.
- Cowan, D. P. (1987). Aspects of the social organisation of the European wild rabbit (*Oryctolagus cuniculus*). *Ethology*, 75, 197–210.
- Delibes, M., & Hiraldo, F. (1981). The rabbit as a prey in the Iberian Mediterranean ecosystem. In K. Myers, & C. D. MacInnes (Eds.), *Proceedings of the first world Lagomorph conference* (pp. 614–622). Guelph, Ont., Canada: University of Guelph.
- Fedriani, J. M., Palomares, F., & Delibes, M. (1999). Niche relations among three sympatric Mediterranean carnivores. *Oecologia*, 121, 138–148.
- Fernández, N. (2005). Spatial patterns in European rabbit abundance after a population collapse. *Landscape Ecology*, 20, 897–910.
- Fernández, N., Delibes, M., Palomares, F., & Mladenoff, D. J. (2003). Identifying breeding habitat for the Iberian lynx: Inferences from a fine-scale spatial analysis. *Ecological Applications*, 13, 1310–1324.
- Forero, M. G., Donazar, J. A., & Hiraldo, F. (2002). Causes and fitness consequences of natal dispersal in a population of black kites. *Ecology*, 83, 858–872.
- Gibb, J. A. (1993). Sociality, time and space in a sparse population of rabbits (*Oryctolagus cuniculus*). *Journal of Zoology (London)*, 229, 581–607.
- Holmes, W. (1980). *Grass, its production and utilization*. London, UK: Blackwell Scientific Publications.
- Hulbert, I. A. R., Iason, G. R., Elston, D. A., & Racey, P. A. (1996). Home-range sizes in a stratified upland landscape of two lagomorphs with different feeding strategies. *Journal of Applied Ecology*, 33, 1479–1488.
- Jacobs, J. (1974). Quantitative measurement of food selection. *Oecologia*, 14, 413–417.
- Jaksic, F. M., & Soriguer, R. C. (1981). Predation upon the European rabbit (*Oryctolagus cuniculus*) in Mediterranean habitats of Chile and Spain: A comparative analysis. *Journal of Animal Ecology*, 50, 269–281.
- Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61, 65–71.
- Kotler, B. P. (1997). Patch use by gerbils in a risky environment: manipulating food and safety to test four models. *Oikos*, 78, 274–282.
- Lima, S. L. (1998). Stress and decision making under the risk of predation: recent developments from behavioral, reproductive and ecological perspectives. *Advances in the Study of Behavior*, 27, 215–290.
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68, 619–640.
- Littell, R. C., Milliken, G. A., Stroup, W. W., & Wolfinger, R. D. (1996). *SAS system for mixed models*. Cary, NC: SAS Institute Inc.
- Lombardi, L., Fernández, N., Moreno, S., & Villafuerte, R. (2003). Habitat-related differences in rabbit (*Oryctolagus cuniculus*) abundance, distribution, and activity. *Journal of Mammalogy*, 84, 26–36.
- McCullagh, P., & Nelder, J. A. (1989). *Generalized linear models* (2nd ed). London: Chapman & Hall.
- 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., & Delibes, M. (1996). Cover is safe during the day but dangerous at night: The use of vegetation by European wild rabbits. *Canadian Journal of Zoology*, 74, 1656–1660.
- Moseby, K. E., De Jong, S., Munro, N., & Pieck, A. (2005). Home range, activity and habitat use of European rabbits (*Oryctolagus cuniculus*) in arid Australia: Implications for control. *Wildlife Research*, 32, 305–311.
- Murray, D. L., Boutin, S., O' Donoghue, M., & Nams, V. O. (1995). Hunting behaviour of a sympatric felid and canid in relation to vegetation cover. *Animal Behaviour*, 50, 1203–1210.
- Palomares, F. (2003). Warren building by European rabbits (*Oryctolagus cuniculus*) in relation to cover availability in a sandy area. *Journal of Zoology (London)*, 259, 63–67.
- Palomares, F., & Delibes, M. (1997). Predation upon European rabbits and their use of open and closed patches in Mediterranean habitats. *Oikos*, 80, 407–410.
- 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.
- Sas Institute Inc. (1990). *SAS/STAT user's guide*, version 6. Cary, NC: SAS Institute Inc.
- Soriguer, R. C. (1981). Estructuras de sexos y edades en una población de conejos (*Oryctolagus cuniculus* L.)

-
- de Andalucía Occidental. Doñana, *Acta Vertebrata*, 8, 225–236.
- Stott, P. (2003). Use of space by sympatric European hares (*Lepus europaeus*) and European rabbits (*Oryctolagus cuniculus*) in Australia. *Mammalian Biology*, 68, 317–327.
- Villafuerte, R., Calvete, C., Gortázar, C., & Moreno, S. (1994). First epizootic of rabbit hemorrhagic disease in free living populations of *Oryctolagus cuniculus* at Doñana National Park, Spain. *Journal of Wildlife Diseases*, 30, 176–179.
- Wallage-Drees, J. W. (1983). Effects of food on onset of breeding in rabbits, *Oryctolagus cuniculus* (L.), in a sand dune habitat. *Acta Zoologica Fennica*, 174, 57–59.
- White, P. C. L., Newton-Cross, G., Gray, M., Ashford, R., White, C., & Saunders, G. (2003). Spatial interactions and habitat use of rabbits on pasture and implications for the spread of the rabbit haemorrhagic disease in New South Wales. *Wildlife Research*, 30, 49–58.
- Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, 70, 164–168.

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