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Influence of herbaceous cover, shelter and land cover structure on wild rabbit abundance in NW Portugal

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The European wild rabbit *Oryctolagus cuniculus* (Linnaeus, 1758) populations in the Iberian Peninsula has suffered a serious decline. Therefore, the knowledge about the factors that influence rabbit distribution and abundance is of major interest for conservation and management programmes. Rabbit relative abundance was evaluated by pellet counting in relation to herbaceous ground cover, shelter availability (tall scrub cover and gaps in rocks) and land cover structure in the Peneda-Gerês National Park (PGNP), NW Portugal. Rabbit abundance was higher at intermediate levels of herbaceous cover, but no significant statistical differences were detected. A strong association between the abundance index and tall scrub cover was verified, and when this cover was rare, an association with gaps in rocks was observed. At the land cover level, rabbit abundance was associated with high interspersion sites of rocks with matorral and high interspersion sites of tall scrubland. Evidence from this study highlighted the importance of shelter and the interspersion of open/shelter habitats for rabbits. This pattern could be interpreted as an anti-predator strategy. Therefore, management actions should favour the growing and establishing of tall scrub patches and the selective cutting in highly continuous areas of tall scrub vegetation.

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Key words: *Oryctolagus cuniculus*, shelter, abundance, food, interspersion

Introduction

The European wild rabbit *Oryctolagus cuniculus* (Linnaeus, 1758) is native to the Iberian Peninsula (Arthur 1989). This lagomorph is a key species in its environments, since it is an important prey for a large number of predators, some of them threatened, eg Iberian lynx *Lynx pardinus* and the Imperial eagle *Aquila adalberti* (Delibes and Hiraldo 1981, Iborra *et al.* 1990, Palomares 2001a), and also an important game species (Rogers *et al.* 1994). However, rabbit populations are seriously depleted in result of several factors, largely habitat destruction, over-hunting and diseases, such as, myxomatosis and more recently RVH (rabbit viral haemorrhagic) disease (Blanco and Villafuerte 1993). In some depleted populations, generalist predators may exert a regulating influence on rabbits retarding their recovery (Trout and Tittensor 1989, Pech *et al.* 1992, Banks *et al.* 1998, Banks 2000). The investigation of which habitat factors influence rabbit distribution and abundance are crucial for management and recovery plans for its populations.

Distribution and abundance of rabbits have been studied in various Mediterranean regions of the Iberian Peninsula (Rogers and Myers 1979, Soriguer 1983, Moreno *et al.* 1996, Palomares *et al.* 1996, Martins and Borralho 1998, Palomares *et al.* 2001), but little in areas with different biogeoclimatic conditions, like the North of Portugal. In Mediterranean regions rabbits were more abundant in areas suitable for warren building or which could provide an abundant supply of tall shrub vegetation well interspersed with areas dominated by herbaceous vegetation and/or agricultural lands (Rogers and Myers 1979, Soriguer 1983, Moreno *et al.* 1996, Palomares *et al.* 1996, Martins and Borralho 1998, Palomares *et al.* 2001). Although, the interspersion factor, between openfield patches (utilized for foraging) and cover (utilized for refuge against predators), has been implicitly recognized in these studies, no attempt has been made to measure this variable in relation to rabbit abundance. A study carried out on a large scale in Spain concluded that the distribution and abundance of rabbits is related to soil and climate (Blanco and Villafuerte 1993). However, Fa *et al.* (1999) argued that on a smaller scale habitat conditions, such as availability of food and shelter, might be determinant.

The aim of this paper is to clarify the influence of herbaceous cover, shelter availability and land cover structure (with emphasis on the interspersion between open/shelter habitats) on rabbit abundance in a transition region between Atlantic and Mediterranean vegetation, at a local scale, within the NW Portugal.

Material and methods

Study area

The study was carried out in the Peneda-Gerês National Park (PGNP), NW Portugal, near Montalegre (41°49'N, 07°47'W). The region (4606 ha) is located in a plateau, interrupted by mountains and small valleys, where the dominant lithological type is the granite, between 800 and 1400 m in altitude. Vegetation falls in the transition zone between Ibero-Atlantic acidiphilous oak woodlands and Supra-Mediterranean vegetation (Ozenda and Borel 2000). The area is dominated by matorral scrub composed of *Erica cinerea*, *Ulex* sp. and *Chamaespartium tridentatum*, within a mosaic of oakwoods (*Quercus pyrenaica* and *Quercus robur*) interspersed with pastures, agricultural fields and patches of tall scrubs of *Genista* sp. and *Cytisus* sp. Annual rainfall is about 2000 mm and annual average temperature is between 7.5 and 10°C.

A land cover map was developed from rectified orthophotomaps (freely available in http//:ortos.igeo.pt/ortofotos), with a cell resolution of 16 m^2, by supervised classification for all pixels, in order to allow sampling procedures and land cover analysis (Fig. 1). Based on vegetation cover and land use, six land cover units were considered: deciduous forest, forest in regeneration, matorral, tall scrubland, pasture/agriculture fields, and rocks (a brief description of the land cover units is presented in Table 1). The map was extensively ground checked and corrected. Only minor corrections were required since the high resolution of the orthophotomaps allowed a precise classification.

Rabbit abundance

Pellet counts provide a simple and reliable means for estimating rabbit abundance (Palomares 2001b). We counted all the pellets observed along 86 belt transects of 400 × 4 m. The length of the transect was determined after initial trials. These trials revealed that rabbits were at very low densities, and for that reason, a longer transect was selected in order to maximize the detection of

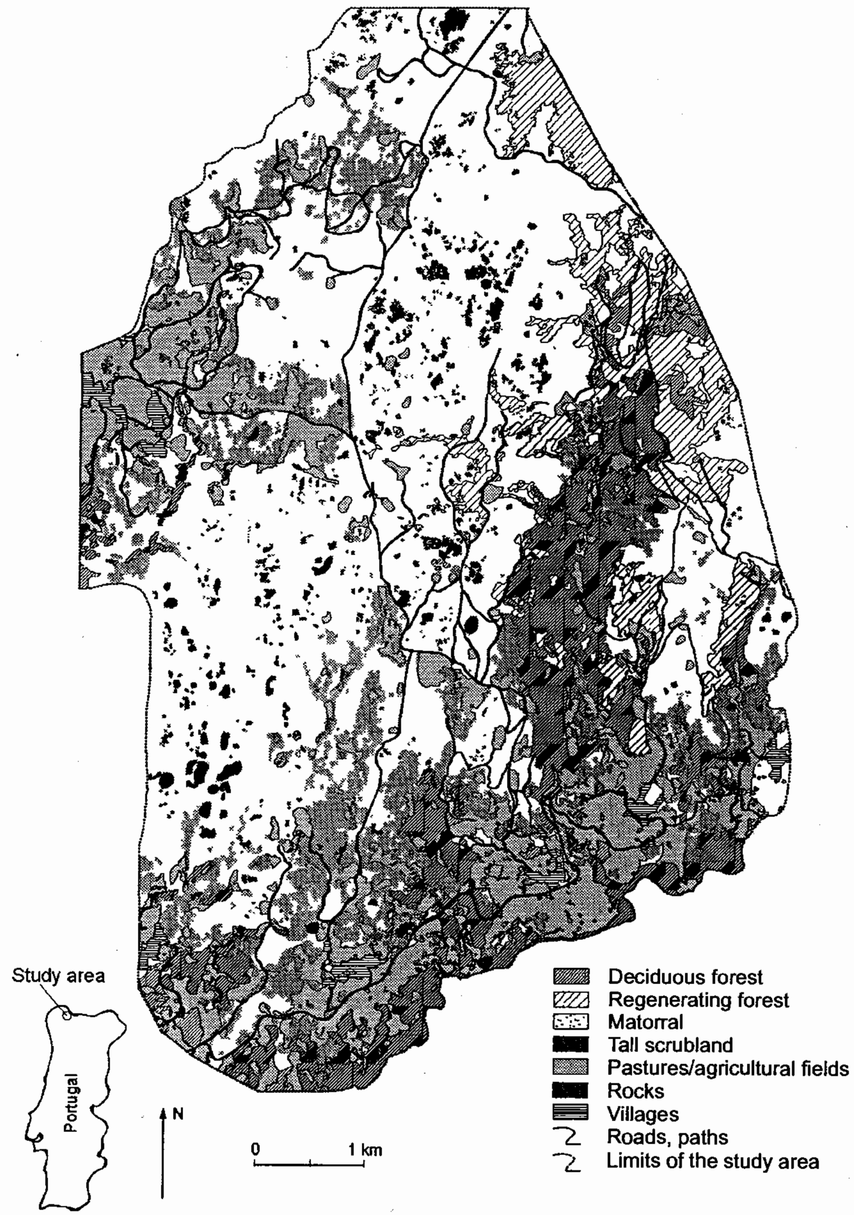

Fig. 1. Land cover map of the study area (northeastern part of Peneda-Gerês National Park), obtained by supervised classification of aerial ortophotomaps (1995 flight) and field validation.

Table 1. Land cover units description.

Land cover unit	Description	Occupied area (ha)	Percentage of the total area (%)
Deciduous forest	Patches of oakwood (*Quercus pyrenaica* and *Quercus robur*) with a mean tree height superior to 4 m. The understorey cover is mainly composed by *Ilex aquifolium* and *Crataegus monogyna*.	578.7	12.6
Regenerating forest	Patches of oakwood in regeneration after fire or cut, with a mean tree height inferior or equal to 4 m.	309.9	6.7
Matorral	Short scrubland dominated by *Erica cinerea*, *Ulex* sp. and *Chamaespartium tridentatum*; mean scrub height inferior or equal to 1 m.	2267.6	49.2
Tall scrubland	Patches of tall scrubs of *Genista* sp. and *Cytisus* sp. resulting from forest degradation or abandoned fields.	427.3	9.3
Pastures/agricultural fields	Fields of grassland utilized for grazing bovine cattle interspersed with cereal fields of *Solanum tuberosum*, *Secale cereale* and *Zea mays*.	688.9	15.0
Rocks	Emerged rocks of granite dispersed mainly in the matorral.	145.8	3.2
Others	Mainly small villages and roads.	187.5	4.0

rabbit pellets. The width of the transect was selected in order to maximize the observation of pellets by the researcher. The relative density of rabbits is expressed as the number of pellets/m^2.

Stratified sampling was followed by dividing the study area into 1 × 1 km units and randomly selecting one transect for each vegetal/landscape formation in each plot. The land cover map was used as a support for this procedure. In general, only those units covering more than 25% of the plot were sampled, although some minor units potentially used by rabbits were considered (rocks and patches of tall scrubland). A Global Positioning System (GPS; model Garmin 12XL, Garmin Corp., Olathe, Kansas, USA) was used to record the mean point position (ie the centre) of each transect. Only records with a GPS error lesser than 5 m were considered. When GPS error was greater than 5 m, we made subsequent records until the defined error limit was reached.

Herbaceous cover

Rabbits use a wide spectrum of foods, but mostly consume herbaceous plants (Soriguer 1988, Chapuis and Gaudin 1995). Seasonal and spatial variation in the diet of the wild rabbit in Portugal demonstrated also the importance of grass-forbs (Martins *et al.* 2002). These studies indicated that the genera *Lolium*, *Holcus*, *Bromus*, *Briza*, *Vulpia*, *Agrostis*, *Senecio*, *Echium* and *Leontodon* are usually consumed by rabbits. These plants are abundant in the herbaceous communities of the northeastern PGNP. By this reason we used the percentage of herbaceous ground cover as an index of food supply.

The sampling procedure consisted in dividing each belt transect into 10 (10 × 4 m) segments and estimating the percentage of herbaceous cover by visual observation following Higgins *et al.* (1996). These values were averaged for the 10 segments and then reclassified in 5 classes to reduce bias produced by visual estimation: 0–20%, 21–40%, 41–60%, 61–80%, 81–100%.

Shelter availability

Rabbits use tall shrub vegetation for refuge but could also use gaps between rocks (Rogers *et al.* 1994). Therefore, shelter availability was estimated by assigning to each transect, a class of percentage of ground covered by tall shrub vegetation, using the same procedure as for the estimation of herbaceous cover. Four classes of shelter availability were considered: 0–20%, 21–40%, 41–60%, > 60%. When shelter availability was = 20%, the presence or absence of other alternative refuges (gaps between rocks) was also recorded.

Land cover structure

The percentage cover by each land cover unit was measured on 3.14 ha circular plots (approximately the allometric home range of rabbits, Villafuerte 1994) around the mean point position (ie the centre) of each transect. Transects were located in sites where the immediately surrounding vegetation was similar to the area covered by the circular plot. Therefore, we assumed that the land cover data evaluated in the circle was representative of the surface crossed by the transect.

The interspersion between food patches and shelter patches was determined by the index of Patton (described in Litvaitis *et al.* 1996). This index measures the irregularity of a patch, based on the area-to-perimeter ratio of a circle, and has the following form:

$$I = P/2(\pi A)^{1/2}$$

where P is the perimeter of the edge between shelter patches (tall scrubland, rocks and forest) and foraging patches (pasture/agricultural fields and matorral) and A is an area of reference of 3.14 ha. All variables were estimated by GIS analysis with the software package MF-Works, version 2.6.3 (Keigan Systems, London, Ontario, Canada).

Statistical analysis

After testing the normality of the frequency distribution of the data on pellet-counts with the Kolmogorov-Smirnov test, the non-parametric analysis of variance (Kruskal-Wallis test) was chosen for detecting statistical differences between herbaceous cover and shelter availability; pairwise comparisons were made by Dunn test. Mann-Whitney *U*-test was also used to compare sites without any shelter alternative to shrubs and sites with alternative refuge (gaps between rocks). All these statistical procedures were performed in the Prism (version 3) software package (Motulsky 1999) with a significant level of 0.05.

The multidimensional characteristic of the land cover data requires a multivariate approach, in order to avoid the problem of the non-independence of variables. Therefore, a PCA (Principal Component Analysis) was performed from the land cover data. PCA creates independent factors which are a linear combination of the original variables. Prior to the PCA, land cover variables were arcsine transformed (Zar 1998). The PCA factors obtained were related with the rabbit relative abundance index, using the Spearman correlation coefficient, so that the distribution of the species could be described in relation to the land cover structure. Nevertheless, in order to search for humped shaped relationships between rabbit abundance and land cover data, non-parametric regression smoothing was used. These methods provide versatile techniques to explore general non-linear relationships between two variables (Hardle 1990). The LOWESS (LOcally WEighted Scatter plot Smoothing) was used to describe the relationship between the rabbit relative abundance (ie response variable) and the PCA factors (ie explanatory variables). The LOWESS technique is a k-nearest neighbour smoother adequate for handling data sets with outliers and a "noisy" relationship between variables, like the one here reported (for more details see Hardle 1990). PCA and LOWESS analysis were performed using the software ADE-4 (Thioulouse *et al.* 1997). The ADE-4 allows to select the number of neighbours, to use in the LOWESS procedure, in order to minimize the average error of the smoother curve in relation to the observed data.

Results

Herbaceous cover and shelter availability

A total of 86 transects was surveyed. Pellets were found in 40 transects (46.5%) with a mean relative density of 1.83 pellets/m^2 (SD = 3.71). Frequency distribution of data on pellet counts was not normally distributed (Kolmogorov-Smirnov test: $D = 0.3249, p < 0.0001$) justifying the choice for non-parametric statistical tests.

Rabbit abundance was highest at intermediate levels of herbaceous cover (the maximum abundance was found in the class of 41–60%), suggesting a possible humped shaped relationship between the two variables. A remarkable low value of rabbit abundance was observed in the highest class of herbaceous cover. Nevertheless, abundance of rabbits was highly variable (large SD values) and no significant statistical differences were found among the five classes considered (Table 2).

Results on pellet counts indicated that mean relative rabbit densities increased with increasing tall scrub cover. Statistical differences were detected among the 4 classes of percentage of ground covered by tall scrubs. Interclass comparisons with Dunn test showed significant differences between the two major classes (41–60% and > 60%) and the minor class (0–20%) of tall scrub cover (Table 2).

In places where tall shrub cover was = 20%, rabbits were more abundant when an alternative shelter existed (gaps between rocks). Mean (± SD) relative density of rabbits was 0.27 ± 0.93 pellets/m^2 in areas with no gaps between rocks ($n = 40$), and 1.23 ± 2.17 pellets/m^2 in areas with gaps between rocks ($n = 16$). These differences were statistical significantly (Mann-Whitney U-test: $U = 155.50, p < 0.05$).

Land cover structure

From the PCA on the land cover data, three factors were retained for subsequent analysis. The three PCs explain 66.6% of the total variance (Table 3). The first

Table 2. Comparison of mean relative densities of rabbits (pellets/m^2) as a function of 5 classes of percentage of herbaceous cover and 4 classes of percentage of tall scrub cover.

Variable	Class (%)	n	Mean ± SD	Kruskall-Wallis test		Dunn test – significant different pairs ($p < 0.05$)
				H	p	
Percentage of herbaceous cover						
	0–20	10	1.99 ± 2.81			
	21–40	18	2.17 ± 4.53			
	41–60	23	2.44 ± 4.47	8.273	ns	none
	61–80	13	2.35 ± 3.87			
	81–100	22	0.59 ± 1.92			
Percentage of tall scrub cover						
	0–20	56	0.64 ± 1.81			
	21–40	6	1.55 ± 2.14	25.158	< 0.0001	0–20% vs 41–60%
	41–60	18	3.56 ± 4.61			0–20% vs > 60%
	> 60	6	8.12 ± 6.80			

Table 3. Results of PCA from land cover data. The correlation between the original variables and the 3 first PC factors, along with eigenvalues and the cumulative percentage of variance explained, are presented.

Variable	PC-1	PC-2	PC-3
Eigenvalue	1.8798	1.5968	1.1867
Cumulative % of variance	26.9	49.7	66.6
% cover by deciduous forest	−0.5837	0.1813	0.5653
% cover by regenerating forest	0.0160	0.0159	0.5115
% cover by matorral	0.5970	−0.7393	−0.1862
% cover by tall scrubland	0.2305	0.6667	−0.4388
% cover by pasture/agricultural fields	−0.6799	0.1217	−0.4388
% cover by rocks	0.5996	0.1106	0.2686
Interspersion	0.5896	−0.6793	0.2123

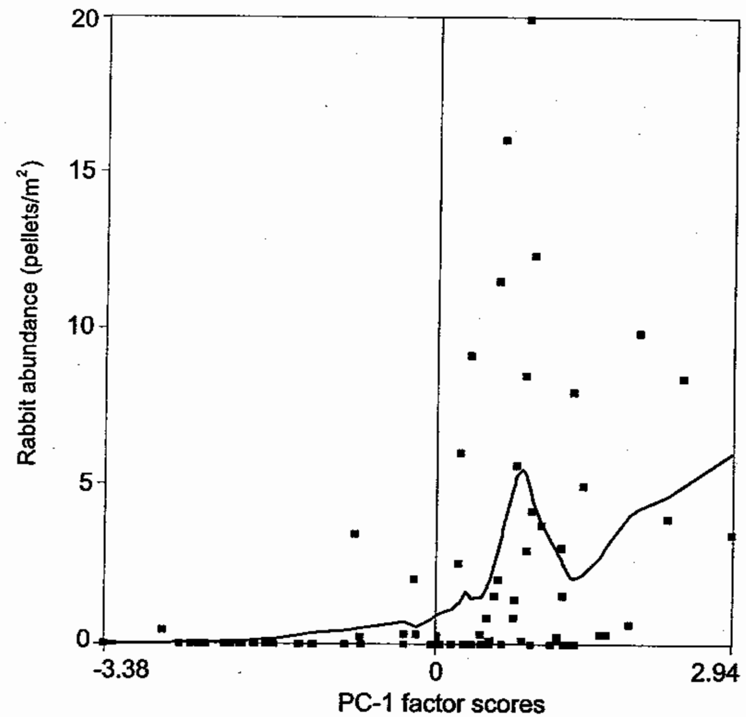

Fig. 2. Relationship between rabbit abundance (pellets/m^2) and the first PCA factor. A LOWESS smoother curve is superposed. The vertical line in the middle of the graph separates negative and positive PC factor scores.

factor shows a gradient from sites characterized by a high interspersion between matorral and rocks (positive scores) towards sites dominated by continuous areas of deciduous forest and pastures/agricultural fields (negative scores). The second factor describes a gradient from high interspersion sites of tall scrubland (positive scores) to sites dominated by continuous areas of matorral (negative scores). The third factor generates a gradient from places dominated by tall scrubland and pastures/agricultural fields (negative scores) towards places dominated by deciduous forest and forest in regeneration (positive scores). The rabbit relative abundance index is significantly correlated with the first two factors ($r_S = 0.5575, p < 0.0001$ for PCA-1; $r_S = 0.4633, p < 0.0001$ for PCA-2), but was not correlated with the third factor ($r_S = -0.1810, p > 0.05$).

In Figs 2 and 3, two scatterplots of rabbit relative abundance index versus PCA – scores (factor one and two) are presented. Superposed are LOWESS smoother curves which allow a more easily interpretation of the relationship between variables. Hence, higher pellet densities were clearly associated with positive scores of the first and second factors.

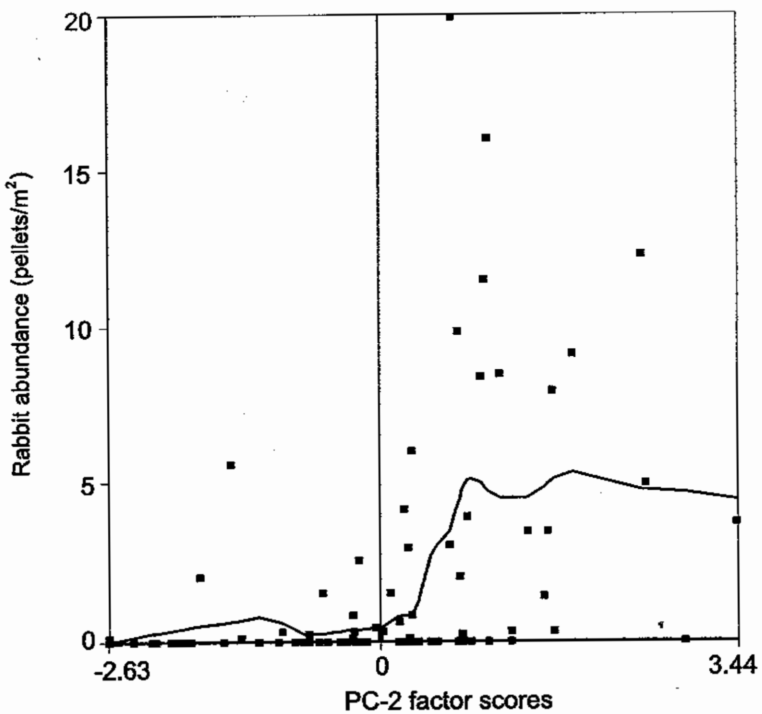

Fig. 3. Relationship between rabbit abundance (pellets/m^2) and the second PCA factor. A LOWESS smoother curve is superposed. The vertical line in the middle of the graph separates negative and positive PC factor scores.

Discussion

In Mediterranean regions, habitat selection by rabbits may be determined by a compromise between food availability and protection from predators (Moreno *et al.* 1996) provided both by bushes and warrens (Palomares and Delibes 1997). In the northeastern PGNP, rabbit abundance seems to have a humped shaped relationship with an index of food supply (percentage of herbaceous cover). This means that rabbits are less abundant in places where herbaceous cover reaches extreme values. Low herbaceous cover could be a limiting factor when rabbits are at high densities, since it may result in a food shortage. High herbaceous cover are associated with openfield, where shelter is not available, and rabbits are more vulnerable to predation (by humans and native predators) (Lombardi *et al.* 2003).

Despite the above considerations, a highly variable response of rabbits to herbaceous cover, in the northeastern PGNP, was observed (large SD values), so that no significant statistical differences were found. This could be a consequence of two factors. Firstly, rabbit abundance appears to be very low in comparison with previous studies. The mean and maximum pellet densities recorded in our study area were well bellow the values recorded for southern Spain and southern France (Rogers and Myers 1979, Rogers 1981, Palomares *et al.* 1996, Fa *et al.* 1999). Hence, rabbit populations in northeastern PGNP are probably far from the habitat carrying capacity limit in food supply terms. Secondly, the northeastern PGNP is situated in a transition area between Ibero-Atlantic acidiphilous oak woodlands vegetation and Supra-Mediterranean vegetation (Ozenda and Borel 2000) and seasonality of rainfall and herbaceous vegetation production are not so marked as in Mediterranean habitats. Therefore, the availability of herbaceous plants for rabbits to eat is probably more limited in Mediterranean regions. However, it should be noticed that only the percentage of ground cover by herbaceous plants was estimated and related with rabbit abundance in this study. This is a rough measure of food supply. Some aspects more meaningful, such as herbaceous biomass or volume and food quality, were not evaluated. Therefore, we argue that this subject needs more intensive research to clarify the influence of food supply on rabbit abundance in other areas outside the Mediterranean region.

Rabbit abundance was positively associated with shrub cover and, in the absence of this cover, a positive association with gaps in rocks was verified. The importance of shrub cover has also been observed in Mediterranean habitats but, in these regions, rabbits may also use open areas if warrens were available nearby (Palomares and Delibes 1997). Lombardi *et al.* (2003) found that in grassland rabbits lived in groups linked to aggregated burrows. However, in our case warrens were detected only in < 10% of the 86 transects, which could be a consequence of the soil characteristics. Two main types of soil situation were found: deep and very humid soils, corresponding to the valleys were oak wood forest or permanent pastures/agricultural fields were present, and squeletic soils scattered with rocks of various sizes, dispersed throughout the matorral, in the highest part of the region. Thus, contrary to Mediterranean regions, in northeastern PGNP the nature of the soil makes warren construction difficult not allowing them to explore open areas. Therefore, rabbits may react by staying closer to shrub cover and gaps between rocks.

The analysis at the land cover level showed that rabbit abundance was associated to sites of high interspersion between rocks and matorral (first PCA factor) and high interspersion sites of tall scrubland (second PCA factor). These results clearly highlighted the importance of shelter and the interspersion between open/shelter habitats for rabbits, as hypothesized in other studies for Mediterranean zones of Iberian Peninsula (Rogers and Myers 1979, Soriguer 1983, Moreno *et al.* 1996, Palomares *et al.* 1996, Martins and Borralho 1998, Palomares *et al.* 2001).

The abundance pattern of wild rabbit in the PGNP seems to be determined by an anti-predator strategy (Jaksic and Soriguer 1981, Villafuerte 1994, Villafuerte and Moreno 1997, Banks *et al.* 1999). This strategy consists in the utilization of closed areas during daylight (and gaps in rocks) for protection against diurnal birds of prey (and human hunting), but not from nocturnal or crepuscular carnivores (the red fox and the wild cat are the main mammal predators of rabbits in the PGNP; Carvalho 2001) whose prey tactics are favored by shrub vegetation (Villafuerte 1994, Moreno *et al.* 1996). Hence, during the night, rabbits tend to use edges between open/closed areas for hiding in bushes or gaps in rocks, foraging and/or run in openfield (Moreno *et al.* 1996, Villafuerte and Moreno 1997, Martins and Borralho 1998).

The results obtained in this study suggested that management actions should favor the growth and establishment of patches of natural shrubs (Palomares *et al.* 2001), similar in structure to tall scrubland of *Genista* sp. and *Cytisus* sp., scattered in areas of continuous matorral and pastures/agricultural fields. This strategy may enhance the availability of shelter conditions and the interspersion of open/closed areas. Continuous areas of tall scrubland, where interspersion is lower, can also be a problem for rabbits, since the risk of predation by nocturnal carnivores is higher (Moreno *et al.* 1996). Therefore, in these places selective vegetation cutting should be undertaken to the level where interspersion reaches an appropriate value. We suggest, an interspersion value, calculated according to the method here described, equal or superior to 1.

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Seasonal and spatial pattern of shelter use by badgers *Meles meles* in Białowieża Primeval Forest (Poland)

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In 1997–2001, we investigated the use of day-time shelters by radio-collared badgers *Meles meles* (Linnaeus, 1758) in the Białowieża Primeval Forest, eastern Poland. Each social group of badgers utilised, on average, 9 different shelters per territory (range: 4–20). The main setts, occupied for breeding and winter sleep, were also most frequently used for day-time rest throughout the year (73% of days). Badgers living in the pristine oldgrowth stands utilised larger number of shelters and spent more days in hollow trees (mainly lime *Tilia cordata*), compared to badgers inhabiting younger secondary tree stands. Number of shelters used by individuals varied between seasons and depended on sex and age of animals. In summer, badgers used more shelters than in spring and autumn. In winter, they stayed in their main setts only. Adult males occupied more shelters and spent fewer days in the main sett than other badgers. In spring, females rearing young used only the main setts. The average underground space used by badgers within the main sett was 128 m^2. It was largest in summer and smallest in winter, and also varied between males and females. We proposed that, in a low-density population, badgers used several setts and other daily shelters to reduce energy expenditure when exploring their large territories and foraging. Furthermore, setts may play a role of marking sites. Analysis of the biogeographical pattern of sett use by European badgers showed that the number of setts used by social groups increased with increasing territory size, whereas the density of setts (*n* setts/km^2) was negatively correlated with territory size. We proposed that different factors could shape the utilisation of setts by badgers in low- and high-density populations.

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Introduction

Eurasian badgers *Meles meles* (Linnaeus, 1758) are semi-fossorial animals. Their burrows called setts are used for breeding, winter sleep, and – year round – as a shelter during day-time resting. The setts are often inherited by generations of badgers. Within their territories, social groups of badgers may construct and use from one to over 25 setts of different type and size (Roper 1993, Ostler and Roper 1998, Revilla *et al.* 2001). Main setts are essential components of badger territories used by all group members, and if complex enough, they secure successful