Rabbit Oryctolagus Cuniculus Habitats in Mediterranean Scrubland: The Role of Scrub Structure and Composition

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Rabbit *Oryctolagus cuniculus* habitats in Mediterranean scrubland: the role of scrub structure and composition

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Although scrub cover is generally regarded as an important habitat component of the European wild rabbit *Oryctolagus cuniculus*, little is known about the species' responses to variation in scrub structure and composition. Such information is required for conservation management of rabbits in Mediterranean scrublands of the Iberian Peninsula (southwestern Europe), where the species is both a key resource for a range of endangered predators and a popular game species. To address this issue, we estimated the effects of variables characterising scrub vegetation on the occurrence and number of rabbit latrines in 60 250-m transects distributed in a 5,000-ha scrubland-dominated landscape in southwestern Portugal. The strongest effect was that of cover by the shrub *Cistus ladanifer*, which was positively related to both the occurrence and relative abundance of rabbits. Conversely, rabbits showed negative responses to cover by *Chamaespartium tridentatum*, ericoid and other broad-leaved shrubs. Rabbits favoured scrubs with a low density of woody vegetation at the ground level, but with a dense overhead cover. The herbaceous layer was also influential with positive effects of cover by grasses under the scrub and by forbs at the edge of the scrub. Taken together, our results suggest that conservation management of rabbit habitats in southwestern Portugal should strive to maintain scrub patches with a combination of favourable characteristics, including dense overhead cover but open access at the ground level, a developed herbaceous layer and woody species providing feeding opportunities during the summer period.

Key words: Cistus ladanifer, conservation, habitat management, Iberia, lagomorphs, Portugal, rabbit

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In the European Mediterranean region, major conservation challenges have emerged in recent decades from the pervasive trend for the abandonment of agricultural land and its subsequent occupation by scrubland and woodland (González Bernáldez 1991, Krohmer & Deil 2003, Romero-Calcerrada & Perry 2004). This has resulted in habitat losses for species associated with early-successional vegetation and edge habitats, which had benefited from the mosaic structure created by the traditional management of Mediterranean landscapes (Farina 1997, Sánchez-Zapata & Calvo 1999, Moreira et al. 2005). One such species is the European wild rabbit *Oryctolagus cuniculus*, which has declined since the 1950s due essentially to diseases, excessive hunting and changes in traditional land uses (Blanco & Villafuerte 1993, Calvete et al. 2004).

The rabbit is native to the Iberian Peninsula where a considerable effort is devoted to its conservation management. This is primarily because the rabbit is an important prey for a wide range of avian and mammalian predators of conservation concern (Delibes & Hiraldo 1981), and a key resource for globally threatened species such as the Spanish imperial eagle *Aquila adalberti* and the Iberian lynx *Lynx pardinus* (González et al. 1990, Palma et al. 1999). The rabbit is also a popular game species, providing an important source of income in rural areas. Therefore, a detailed understanding of rabbit habitat requirements has been actively sought in recent years in order to develop management prescriptions to enhance its populations (Moreno & Villafuerte 1995, Moreno et al. 1996, Martins et al. 2003, Calvete et al. 2004).

Favourable rabbit habitats are judged to include herbaceous patches providing adequate food resources, combined with some kind of scrubland cover or warrens offering protection against predators (Rogers & Myers 1979, Palomares & Delibes 1997). Given these general ecological conditions, rabbits can occur over a wide variety of habitat configurations, ranging from open grasslands, where protection is provided primarily by warrens, to areas dominated by scrubland interspersed with small herbaceous patches (Lombardi et al. 2003). Habitat management strategies vary accordingly; efforts focusing to a large extent on reducing predation risk in open habitats, frequently by providing artificial warrens, whereas increasing food resources is usually the main goal in closed habitats (Moreno & Villafuerte 1995).

In landscapes resulting from the abandonment of traditional land uses, clearing scrubland patches and eventually sowing nutritious herbs are usually the main management prescriptions (Moreno & Villafuerte 1995). Recommendations tend to ignore the scrubland component, implicitly assuming that scrub cover is plentiful and so unlikely to limit rabbits. This view, however, may not be correct, as different kinds of scrub may vary widely in the habitat conditions they offer to rabbits. For instance, variation in stem density may affect the potential of scrubland to provide concealment and escape routes against predators (Villafuerte & Moreno 1997). Also, rabbits consume woody plants during some periods of the year, and so the temporal and spatial availability of important food resources may be influenced by the distribution, abundance and nutritional value of different shrub species (Martins et al. 2002). It is likely, therefore, that a greater consideration should be given to the scrub component for effectively managing rabbit habitats. However, taking this approach is difficult at present, due to a very poor understanding of the ways in which rabbits may be influenced by scrub attributes.

Our present study addressed this issue, quantifying the influences of scrub structure and composition on the distribution and abundance of rabbits, in a scrubland dominated landscape of southwestern Portugal. Our results were then used to evaluate the importance of the scrub component when managing rabbit habitats for conservation in this region, and to suggest Mediterranean scrubland management guidelines favouring rabbits.

Methods

Study area

A study area representative of the vast scrublands occupying former arable land in the mountain ranges of southwestern Portugal was selected at the foothills of the Monchique massif (902 m; Fig. 1). This is a rugged landscape situated at 100-300 m a.s.l. It is crossed by the entrenched valleys of the Seixe River and its numerous small tributaries. Mean temperature is 16°C and the average annual rainfall is about 750 mm; only 6-7% of the annual rain falls during June-September, the hottest period of the year, causing a water deficit at the end of the dry season. The potential vegetation on the schist-siliceous soil prevalent in the region is a mixed oak forest dominated by cork oak *Quercus suber* (Rivas-Martinez et al. 1990, Seng & Deil 1999), but natural vegetation was largely cleared for cereal cropping from the 1930s up to the 1960s, and presently occur at various stages of recovery from past agricultural disturbance (Krohmer &

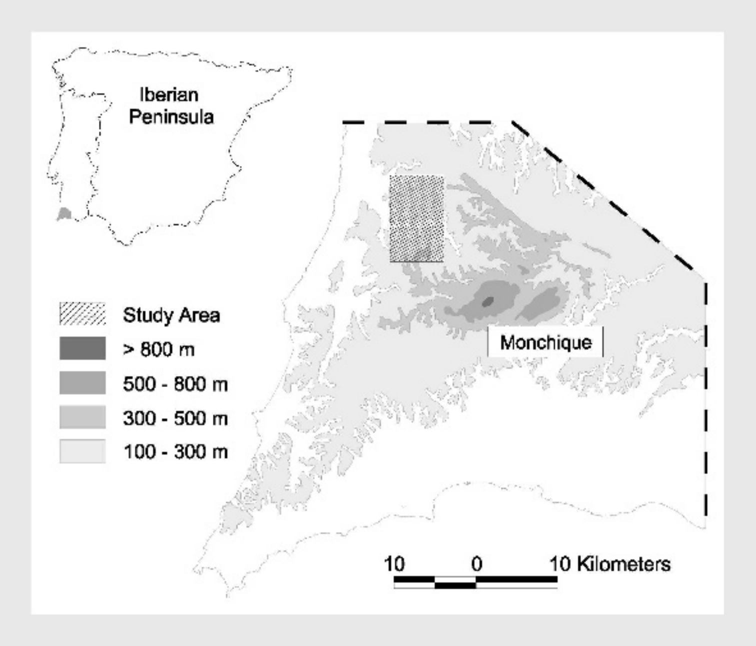

Figure 1. Study area in southwestern Portugal from which rabbits were sampled during June-August 1997.

Deil 2003). Evergreen sclerophyllous shrubs dominate the landscape with a shrub composed by *Cistus ladanifer* occupying vast dry areas with strongly eroded soils. Depending on soil, moisture and disturbance conditions, there is also a variety of more diverse shrub types, the most representative being gorse-heaths composed of several species of *Ulex, Genista, Erica* and Cistaceae (Rivas-Martinez et al. 1990, Seng & Deil 1999). The most developed vegetation is largely confined to north-facing slopes, including cork oak woods and a tall and dense thicket dominated by *Arbutus unedo* and *Erica arborea*. During the 1970s and 1980s there was large-scale afforestation with eucalyptus *Eucalyptus globulus* which replaced abandoned cereal fields and natural vegetation that had been spared from past human activities (Krohmer & Deil 2003). Agricultural activities are now extremely reduced, and human occupation is restricted to a few isolated houses and sparsely cultivated valleys. Hunting pressure on rabbits is apparently low and localised, and there is no game management.

Study design and rabbit survey

The study was carried out in an area of about 5,000 ha in which a systematic rabbit survey recorded the presence of 30 discrete sites occupied by rabbits (see below). The effects of scrub vegetation structure and composition on rabbit distribution were then estimated by comparing habitat conditions at sites occupied by rabbits with an equal number of random sites within the study area from which the species was absent. Variation in habitat conditions within rabbit sites was used to estimate the factors affecting rabbit abundance.

Rabbit distribution was surveyed during June-August 1997, i.e. after the end of the breeding season (Gonçalves et al. 2002), by systematically searching for activity signs (footprints, faecal pellets, scratches and direct observation of animals) along the network of dirt roads and firebreaks crossing the study area. These tracks provided the main discontinuities in otherwise densely vegetated terrain where rabbit signs appeared largely absent and systematic surveys were virtually impossible. Warrens were not used in surveys, as the thin and rocky soils largely prevented rabbit digging. The distribution of signs was noted on 1:25,000 maps, and discrete rabbit sites were identified as clusters of signs separated from the nearest cluster by at least 300 m with no evidence of rabbit activity in-between. The 300-m distance was chosen because movements by rabbits in similar habitats tend to be shorter than this (e.g. Gibb 1993), though dispersing animals may eventually travel much longer distances (e.g. Moreno et al. 2004). Nevertheless, the lack of any rabbit sign in-between sites suggested that movements among sites separated by this distance were at most sporadic, and so they could be taken as independent locations. As this assumption could not be tested, eventual spatial dependencies among sampling sites were controlled for statistically in the data analysis (see below).

After the survey, 30 random points were distributed across the network of dirt roads and firebreaks crossing the study area, at a minimum distance of 300 m from the nearest site occupied by rabbits. At each rabbit site, the relative abundance of rabbits was indexed from a latrine count along a 250-m transect, counting as a latrine any group of > 20 pellets within a circle with a 10-cm radius. Latrines are special communal sites where rabbits deposit faecal pellets for social reasons, in addition to depositing faeces apparently at random throughout their range (Sneddon 1991), and they have been widely used to index rabbit abundances (e.g. Iborra & Lumaret 1997). This indirect method was used because the actual observation of individuals in the study area was not feasible due to dense vegetation cover.

Vegetation structure and composition

The scrub bordering dirt roads along the 250-m transects set at rabbit sites and at random sites, was characterised from 11 variables quantifying the woody vegetation vertical structure and the herbaceous layer (Table 1). In each transect, vegetation variables were estimated at six sampling points, located at 50-m intervals on alternating sides of the road. At each point, the overall woody cover and the proportion of different scrub types was estimated at four 0.25-m vertical strata (0-0.25 m - 0.75-1.0 m), using a vegetation profile board (Hays et al. 1981). We recognised six shrub types: 1) ericoid shrubs (heather *Calluna vulgaris* and *Erica* spp.); 2) thorny shrubs (e.g. *Ulex* spp. and *Genista* spp.); 3) *Cistus ladanifer*; 4) other broad-leaved evergreen shrubs (e.g. *Arbutus unedo, Quercus* spp. and Cistaceae except *C. ladanifer*); 5) *Chamaespartium tridentatum*; and 6) *Dittrichia revoluta*. The herbaceous layer was quantified in terms of percentage cover made up by grasses (Gramineae) and forbs (non-grassy and herbaceous species, e.g. legumes and composites), both at the edge of the scrub and under the scrub at 5 m from the edge. The same observer carried out all measurements, thereby minimising methodological variations. Vegetation variables were averaged across the four strata and the six points measured in each transect, except where indicated otherwise.

Data analysis

The angular transformation was used for proportional data to reduce the weight of a few large values in subsequent statistical analysis and to overcome the unity sum constraint. The interrelationships among vegetation variables were then evaluated using Principal Components Analysis (PCA; Legendre & Legendre 1998). Generalised linear modelling was used to examine the effects of vegetation variables on the distribution and abundance of rabbits (GLM; McCullagh & Nelder 1989). The occurrence data were modelled with logistic regression, whereas models for latrine counts were based on Poisson regression corrected for overdispersion. Model development involved a preliminary selection of significant variables using likelihood-ratio statistics, testing both the linear and unimodal effects of each vegetation variable.

Table 1. Scrubland vegetation structure and composition at sites used (N = 30) and non-used (N = 30) by rabbits in southwestern Portugal during June-August 1997. The distance was measured to the nearest site occupied by rabbits.

	Mean ± SD (Min-Max)	
Variables	Used sites	Non-used sites
Scrub cover (%)	62.7 ± 13.7 (35.2-82.9)	70.4 ± 14.7 (39.8-98.1)
Scrub composition (%)		
Ericoid shrubs	13.0 ± 14.1 (0.0-61.7)	25.5 ± 19.4 (0.8-81.1)
Thorny shrubs	5.1 ± 6.65 (0.0-26.4)	6.0 ± 8.69 (0.0-36.8)
Cistus ladanifer	63.4 ± 27.2 (0.0-100.0)	37.5 ± 30.3 (0.0-90.7)
Other broad-leaved shrubs	10.3 ± 17.3 (0.0-75.7)	22.2 ± 26.0 (0.0-77.9)
Chamaespartium tridentatum	3.6 ± 6.33 (0.0-22.3)	5.7 ± 8.10 (0.0-35.8)
Dittrichia revoluta	4.6 ± 7.14 (0.0-22.3)	3.2 ± 4.26 (0.0-12.4)
Herbaceous cover (%)		
Grasses, edge	45.2 ± 21.9 (10.0-83.3)	37.0 ± 20.5 (6.7-73.3)
Grasses, interior	41.0 ± 25.7 (0.0-86.7)	26.2 ± 22.6 (0.0-83.3)
Forbs, edge	9.8 ± 8.71 (0.0-33.3)	4.4 ± 5.49 (0.0-16.7)
Forbs, interior	4.1 ± 5.85 (0.0-23.3)	1.8 ± 2.59 (0.0-10.0)
Distance (km)	0.9 ± 0.58 (0.3-2.2)	0.6 ± 0.24 (0.3-1.2)

Combinations of significant variables and their interaction terms were selected using stepwise procedures, and the Akaike Information Criteria (AIC) was used to select the best multivariate models (Burnham & Anderson 1998). Percentage reduction in deviance between the null model (model fitted to the intercept only) and each model tested was taken to indicate the amount of variability explained by the models. In the modelling procedure, the log-transformed distance from each sampling point to the nearest site occupied by rabbits was used to test for spatial structure in rabbit distribution. The marginal effects of vegetation variables in models including the spatial term were then tested, thereby accounting for potential confounding effects of spatial autocorrelation (Legendre & Legendre 1998). Throughout the study, the significance level was set at $P < 0.05$. Analyses were made using S-Plus 2000 (MathSoft 1999).

Table 2. Loadings of vegetation variables on the first four axes (PC 1-PC 4) extracted by PCA, and the proportion of variance accounted for by each axis, for 60 rabbit habitat sampling sites in southwestern Portugal during June-August 1997. Values in italics indicate loadings >|0.40|.

Variables	PC1	PC2	PC3	PC4
Scrub layer				
C. ladanifer	*0.74*	0.20	*-0.59*	-0.15
C. tridentatum	-0.34	*0.54*	0.08	*-0.54*
Ericoid shrubs	*-0.61*	0.17	0.39	-0.25
Thorny shrubs	0.30	0.10	0.36	*0.67*
Broad-leaved shrubs	*-0.58*	-0.18	0.32	0.36
Dittrichia revoluta	0.24	-0.32	*0.44*	-0.25
Scrub cover	*-0.62*	0.07	-0.07	-0.09
Herbaceous layer				
Grasses, edge	*0.53*	*-0.49*	*0.52*	-0.27
Grasses, interior	*0.71*	0.27	*0.41*	-0.19
Forbs, edge	*0.66*	*0.61*	0.04	0.00
Forbs, interior	0.41	*0.72*	0.11	0.14
Eigenvalue	3.29	1.72	1.39	1.15
% Var.	29.9	15.6	12.6	10.5

Results

The PCA for vegetation variables highlighted a dominant gradient primarily related to the proportional cover by *C. ladanifer* (Table 2). The first PC accounted for 29.9% of the variance in the data, contrasting scrubland dominated by *C. ladanifer* with scrubland covered primarily by ericoid and other broad-leaved shrubs. *C. ladanifer* scrubland tended to be less dense and to have a higher soil coverage by grasses and forbs, both within and at the edge of the scrub, than ericoid and other broad-leaved shrubs. The second PC accounted for 15.6% in variance and it was primarily related with the herbaceous layer, contrasting areas dominated by either forbs or grasses. The third PC (12.6%) contrasted *C. ladanifer* scrubland with long-term fallows, dominated by *Dittrichia revoluta* and with a well-developed grassy layer. The fourth PC (10.2%) depicted a weak gradient of increasing cover made up by thorny shrubs and decreasing cover made up by *Chamaespartium tridentatum*.

The strongest influence on rabbit distribution was that of *C. ladanifer* (Table 3), with the highest estimated probabilities of occurrence recorded for scrub-

Table 3. Summary of univariate Generalised Linear Models for the effects of vegetation and spatial structure on rabbit occurrence (logistic regression) and relative abundance (Poisson regression) in southwestern Portugal during June-August 1997. Signs indicate the directions of the association between the dependent and the explanatory variables, and % DEV is the percentage of explained deviance. Significant variables ($P < 0.05$) are given in italics, and * indicate variables that remained significant ($P < 0.05$) after accounting for spatial structure in rabbit distribution.

	Occurrence models (N = 60)			Abundance models (N = 30)		
		% Dev	P-value		% Dev	P-value
Scrub layer						
Scrub density	(-)	*5.8*	*0.027*	(-)	1.5	0.520
Ericoid shrubs	(-)	*11.6*	*0.002**	(-)	11.6	0.062
Thorny shrubs	(-)	0.0	0.955	(-)	7.3	0.149
Cistus ladanifer	(+)	*13.3*	*<0.001**	*(+)*	*23.8*	*0.007**
Broad-leaved shrubs	(-)	*4.8*	*0.046*	(-)	6.1	0.198
Chamaespartium tridentatum	(-)	1.5	0.182	(-)	7.0	0.157
Dittrichia revoluta	(+)	0.5	0.505	(-)	1.8	0.482
Herbaceous layer						
Grasses, edge	(+)	3.0	0.113	(-)	2.3	0.421
Grasses, interior	(+)	*6.5*	*0.020**	(-)	4.0	0.297
Forbs, edge	(+)	*10.0*	*0.004**	(+)	0.1	0.868
Forbs, interior	*(+)*	3.6	0.084	(-)	0.1	0.883
Distance	(-)	*8.0*	*0.010*	(-)	3.0	0.374

land dominated by this species (Fig. 2). However, there was also a negative response to scrub density, suggesting that rabbits were favoured by more open scrub. Ericoid shrubs showed a negative effect with very low estimated probabilities of rabbit occurrence (< 0.4) noted for scrubland with > 25% cover made up by these shrubs (see Fig. 2). A similar pattern, though not as strong, was found for broad-leaved shrubs. The herbaceous layer was also influential with a strong positive effect of cover made up by forbs at the scrub edge, and less so by grasses under the scrub (see Fig. 2). There was no evidence for unimodal responses of rabbits to any vegetation variable. After accounting for the significant effect of spatial structure, the linear effects of *C. ladanifer*, ericoid shrubs, edge forbs and interior grasses remained significant. The best AIC model included only the significant effects of *C. ladanifer* and edge forbs, reducing the total deviance by 18.3%. No significant improvement could be obtained by adding the spatial term to this model (P = 0.098).

Results of a similar analysis based on woody vegetation variables broken by vertical strata yielded broadly similar results (Table 4). The occurrence of rabbits was favoured by a scrub dominated at all levels by *C. ladanifer* and with reduced cover made up by ericoid shrubs. The broad-leaved shrubs also had an overall tendency to negatively affect the occurrence of rabbits, but this was significant only for the second strata. At the basal level, but not for other strata, there were negative effects of scrub density and cover made up by *Chamaespartium tridentatum*. After accounting for spatial structure in rabbit distribution, the effects of broad-leaved shrubs and *Chamaespartium tridentatum* lost significance. The best AIC model included the basal cover made up by *C. ladanifer* and edge forbs, reducing the deviance by 19.3%. Adding the spatial term to this model did not improve its performance (P = 0.125).

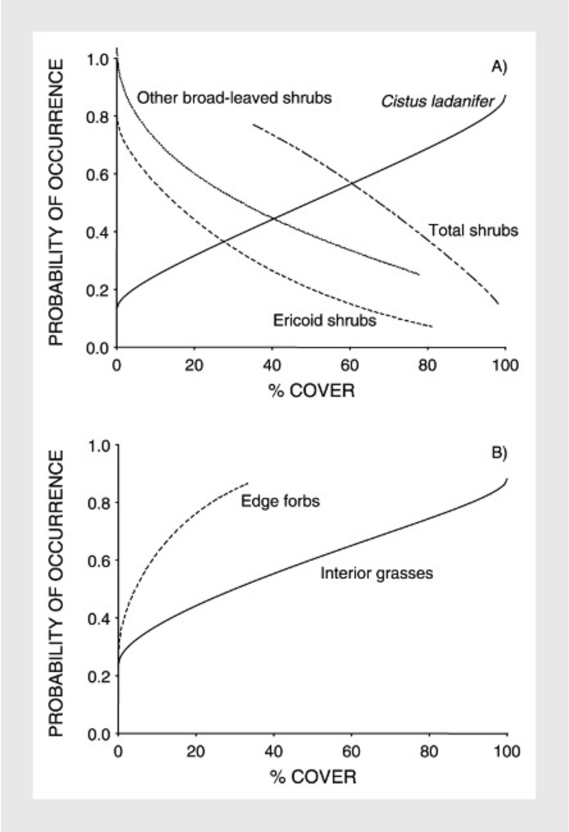

Figure 2. Logistic regression models for the effects of variables characterising the scrub (A) and herbaceous (B) layers on the probability of occurrence of rabbits in Mediterranean scrublands of southwestern Portugal during June-August 1997. The curve depicted for each variable was restricted to the range of observed values.

Table 4. Summary of univariate Generalised Linear Models for the effects of scrub vegetation divided by vertical strata on rabbit occurrence (logistic regression) and relative abundance (Poisson regression) in southwestern Portugal during June-August 1997. Signs indicate the directions of the association between the dependent and significant (P < 0.05; in italics) and nearly significant (0.05 < P < 0.1) explanatory variables, and * indicate variables that remained significant (P < 0.05) after accounting for spatial structure in rabbit distribution.

	Scrub vegetation strata (m)			
Variables	0-0.25	0.25-0.50	0.50-0.75	0.75-1.0
Occurrence				
Scrub density	(-) *0.026**	(-) 0.051	(-) 0.094	(-) 0.098
Ericoid shrubs	(-) *0.019*	(-) *0.005**	(-) *0.002**	(-) *0.002**
Cistus ladanifer	(+) *0.001**	(+)*<0.001**	(+) *0.001**	(+) *0.003**
Broad-leaved shrubs		(-) *0.048*	(+) 0.088	(+) 0.072
Chamaespartium tridentatum	(-) *0.030*			
Abundance				
Scrub density				(+) *0.037**
Ericoid shrubs	(-) 0.067	(-) *0.044**	(-) 0.084	(-) 0.072
Cistus ladanifer	(+) *0.005**	(+) *0.007**	(+) *0.017**	(+) 0.054

The proportion of *C. ladanifer* was the only variable significantly related to variation in rabbit abundance (see Table 2), irrespective of spatial structure, with the highest latrine counts recorded for almost pure stands (> 80%) of this species (Fig. 3). The other variables did not show significant relationships with the latrine counts, though there was a tendency for an inverse relationship with ericoid shrubs. When vegetation variables were broken by vertical strata, the results for *C. ladanifer* remained similar, and the negative effects of the ericoid shrubs became significant at the second level; overall scrub density showed a positive relationship at top level (see Table 3). The best AIC model included the positive effects of *C. ladanifer* and interior grasses, reducing the total deviance by 31.4%. Adding the spatial term to this model did not improve its performance (P = 0.685).

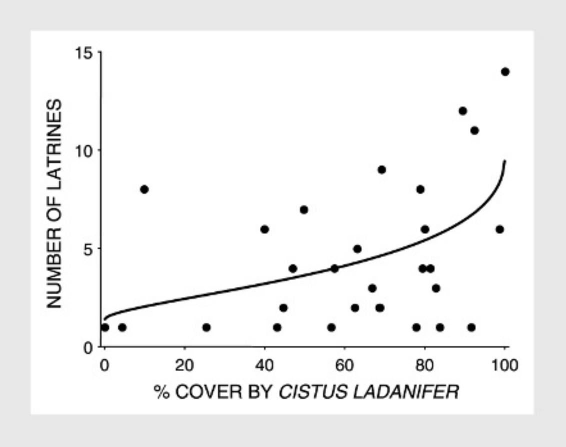

Figure 3. Poisson regression model for the effects of percentage cover made up by *C. ladanifer* on the number of rabbit latrines in Mediterranean scrublands of southwestern Portugal during June-August 1997; sites from which rabbits were absent were excluded.

Discussion

Our study supported the view that the distribution and abundance of rabbits can be influenced to a large extent by scrubland composition and vertical structure. In the uplands of southwestern Portugal, rabbits seemed to be favoured by scrubland dominated by *C. ladanifer*, with relatively sparse woody vegetation at the ground level but with dense overhead cover, and with abundant herbaceous vegetation both at the edge and within scrub patches. The negative responses recorded for ericoid shrubs, other broad-leaved shrubs and *Chamaespartium tridentatum* suggested that rabbits avoided most scrub types available within the region, including the *Arbutus unedo* - *Erica arborea* thicket and several heathlands with *Calluna vulgaris, Erica australis* or *Erica umbellata* (Rivas-Martinez et al. 1990, Seng & Deil 1999).

Although our study had some limitations and potential shortcomings, it is unlikely that these affected significantly the patterns described above. A major limitation was the relatively small size of the study area (5,000 ha), which could have caused the results to be site-specific. However, the study area was much comparable to other landscapes in southern Portugal, particularly in the southwestern uplands where agricultural abandonment resulted in extensive cover made up by dense scrubland, including vast expanses dominated by *C. ladanifer* (e.g. Krohmer & Deil 2003). Also, the main habitat associations uncovered herein have been recorded in more extensive rabbit surveys carried out within the region (P. Beja, L. Palma & M. Pais, unpubl. data), thus suggesting that the patterns observed might be valid over a much wider region. These surveys also suggested that despite the rather limited temporal scope of our present study, the patterns described may be valid across seasons and over the years. These views should be confirmed by future studies analysing larger areas over longer time frames. Another potential problem of our study was the relatively small distance among sampling points which could have introduced confounding effects due to spatial autocorrelation in environmental attributes or rabbit population processes (Legendre & Legendre 1998). This was unlikely to be a major problem, however, as the introduction of a spatial term (distance to the nearest site occupied by rabbits) in the habitat models did not change the statistical significance of habitat variables in the vast majority of cases. Explicitly incorporating spatial terms in ecological models is considered a far better approach to deal with spatial autocorrelation than trying to eliminate spatial dependencies through sampling design (Legendre & Legendre 1998).

Several non-exclusive hypotheses may be put forward to explain the observed association of rabbits with *C. ladanifer* shrub. One possibility is that this shrub might provide a critical food resource, at least during some periods of the year. At first, this seems unlikely, as *C. ladanifer* is usually considered a poor forage due to high leaf lignin, low nutritional value and the presence of toxic flavonoids and terpens (e.g. Gómez-Castro et al. 1978, Sosa et al. 2004), making it little used by rabbits when more profitable foods are available (Martins et al. 2002). However, *C. ladanifer* is extensively consumed by the red deer *Cervus elaphus* in periods of nutritional constraint (Rodríguez 1978a, Bugalho & Milne 2003), and this may also be the case for the rabbit. In Mediterranean climates, the main period of food stress for rabbits is the summer when very dry and hot conditions result in a minimal standing crop of grasses and forbs, and a low nutritional quality of natural forages (Myers & Poole 1963, Alves & Moreno 1996). Under these circumstances, rabbits can not meet their daily water and protein requirements by feeding solely on the herbaceous layer (Alves & Moreno 1996). They must supplement their diet with a number of alternative foods, including the leaves and seeds of scrubs (Cooke 1982). Although the summer leaves of *C. ladanifer* have a minimal nutritional value (Gómez-Castro et al. 1978), the capsules (seeds plus woody walls) produced by this plant are nutritionally very profitable, as they are rich in raw protein and fat (Rodríguez 1978b). This resource is available throughout the dry season, and it may comprise up to 45% of red deer summer diet in habitats similar to that in southwestern Portugal (Rodríguez 1978a). Clearly, further data should be gathered to evaluate whether capsules are a preferred food resource influencing the association of rabbits with *C. ladanifer* scrubland.

Another possibility is that rabbits were influenced by the herbaceous layer, which seemed to be more developed in *C. ladanifer* stands than elsewhere. Indeed, there was a relatively high cover of grasses under *C. ladanifer* which was probably favoured by the lower woody cover recorded in this scrub. The presence of grasses within scrubland may be particularly valuable, allowing rabbits to feed during the day on a preferred resource (Bhadresa 1987) when their activities outside protective cover tend to be severely restricted due to predation risk (Moreno et al. 1996). This view was supported by the positive response of rabbits to grass cover within scrubland, and the lack of a significant relationship recorded for edge grasses.

The value of different scrub types in providing protection against predators is another potential determinant of rabbit distribution and abundance. This may be particularly important in the study area where the thin and rocky soils largely prevented rabbits from digging warrens. Scrub is generally regarded as offering effective protection against avian predators, but increases the risk of predation by stalking mammalian predators (Moreno et al. 1996). Dense scrub may be particularly unsafe because it can hinder the visual perception of approaching predators and obstruct escape movements (Villafuerte & Moreno 1997). This may justify the observed negative responses to scrub cover at the ground level, and the positive relationships with overhead cover. The structure of *C. ladanifer* shrub, dense at the higher level but relatively sparse at ground level, tends to provide this kind of cover, thus probably representing a good compromise in terms of protection from both aerial and terrestrial predators.

Whatever the ultimate causes, the observed association between rabbits and *C. ladanifer* suggests that efforts to increase rabbit populations need to recognise the influential role played by the composition and structure of scrubland vegetation. For instance, the common practice of creating small grassland patches in scrubland landscapes to improve rabbit habitats (Moreno & Villafuerte 1995), would likely be more effective if the preferred scrub patches are not removed and the clearings are opened in their vicinity. Also, favourable scrub patches, with an optimal vertical structure and high herbaceous cover, may be actively created and maintained across the landscape through rotational burning or cutting (e.g. Patón et al. 1998, Tárrega et al. 2001). To design adequate conservation management prescriptions, the most favourable scrubland vegetation needs to be identified in each case as it will probably differ among regions in relation to local habitat conditions. For instance in southern Spain, *C. ladanifer* shrub appears to be little used by rabbits in the Sierra Morena (M. Delibes, pers. comm.), whereas in the Province of Cadiz a positive association was recorded between rabbits and the shrub *Pistacia lentiscus* (Fa et al. 1999). In general, we hypothesise that the preferred scrub for rabbits should have a combination of favourable characteristics, including a developed herbaceous layer, dense overhead cover but open access at the basal level and at least some woody species providing feeding opportunities during the summer period. This view should be confirmed in future studies, preferably through the experimental manipulation of scrub characteristics.

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