Factors shaping European rabbit abundance in continuous and fragmented populations of central Spain

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This study analyses differences in European rabbit *Oryctolagus cuniculus* (Linnaeus, 1758) abundance between fragmented and continuous populations and the relative importance of habitat structure (micro- and macrohabitat) and isolation in determining the abundance pattern in fragmented and continuous areas of central Spain. The species was mainly restricted to mediterranean vegetation habitat. In fragmented areas, rabbit abundance was linked to scrubland cover but was not correlated to pasture/cropland cover. The model explained very little of the observed variance. Distance to continuous populations did not improve the model. Stochastic phenomena or unmeasured factors (predation level, soil type) could be acting in this context. Rabbits were more abundant in continuous areas than in fragmented ones. In continuous areas, rabbit abundance was associated with mosaics of pastures, scrublands, and croplands. These habitat features are linked to shelter and feeding requirements of rabbits. The model explained an important part of the observed variance. This supports that management and conservation strategies should be based on the landscape pattern in each situation.

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Introduction

Over the last 50 years, populations of European rabbit *Oryctolagus cuniculus* (Linnaeus, 1758) have suffered a dramatic reduction in Europe (Trout *et al*. 1986, Villafuerte *et al*. 1994, 1995) due to myxomatosis, rabbit haemorrhagic disease (RHD), and habitat changes (Trout *et al*. 1992, Webb 1993, Villafuerte *et al*. 1995, 1997). In some countries, where rabbits have been introduced and are considered as

a pest, this population crash has favored the conservation of native fauna. However, the rabbit cannot be regarded as a pest in most of its natural distribution range (Angulo 2001). For example, in Spain, the rabbit is a very important food resource for many predators (Delibes and Hiraldo 1981), being the main prey for highly endangered species such as the Iberian imperial eagle *Aquila adalberti* and the Iberian lynx *Lynx pardinus* (Ferrer 1993, Nowell and Jackson 1996). For these species most of the conservation guidelines are based on rabbit population recovery. Moreover, the rabbit is also considered one of the most popular game species (García y Bellido 1986), and its hunting is important economically and socially in large areas of Spain.

Several studies have shown that rabbit abundance and distribution is mainly determined by habitat structure, especially by mosaic areas of typical mediterranean vegetation composed by scrublands and pastures (Rogers and Myers 1979, Soriguer and Rogers 1981). However, this suitable habitat may be continuous or fragmented within a matrix of unsuitable habitats (large forests, mountain etc). Therefore, the rabbit's distribution may show a continuous pattern or a fragmented one (Blanco and Villafuerte 1993). The spread of RHD since 1988 appears to have intensified fragmentation of rabbit populations causing extinction of some populations and changes in the distribution pattern of others.

Continuous and fragmented populations are subjected to different environmental and stochastic processes (Hanski 1991, Saunders *et al*. 1991), thus management of fragmented populations may be drastically different from continuous ones (Caughley 1994). For example, fragmentation leads to a reduction of the area and an increase of isolation, which implies the reduction of population size and an increase in the likelihood of extinction (Wilcox and Murphy 1985, Hanski 1991).

Up to date, there have been few studies aimed at analysing the role of habitat types and different degrees of fragmentation in explaining rabbit abundance. Even fewer have used several spatial scales simultaneously (but see Fa *et al*. 1999). Nevertheless, the importance of habitat features may disappear or take on a different structure according to the scale on which species distribution is measured (Kotliar and Wiens 1990). The importance of taking into account several scales in habitat-species studies has been pointed out in most studies (eg Wiens *et al*. 1987, Kotliar and Wiens 1990).

This study analysed rabbit abundance and distribution in continuous and fragmented populations and discussed the relative importance of habitat features and isolation, by simultaneously considering microhabitat and macrohabitat descriptors of the environment. In particular, we aimed to check whether rabbit abundance was lower in fragmented than in continuous populations and, if so, whether isolation was an additional key factor in explaining rabbit abundance in fragmented populations. In addition, we explored whether a multi-scale approach would explain an important part of variation seen in rabbit abundance.

Study area

The study was conducted in central Spain (Madrid province) in 1998–1999 during winter and early spring. Sites to be surveyed were chosen within the most abundant habitat types in central Spain. These included: (a) mediterranean vegetation composed by holm oak forests (*Quercus ilex*) and associated scrubland (*Cistus ladanifer, Retama sphaerocarpa*) shown *a priori* to be the most suitable habitat for rabbits (see above); (b) Pyrenean oak forests (*Quercus pyrenaica*); and (c) pine forests (mainly *Pinus sylvestris*). Mediterranean vegetation is located in low-lying areas (500–900 m a.s.l.), Pyrenean oak forests between 900–1200 m a.s.l. and pine forests between 1000–1700 m a.s.l (for details about vegetation see Rivas-Martínez 1982). Mediterranean vegetation habitat is mainly used for hunting of game species (rabbits being one of the most important) and agricultural use. Pyrenean oak forests are used for livestock, mainly cows, and pine forests are used for forestry and recreational activities. Soil type and climate features correlated with habitat type in central Spain (Rivas-Martínez 1982, Monturiol 1987).

Two contrasting regions were studied: (1) a mountainous area in the north of the province where the three habitat types are represented, (2) plain areas in the south-west, with lower relief and a landscape that mainly consisted of mediterranean vegetation with scrublands and croplands interspersed. Rabbit distribution between the two regions is clearly different; in the north of the province rabbits occur in naturally fragmented populations (hereafter fragmented area) presumably due to the patchy distribution of suitable habitat (mediterranean vegetation composed by holm oak forests and scrublands). In the south rabbits are widespread (Blanco and Villafuerte 1993) (hereafter continuous area).

Material and methods

Sampling protocol

We surveyed 78 areas using transects 1-km length: 62 in fragmented areas and 16 in continuous areas. Surveys in the fragmented areas were conducted in the different habitat types above described: 16 in mediterranean vegetation habitat, 21 in Pyrenean oak forests, and 25 in pine forests. Minimum distance between all sampled areas was 1 km. Rabbit abundance was estimated through latrine counts. Latrine counts have been previously used as an index to estimate rabbit abundance (Palma *et al*. 1999) and appear to be a useful indirect estimator of rabbit abundance in large-scale studies, despite the potential problems with decay rates or age of rabbit pellets (Palomares 2001, S. Cabezas-Díaz and E. Virgós, unpubl.). A latrine was defined as any faecal accumulation having at least 20 pellets over a surface of 200 × 300 mm. Latrine counts were performed each 200 m along the 1-km length path, by means of two perpendicular belt transects (25 m long × 2 m wide) on opposite sides of the track ($n = 10$ belt transects per 1-km path surveyed).

Microhabitat variables relating to food resources or shelter for rabbits (Rogers and Myers 1979, Moreno and Villafuerte 1995, Fa *et al*. 1999) were estimated each 200 m along the 1-km path. We estimated tree, shrub (higher than 50 cm), herb, and rock cover (all of them in %). Coverage was estimated by eye in circular plots of 25-m radius following similar protocols to general habitat-species studies (Morrison *et al*. 1992). Estimation of microhabitat was made by different observers after a calibration of their assessments. To quantify macrohabitat variables each 1-km length path was located in the middle of a 3 × 3 km surface, which may be considered as a landscape scale that covers several rabbit home-ranges (see Parer 1982, Gibb 1993). The macrohabitat variables that were quantified on 1:50 000 land use maps included cover of forests, scrublands, pastures, and croplands (all of them in %); a roughness index and number of watercourses. These variables have been hypothesized that determine the habitat suitability for rabbits at large-spatial scales (Rogers and Myers 1979, Fa *et al*. 1999). Cover of the different variables was measured using a grid with points evenly spaced over the 3 × 3 km surface, where we counted the number of points of each cover type. Roughness was measured as the average number of 20-m elevation lines recorded in 4 evenly spaced lines (2 N–S and 2 E–W

orientation) on the 3×3 km grid square. Watercourses were quantified as the total number recorded in each 3×3 km area.

In addition to habitat descriptors, we used – as an isolation measure – the distance between each 1-km length path surveyed and assumed 'core' area. We considered a 'core' area as an area, where rabbit population showed a fairly continuous distribution over an area of 50 km^2. Two core areas have been defined surrounding or near to the transects surveyed, both located in mediterranean vegetation habitat. Thus, all paths surveyed in the continuous area were included in one of the 'core' areas considered, so isolation was registered as zero for those paths. Distances among paths located in the fragmented area and 'core' areas were measured on 1:100 000 topographic maps, taking the minimum distance between them.

Statistical analyses

We compared rabbit abundance (number of latrines counted in each area) between the different habitat types in the fragmented area through a one-way ANOVA. In addition, we evaluated the effect of fragmentation *per se* on rabbit abundance comparing mediterranean vegetation habitat in continuous and fragmented areas through a one-way ANOVA. Effects of habitat features and isolation on rabbit abundance (number of latrines/km) were analysed through stepwise multiple regression. Two regression models were undertaken: (a) a model for mediterranean vegetation habitat in fragmented area ($n = 16$), (b) a model for mediterranean vegetation habitat in continuous area ($n = 16$). Previously, we performed PCA analyses (varimax rotated) in both areas to obtain independent variables used as predictors in multiple regression analyses. We made two PCA analyses for each area, one using macrohabitat descriptors and another with microhabitat ones. In addition, the model for the fragmented area also included the distance to 'core' populations as a measure of isolation. In both cases, a forward stepwise procedure was followed in order to select the variables that enter the final model (F to enter = 4.00, F to remove = 3.99; Neter *et al*. 1985). Variables were transformed in order to attain normality and homocedasticity. When variables were not normally distributed despite transformation, we used only those with positive skewness (Underwood 1997). All analyses were performed with STATISTICA 5.0 package, using the standard criterion of probability ($p < 0.05$).

Results

Rabbit abundance strongly varied between habitats in fragmented areas (ANOVA: $F_{2,75} = 10.40$, $p < 0.001$). Rabbits were mainly located in areas dominated by mediterranean vegetation habitat, were not present in pine forests, and were very scarce in the pyrenean oak forest (only found in one of the sampled areas within this habitat).

Rabbit abundance was significantly different between mediterranean vegetation habitat in fragmented and continuous areas ($F_{1,30} = 4.57$, $p = 0.04$), with higher abundance in the continuous areas (mean ± SD: 9.19 ± 8.52, range 0–24) than in the fragmented ones (4.06 ± 4.40, range 0–13). In addition, the distribution of numbers of latrines in the transects was different between the two areas. In continuous areas, 7 transects showed more than 10 latrines, whereas in fragmented areas only 3 transects showed more than 8 latrines. Transects without rabbit latrines showed similar numbers in both areas (4 in continuous and 6 in fragmented ones).

PCA analysis in fragmented areas with microhabitat descriptors yielded one factor (Table 1), which separated areas with high shrub and herb cover (positive scores) from areas with high tree and rock cover (negative scores). The PCA with

Table 1. Results of PCA analyses (VARIMAX rotation) from microhabitat and macrohabitat variables used in fragmented areas surveyed in this study (* indicates significant correlations).

Microhabitat variables	PCA factor 1	Macrohabitat variables	PCA factor 1	PCA factor 2
Tree cover (%)	−0.889*	Forest cover (%)	−0.932*	0.252
Shrub cover (%)	0.904*	Scrub cover (%)	0.825*	0.333
Herb cover (%)	0.704*	Pasture cover (%)	0.056	−0.960*
Rock cover (%)	−0.785*	Cropland cover (%)	0.559*	0.426
		Number of watercourses	0.846*	0.121
		Roughness index	0.230	0.891*
Eigenvalue	2.720	Eigenvalue	2.634	2.088
Variance explained	0.680	Variance explained	0.440	0.348

macrohabitat descriptors yielded two factors, the first separated cultivated and scrub areas (positive scores) from forested ones (negative scores). The second factor segregated roughness of areas (positive scores) from areas with high pasture cover and plain terrain (negative scores) (Table 1).

Stepwise multiple regression analysis between rabbit abundance and PCA factors and isolation only included factor 1 of macrohabitat ($R^2 = 0.48$, $\beta = 0.69$, $p = 0.003$). Rabbit abundance was higher in areas dominated by scrubland--cropland mosaics with abundant number of watercourses (positive scores of the PCA). The distance to 'core' areas (isolation) or microhabitat PCA descriptors were not significant.

PCA analysis in continuous areas with microhabitat descriptors yielded one factor (Table 2), which was interpreted as a gradient from areas with high tree and herb cover (positive scores) to shrub and rock cover (negative scores). The PCA

Table 2. Results of PCA analyses (VARIMAX rotation) from microhabitat and macrohabitat variables used in continuous areas surveyed in this study (* indicates significant correlations).

Microhabitat variables	PCA factor 1	Macrohabitat variables	PCA factor 1	PCA factor 2
Tree cover (%)	0.686*	Forest cover (%)	0.719*	0.656*
Shrub cover (%)	−0.789*	Scrub cover (%)	−0.984*	0.028
Herb cover (%)	0.578*	Pasture cover (%)	−0.914*	−0.242
Rock cover (%)	−0.599*	Cropland cover (%)	0.222	−0.926*
		Number of watercourses	−0.891*	0.057
		Roughness index	0.257	0.863*
Eigenvalue	1.80	Eigenvalue	3.230	2.095
Variance explained	0.450	Variance explained	0.538	0.350

with macrohabitat descriptors yielded two factors. Factor 1, separated areas of high forest cover (positive scores) from areas of high scrub and pasture cover (negative scores). Factor 2, segregated areas with a high roughness index and forest cover (positive scores) from areas with high cropland cover (negative scores) (Table 2).

Stepwise multiple regression between rabbit abundance and PCA factors included only macrohabitat factors (factor 1: β = –0.59; factor 2: β = –0.62; R^2 = 0.74, p < 0.001). Rabbits were more abundant in areas where the cover of pastures, scrubland and cropland was high.

Discussion

Rabbits are practically restricted to mediterranean vegetation habitat and associated vegetation both in fragmented and continuous areas. This fact supports earlier studies on the habitat preferences of rabbits. Probably, the absence of rabbits in other habitats is a consequence of their higher elevation. It has been shown elsewhere that elevation may negatively affect rabbit distribution and abundance (Fa *et al*. 1999, Trout *et al*. 2000). Moreover, in the case of pine forests, it could be suggested that in addition to elevation, the low suitability of this habitat might be related with its low protection cover and low share of grazing areas.

According to our hypothesis, rabbits show lower abundance in mediterranean vegetation habitat located in areas where habitat is fragmented. This conforms to general theories about species abundance in fragmented areas (Wilcox and Murphy 1985). In general, fragmentation produces an increase in isolation (lower potential immigration) and a reduction in patch size, which may reduce density and increase the likelihood of extinction (Wilcox and Murphy 1985, Hanski 1991). Both processes may occur within the low density rabbit populations in the fragmented area.

On the other hand, our results showed that rabbit abundance was explained by slightly different factors depending on the degree of fragmentation. Other vertebrate species show a different response to environmental variables according to the level of fragmentation (Tellería and Virgós 1997, Virgós 2001), but in most cases, the main difference is related to the relative role of habitat variables against isolation with higher preponderance of isolation in the fragmented situations. In the present study, isolation was not linked to changes in abundance in the fragmented area. This could be explained by the fact that average distance among fragmented and 'core' populations (15.36 km) was higher than dispersal range of the species (maximum 2 km; see Parer 1982, Calvete and Estrada 2000), reducing connectivity among populations (Merriam 1991). In this context, rabbit populations in fragmented areas of central Spain can not be considered as a typical mainland ('core')-island system (Harrison 1991). Maybe each population is linked to other small populations in the fragmented area and they constitute a metapopulation without a clear 'core' area (Hanski 1991). We were not able to test this possibility further.

In fragmented areas rabbits are more abundant where scrubland cover with cropland land and number of watercourses was high, whereas pastureland appears

to be a less suitable habitat for rabbits. In continuous populations, mosaics of pasture with crops and scrubs mainly determined abundance. In both cases, forested areas are associated with low rabbit abundance. Previous studies on rabbit abundance and distribution have emphasized the preference of this species for mosaic habitats, where both scrub and pastures are interspersed and provide shelter (high scrub cover) and food (high herb or pasture cover) (Rogers and Myers 1979, Moreno *et al*. 1996, Villafuerte and Moreno 1997, Fa *et al*. 1999). In relation to cropland areas, Boag (1987) noted that non-intensive agriculture could benefit rabbit abundance by increasing feeding areas.

Nevertheless, our results indicate a lack of association between rabbit abundance and pastureland in fragmented areas of the mountains. This may not be linked to fragmentation *per se*, it may rather be explained by the different human use of pastureland in each area. In fragmented areas (mountains), the pastureland is heavily used by cattle for grazing. This fact could prevent use of pastures by rabbits, as it has been proved that competition with other herbivores is an important factor in rabbit mortality and density (Gibb 1977, 1981, Wallage-Drees and Croin Michielsen 1989).

The other main conclusion of this study is that landscape variables add an important source of explanatory power to rabbit-habitat models. Microhabitat variables did not emerge as useful variables in our analyses. This suggests that if macrohabitat descriptors were not used, rabbit-habitat models would be less useful for managers. Previous studies on rabbits indicated that landscape variables are very important to explain rabbit distribution and abundance (Myers and Parker 1975, Rogers and Myers 1979, Soriguer and Rogers 1981), but no study has previously analysed the relative role of microhabitat and macrohabitat factors simultaneously. Future studies may gain from this multi-scale approach but the data indicate that macrohabitat descriptors might be more useful, when money or time-constraints prevent the sampling of microhabitat variables in the field. On the other hand, this study supports previous suggestions about the importance of factors acting at large scales in shaping the distribution of species (eg Wiens *et al*. 1987, Kotliar and Wiens 1990).

The relatively low predictive power of the fragmented population model is supported by several theoretical studies (Wilcox and Murphy 1985, Hanski 1991). They indicated that species abundance in fragmented populations may be mainly shaped by stochastic events: genetic, demographic and environmental risks. Possibly, myxomatosis and RHD could also represent important stochastic factors shaping rabbit abundance pattern in fragmented populations. The effects of these diseases have been suggested as very critical in small populations (Villafuerte *et al*. 1995, Calvete and Estrada 2000). Alternatively, the low predictive value compared to continuous populations may be a consequence of the effect on abundance of the distance to other near isolated populations. A complete sampling of all populations and an extensive survey on the prevalence and effect of diseases in this area may greatly improve our knowledge on the determinants of distribution of rabbits in fragmented and small-sized populations.

In conclusion, management and conservation strategies should be carefully based on landscape pattern in each situation, as rabbit abundance is different between fragmented and continuous areas. In order to raise current density of rabbits, management practices in continuous areas need to promote mosaics of pastures or croplands and scrubs. Controlled burning or cultivation in selected areas may be adequate management as has been shown in other Mediterranean areas (Moreno and Villafuerte 1995). Cleared areas may be colonized by native herbs (pastures) or cultivated with cereals.

In the fragmented areas, a reduction in cattle density may improve the suitability of pastures for rabbit grazing but this management may be difficult to perform because traditional cattle management is an important economic activity (Valenzuela 1987). Alternatively, the reintroduction of rabbits in some areas, where the species have disappeared in the last decade due to RHD spread, may be an interesting tool. This would reduce the distance between populations and enhance the likelihood of effective dispersal and re-colonisation of patches where rabbits had become extinct.

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