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Research article

Habitat factors related to wild rabbit conservation in an agricultural landscape

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Abstract

Populations of European wild rabbit (*Oryctolagus cuniculus*) have been decreasing since the 1950s. Changes in agricultural practices have been suggested as reasons for their decline in Mediterranean landscapes. We evaluated the environmental variables affecting rabbit distribution in a semiarid agricultural landscape of Northeastern Spain. Sampling was performed in 147 sites randomly distributed across Zaragoza province. At each site, data were recorded in five 100 m segments along a 1 km transect, following ecotones between crops and natural-vegetation areas. A rabbit abundance index was estimated from latrine count, pellet density and number of plots with pellets. In addition to environmental variables that have been shown to be related to rabbit abundance in other habitats, as climate, soil hardness and topography of the site, we measured landscape components related to agricultural use, such as structure of natural vegetation in remaining areas non-devoted to agricultural use and distances to different types of crops and to ecotone between crop and natural vegetation. Our results showed that rabbit abundance was positively correlated to yearly mean temperature, February and May mean rainfall, and negatively correlated to September and November mean rainfall, hardness of soil, and site topography. In relation to agricultural use, rabbit abundance was positively correlated to the scrub structure of natural-vegetation areas and negatively correlated to distance to edge between cultivated unirrigated cereal crops (wheat or barley) and yearly resting cereal crops. Rabbit abundance increased only when the edge between alternate cereal crops was less than 50 m from the ecotone between crops and natural vegetation.

Introduction

In recent decades, changes in agriculture in Southern Europe have been characterized by intensification of cultivation, and exploitation of natural-vegetation areas with the help of agricultural mechanization (Wilcove et al. 1986). The Mediterranean Basin is usually regarded as the most conserved region in Europe, with high biodiversity, a high degree of endemism, and many species of endangered wildlife. However, one of the main conservation problems in the Mediterranean is loss of habitat caused by the intensification of agricultural practices (Myers et al. 2000).

Changes in land-use and agricultural practices have been suggested as reasons for the decline of several species (Chamberlain and Fuller 2000; Palma et al. 1999; Smith and Bruun 2002), and in some cases, spatial variations of specific landscape components have been identified as the causes of wildlife decline (Hones et al. 1996; Rands 1986). This is especially true in the agricultural semiarid landscape, which provides breeding grounds for many species of conservation concern (Nadal et al. 1996; Suárez et al. 1997; Tella et al. 1998). Examples of changes in the abundance and distribution of Mediterranean wildlife as a result of agricultural changes include reductions in range and numbers of several bird species (Nadal et al. 1996; Tella et al. 1998; Carrete et al. 2002), and endangered predators such as the Iberian lynx (*Lynx pardina*) (Palma et al. 1999).

In the Mediterranean, wild rabbit is usually the staple prey of a wide variety of predators, some of which are threatened with extinction, as the imperial eagle (*Aquila adalberti*) and the Iberian lynx (Delibes and Hiraldo 1981). It is also the most important small game species in sport hunting in Spain. Wild rabbit populations have been declining since mid 20th century. This decline has been recorded since the arrival of *Myxomatosis* in the 1950s (Ratcliffe et al. 1952; Muñoz-Goyanes 1960) and Rabbit Haemorrhagic Disease (RHD) at the end of the 1980s (Argüello et al. 1988). Considerable efforts have been made to enhance wild populations for hunting and conservation purposes. Management strategies include predator control, vaccination campaigns and restockings (Calvete et al. 1997; Angulo 2003). However, habitat management is the main management strategy, as landscape changes and habitat loss exacerbate the effects of disease and hinder the recovery of wild rabbit populations (Moreno and Villafuerte 1995; Palma et al. 1999).

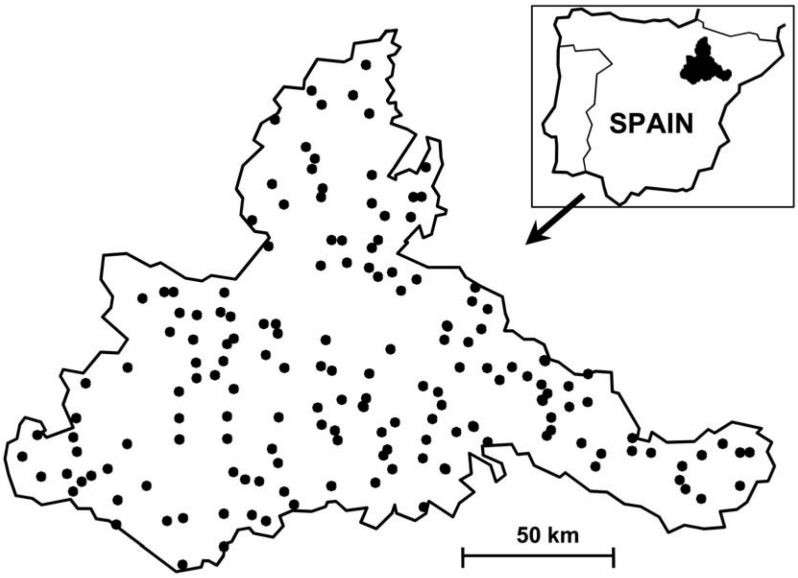
To date, no research has identified which specific landscape components related to agriculture are determining the maintenance of wild rabbit populations in the Mediterranean. Some studies in Northern Europe have focused on the impact of agricultural practices on rabbit populations through changes on habitat structure (Boag 1987; Trout et al. 2000). Palma et al. (1999) suggested that, in Mediterranean ecosystems, changes in land uses in recent decades might be one of the main causes favouring the recent fragmentation and the lack of recovery of rabbit populations. After the appearance of RHD in wild populations, only the surveys of Fa et al. (1999) and Virgós et al. (2003) tried to determine the correlates between rabbit abundance and habitat variables in Mediterranean landscapes, but their results were not very conclusive. Given that Mediterranean landscapes consist of a mosaic of crops and natural-vegetation areas, detecting which agricultural landscape components determine the conservation of rabbit populations could help in the compatibility between agriculture practices and wildlife conservation.

In this paper we aimed to identify the most important factors that determine current wild rabbit abundance in semiarid agricultural landscapes of Mediterranean Spain, a decade after the arrival of RHD. Taking into account factors such as climate, topography and hardness of soil that are known to affect wild rabbit distribution (Rogers and Myers 1979; Parer and Libke 1985; Trout and Smith 1995; Trout et al. 2000), we focussed on the landscape components that were related to agriculture practices. These components were remaining natural vegetation structure and cover, and presence of different types of crops. Determining such relationships could help to guide specific habitat management strategies that aim to enhance wild rabbit populations in semiarid agricultural landscapes. As a prey species, it is known that the wild rabbit maximizes the time between refuge patches and food patches (Moreno et al. 1996; Villafuerte and Moreno 1997). In semiarid agricultural landscapes, crops provide the main food for rabbits while natural vegetation and field margins provide refugia and breeding sites. Thus, in these landscapes it can be predicted that rabbit abundance would be positively affected by the presence of a good cover in the natural areas, which reduces their risk of predation, and by the amount of crops offering high quality food, which favors physical condition and reproduction.

Methods

The study site was located in Zaragoza province (17,274 km^2), northeastern Spain (Figure 1). Geographical range of sampled sites was from 2º 7′W to 0º 18′E longitude and from 40º 58′ to 42º 32′N latitude. The climate is Mediterranean and predominantly semiarid, with yearly mean rainfall and temperature of 377 mm and 13.5 °C, respectively, for the entire study area. By area, 47% of the province is devoted to agricultural use, mainly the production of wheat and barley on unirrigated land. Because of climatic and soil conditions in the area, non-irrigated cereal crops are produced once every two years, with a resting year between consecutive harvests. During resting years the ground is ploughed but not sown.

To select sampling sites, the province was subdivided into 179 100 km^2 areas (10 km $\times$ 10 km). Eleven areas located on the irrigated plain of the Ebro and Gallego rivers and near Zaragoza city were excluded because intensively irrigated crops in these areas have never been suitable for rabbits. Ninety-one from the 168 remaining areas were randomly selected. With this sampling protocol more than 50% of suitable areas were sampled, and their distribution was uniform across the province surface.



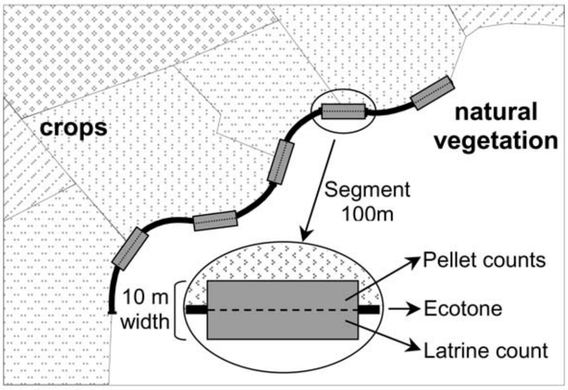


Figure 1. Study area and scheme of a 1-Km transect with the five segments where latrine and pellet counts were performed. Environmental variables were recorded from the center of each segment.

Two sites were sampled in each 100 km^2 selected area, except when the agricultural landscape accounted for less than 50% of the area. In these cases, in order to avoid the sampling of very close sites, only one site was sampled per area. Thus, two sites were sampled in 56 of the 91 squares, and a total of 147 sites were sampled across whole province (Figure 1). Each site consisted of a 1 × 1 km surface. These sites were selected on 1:25,000 topographic maps according to the following three criteria: (1) for ease of access, to be within 500 m of a road or track, (2) to have, at least, 1 km length of ecotone between crops and natural-vegetation area and (3) to be representative of the agricultural use of the soil within the 100 km^2 area. A site was considered representative of the agricultural use when the types of crops of the site were the most frequent in the area. All sampled sites were at least 2 km away from human habitations and the minimum distance between sites was 3 km.

The best estimation of rabbit abundance by means of pellet count in Mediterranean scrublands is obtained at the edge of scrub with open areas (Palomares 2001). For these reasons in each sampled site a transect 1 km long, 10 m wide, was walked by two observers following ecotones between crops and natural-vegetation areas. We defined natural-vegetation areas as those that were wider than 50 m (measured perpendicular to the ecotone boundary). Along of transect environmental variables and rabbit abundance was estimated. Transects were divided into ten 100 m segments and rabbit abundance and environmental variables were estimated in five alternate segments along each transect (Figure 1). Transects were measured during July-August of 2001, after the rabbit breeding season, and just after rabbit densities had peaked (Calvete et al. 2002).

Estimation of relative rabbit abundance

Latrine and pellet counts have been widely used as indices to estimate rabbit abundance (Taylor and Williams 1956; Iborra and Lumaret 1997; Fa et al. 1999; Palomares 2001), and both methods were used in this survey. To minimize methodological variations, pellet and latrine counts were always performed by the same observer.

Latrine counts were performed along a 2 m wide band in the natural-vegetation areas included in the transect 10 m wide band. Only pellet groups with clear fecal accumulation and at least 100 pellets were considered a latrine. Latrine counts alone are not strictly adequate to compare rabbit abundance between areas, because average size of latrines can differ substantially with rabbit density. In order to obtain a more accurate estimate of rabbit abundance, a corrected count of latrines, taking into account their size, was performed. The corrected count estimated the length of the maximum diameter of each latrine in 30 cm length intervals. Latrines with a maximum diameter < 30 cm were counted as one and no fractions of length were estimated, because counts were rounded up for every latrine. Thereafter, corrected latrine count estimated along each segment was the number of 30 cm intervals length occupied by latrines. This method facilitated a quick estimation of latrine abundance corrected by their size along transects.

Pellet counts were done in ten 0.5 m^2 circular plots for each segment in the crop area included in the transect band. Plots were uniformly spaced at 10 m intervals along the length of the segment, and counts on or near latrines were avoided. The total number of pellets counted in the ten plots within each segment was used as a pellet abundance index. In addition, the number of plots with pellets (positive plots) in each segment was used as a third estimate of rabbit abundance. In the case of transects performed next to cereal crops, in order to avoid biases estimation of pellet abundance due to just ploughed crops in resting year (where pellets were buried), transects were performed next to cultivated cereal crops.

Environmental variables

Environmental variables were estimated at site (1 km transect) and segment (100 m transect) levels. At site level, topography was estimated from 1:25,000 scale maps. Following to Virgós et al. (2003) we recorded the number of 20 m elevation lines in two perpendicular lines (N-S and E-W orientation) crossing the center of the 1x1 km site area. In addition we also calculated the difference (in meters) between the highest and the lowest elevation lines of the site.

Climatological variables were estimated from original data provided by the National Meteorological Institute. Mean monthly rainfall for each site was estimated from monthly pluviometric data recorded from 1980 to 2000 at weather stations ($n = 121$). Distance from each site to the nearest weather station was always < 10 km, and the elevation difference between each site and its weather station was < 100 m. When a site was within 10 km and $\pm$ 100 m of elevation of several weather stations, the arithmetic mean of their data was used.

Thermometric weather stations were more distant than pluviometric stations from sampled sites, and it was not possible to obtain direct monthly estimates of thermometric data for each site. Thus, only yearly mean estimations of temperature were performed. To do this, a linear multiple regression model was fitted to data of all weather stations ($n = 174$) within the geographical range of the study area. Yearly mean temperature of each station, estimated as the arithmetic mean of yearly mean temperatures registered from 1990 to 2000, was introduced in the model as dependent variable, and longitude, latitude and altitude of all weather stations were used as predictor variables. The regression model obtained (adjusted $R^2 = 0.81$; df $= 3$; $F = 254.41$; $P < 0.001$) was used to estimate yearly mean temperature of each site.

At segment level, environmental variables were recorded at the center of every segment. We estimated soil hardness and vegetation structure within a circular plot of radius 50 m in each segment. Soil was classified as soft, compact, hard, or rocky, to reflect its relative suitability for burrow excavation. Soil hardness was measured only in naturally vegetated areas. In an agricultural environment, rabbits can excavate their breeding stops amongst the crops, where soil is usually deeper and softer. However, because of farming works and the higher risk of predation of young rabbits in stops compared to warrens, we considered that breeding success was related to hardness of soil in non-cultivated areas, where permanent and therefore bigger warrens can be dug (Myers and Parker 1965; Wood 1980; Gibb 1993). Vegetation structure in naturally vegetated areas was characterized by estimating by eye mean height and percentage cover of herbs, scrub, and trees, following similar protocols to general habitat-species studies (Morrison et al. 1992). Small trees with branches at soil level were classified as scrub.

We estimated minimal distances from the center of each segment to the following agricultural landscape components: (1) each different kind of crop (the possible outcomes were: unirrigated cereal (wheat or barley), vineyard, almond orchard and/or olive grove, sunflowers, irrigated lucerne, irrigated cornfield, or non-cultivated crop other than yearly resting cereal crop); (2) in the case of unirrigated cereal crops, distance to yearly resting crops (hereafter distance to edge between alternate unirrigated cereal crops); (3) permanent water sources; (4) ecotone between crop and natural vegetation. Distance estimates were recorded as < 50 m, 51-100 m, 101-150 m, 151-200 m or > 200 m. Distance classes > 200 m were not discriminated because, in many areas, landscape topography precluded observations greater than 200 m. To avoid methodological variations, all estimations of environmental variables were performed by the same observer.

Data analyses

Corrected latrine count, pellet abundance, and positive pellet plots were highly correlated. To assess rabbit abundance a principal component analysis (PCA) was performed to express the three correlated variables using a single rabbit abundance index. A principal component, accounting for the 85.83% of original variance of the three variables, was obtained, and its scores were used as rabbit abundance index (Table 1a). To reduce variance, the three variables were square root transformed before applying PCA.

Some tolerance values, estimated to test colinearity among raw environmental variables, were very close to zero (< 0.001), i.e., some raw environmental variables were highly correlated. Therefore, PCA was used to reduce the original raw data set. To facilitate interpretation, several PCAs were performed within groups of related raw variables (topographic-PCA, vegetation-PCA, distances to-PCA and climatological-PCA). The principal components obtained and the explained variance are shown in Table 1. The scores of the principal component obtained from the topographic-PCA increased from plain to hill and mountain sites and were used as a single topographic index. Soil hardness and minimum distance to ecotone between crop and natural vegetation were not included in these PCAs, since they were correlated with no other environmental variable. After PCAs, the tolerance values of new environmental variables obtained from PCAs were higher than 0.92. However, the principal components obtained in the PCA performed with climatological variables were biologically unmeaningful with respect to rabbit ecology. Therefore, raw climatological variables were used in the subsequent analyses.

Associations between rabbit abundance index and environmental variables were tested by fitting a generalized linear mixed model to the data using maximum likelihood estimation of the parameter vector through an iterative process. Computations were performed with SAS Macro program GLIMMIX (Version 25 Sep 1998) which iteratively runs SAS Procedure MIXED (SAS Institute, 1997). The rabbit abundance index obtained from PCA was the dependent variable, and a gamma distribution with log-link function was used as the error distribution. Segments were grouped into transects and data from segments were correlated within each transect. This covariance structure was handled by introducing transects (site level) as random effects into the GLIMMIX. The initial independent variable set comprised the raw variables (Table 1b; soil hardness and minimum distance to the ecotone between crop and natural vegetation); the principal components obtained from the PCAs (Table 1c-e; topographic index, tree, scrub, herb and the five factors obtained in the distances to-PCA), and the raw climatological variables (yearly mean temperature and monthly mean rainfall for every month). All these variables were introduced in the model as fixed effects. A backward elimination procedure was used to obtain the final model. Goodness of fit of the final model was measured as the percent deviance explained from the null model deviance (McCullagh and Nelder 1997).

Because some pairs of climatological variables were highly correlated, we verified that the coefficients for each variable were determined by the true correlation with the dependent variable and not by the sign of the coefficients of the other retained variables.

Table 1. Variables used in the model.

a) Rabbit abundance index					
	Rabbit abundance index				
Latrines/100m	0.91				
Pellets / 5 m^2	0.94				
Positive plots	0.92				
Eigenvalue	2.57				
Rabbit abundance-PCA (unrotated solution)			Explained variance		85.83 %
b) Raw variables					
Yearly mean temperature					
Monthly mean rainfall					
Soil hardness					
Minimum distance to ecotone between crop and natural vegetation					
c) Topographic index					
	Topographic index				
Elevation lines N-S	0.80				
Elevation lines E-W	0.83				
Elevation difference	0.80				
Eigenvalue	1.98				
Topographic-PCA (unrotated solution)			Explained variance		66.14 %
d) Vegetation structure					
	Tree	*Scrub*	*Herb*		
Tree height	0.93	0.10	–0.05		
Tree cover	0.92	0.15	–0.06		
Scrub height	0.10	0.89	0.03		
Scrub cover	0.15	0.85	–0.20		
Herb height	–0.05	0.02	0.83		
Herb cover	–0.05	–0.18	0.81		
Eigenvalues	2.28	1.15	1.31		
Vegetation-PCA (varimax rotation)			Explained variance		79.08 %
e) Crop distances					
	Factor 1	*Factor 2*	*Factor 3*	*Factor 4*	*Factor 5*
Unirrigated cereal crop	–0.16	–0.04	0.83	–0.22	–0.12
Edge between alternate cereal crops	–0.06	0.91	0.24	–0.05	–0.06
Vineyard	–0.05	–0.14	–0.11	0.75	–0.05
Almond orchard or olive grove	–0.08	–0.12	–0.76	–0.11	–0.12
Sunflowers crop	0.05	–0.05	0.01	–0.03	0.97
Irrigated lucerne crop	0.79	–0.03	–0.10	–0.01	–0.14
Irrigated cornfield	0.85	–0.01	–0.08	–0.01	0.19
Non cultivated crop	0.01	0.08	0.04	0.81	0.02
Permanent water source	0.72	–0.09	0.09	–0.04	0.02
Eigenvalues	2.18	1.68	1.42	1.16	1.01
Distances to-PCA (varimax rotation)			Explained variance		74.43 %

To do this, the relationship between every climatological variable retained in the final model and the rabbit abundance index was explored by fitting a new exploratory GLIMMIX (with the same structure covariance and error distribution), and controlling for the effects of all environmental variables selected in the final model, but excluding the remaining climatological variables in the independent variable set.

To test the effect of distances (from the center of segments to landscape components) retained in the final model on the rabbit abundance index, a new generalized linear mixed model analysis was performed using a structure covariance and an error distribution the same as those used in the first analysis. Rabbit abundance index was the dependent variable, and all independent variables retained in the first fi-

Table 2. Mean, variance and range of raw variables and the PCA-estimated abundance index related to rabbit abundance in sampled segments (n = 735).

	Mean	Variance	Range
Corrected latrines /100 m	1.04	8.32	0 − 27
Pellets / 5 m^2	14.68	3518.95	0 − 1013
Positive plots	1.80	8.15	0 − 10
Abundance index	0.70	1	0.06 − 5.84

nal model were included as covariates, except for the PCA variables reflecting distances to habitat elements. These PCA-variables were substituted by the raw variables (the estimated distance intervals) and introduced in the initial model as categorical predictor variables with five levels. A Dunnett's one tailed test was performed to test differences between the estimated distance intervals, being the most distant interval ($>$ 200 m) the control level.

Results

Random sampling of sites across Zaragoza encompassed a broad and representative range of climatological and topographical features, and the agricultural practices within the province. Yearly mean rainfall and temperature at study sites ranged from 260 to 611 mm and from 10.1 to 16.4º C, respectively. Altitude ranged from 160 to 1,180 m a.s.l. Unirrigated cereal cropping (wheat and barley) was the dominant agricultural land use.

The distribution of the raw variables related to rabbit abundance in sampled segments was strongly overdispersed, with low mean values and high variances (Table 2). No sign of rabbit presence (pellets or latrines) was found in 28.57% of the 147 sampled sites. The mean density of pellets and corrected latrine counts per segment for the whole province was very low in comparison to the highest values found in a few segments (Table 2). Corrected counts of latrines and pellet density were higher than the mean values in only 17.82% and 15.65%, respectively, of the 735 segments sampled.

In the GLIMMIX analysis, the final model retained nine of the 23 independent variables included in the initial model (Table 3), and explained 69.9% of variation in abundance index. Of the climatological variables, yearly mean temperature, and February and May monthly rainfall were positively correlated to the rabbit abundance index, whereas September and November monthly rainfall were inversely correlated to it. Each rainfall variable retained the same sign obtained in the final model when the other rainfall variables were removed from it. Rabbits were less abundant when hardness of soil in natural-vegetation areas or topographic index of site were higher. Among variables reflecting vegetation structure in natural-vegetation areas, rabbit abundance index was positively correlated with scrub, and not with tree or herb. Scrub variable was a principal component directly associated with height and cover of scrub vegetation (Table 1).

Among variables reflecting distances to crops, the principal component Factor 3 (unirrigated cereal crops, almond orchard, and/or olive grove) and Factor 2 (edge between alternate cereal crops) were closely associated with rabbit abundance index. The principal component Factor 3 was strongly inversely associated with the dependent variable, but was not retained in the final model (Coefficient $\pm$ SE = -0.092 ± 0.051; t = -1.79; P = 0.074). Only Factor 2, which was inversely correlated to the rabbit abundance index (Table 3), was retained in the final model. This association showed that the rabbit abundance index was highest in those segments nearest to edges between alternate unirrigated cereal crops.

The effects of distance to edge between alternate cereal crops on rabbit abundance index were also tested using GLIMMIX. In this analysis, all independent variables retained in the final model (Table 3) were included as covariates, except the principal component Factor 2, which was substituted by the raw categorical estimation of distance to edge between alternate cereal crops. In the results of this analysis, all independent variables were retained with the same sign of association with rabbit abundance index and with similar statistical signification levels to those obtained in the first GLIMMIX. Comparisons, using the Dunnett's test, of all intervals of distance against the most distant interval ($>$ 200 m) which was considered as the control level, showed that rabbit abundance index increased only when the edge between alternate cereal crops was less than 50 m from the ecotone between cover and crop (t = 3.81; $P < 0.001$) (Figure 2). No statistically significant difference in rabbit abundance index was found when the control level was compared with distance intervals of 51 − 100 m (t = -0.21; P = 0.885), 101 − 150 m (t = -1.48; P = 0.997), and 151-200 m (t = 0.16; P = 0.774).

Table 3. Coefficients of independent variables from the GLIMMIX analysis for rabbit abundance index. Topographic index, Scrub and Factor 2 were principal components estimated from raw variables (see Table 1).

	Coefficient ± SE	t	P
Yearly mean temperature	0.519 ± 0.113	4.59	< 0.001
February mean rainfall	0.006 ± 0.003	2.48	0.013
May mean rainfall	0.006 ± 0.002	3.80	< 0.001
September mean rainfall	–0.004 ± 0.002	–2.88	0.004
November mean rainfall	–0.004 ± 0.002	–2.53	0.012
Hardness of soil	–0.324 ± 0.067	–4.8	< 0.001
Topographic index	–0.273 ± 0.093	–2.95	0.003
Scrub	0.228 ± 0.056	4.05	< 0.001
Factor 2	–0.154 ± 0.047	–3.30	0.001

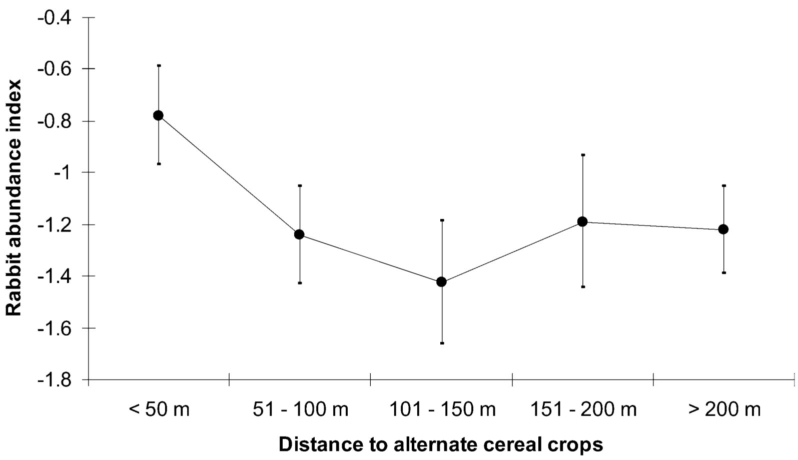


Figure 2. Least squares means (with 95% confidence intervals) of rabbit abundance index, estimated from the GLIMMIX analysis, in relation to distance (in meters) to edge between cultivated and yearly resting unirrigated crops of wheat or barley.

Discussion

Influence of landscape abiotic components on rabbit abundance

The distribution of rabbits in different landscapes is influenced by topography, soil hardness and climatological conditions (Rogers and Myers 1979; Parer and Libke 1985; Trout and Smith 1995; Trout et al. 2000; Virgós et al. 2003). The effects of these factors were also detected and controlled in our study. Controlling these factors was necessary to estimate the effects of landscape components related to agriculture on rabbit abundance.

The lack of rabbits in sites with high topographic index values (mainly mountain sites) may reflect fragmentation and isolation of rabbit populations due to the patchy distribution of suitable habitat at the bottom of valleys. Outbreaks of myxomatosis and RHD or other stochastic events may cause the local extinction of small populations (Lande et al. 1994; Calvete et al. 2002), and the steep topography and patchy distribution of habitat may hinder movement between neighboring populations and, therefore, repopulation of suitable empty habitats (Forys and Humphrey 1999; Virgós et al. 2003).

In addition to soft soil in which to dig warrens or breeding stops, the availability of wild food species affects the breeding success and health of lagomorphs (Eisermann et al. 1993; Lochmiller et al. 1995; Peitz et al. 1997; Villafuerte et al. 1997). Autumn rainfall influences the germination and growth of the annual plants, which, in turn, influences the onset of the rabbit breeding season (Delibes and Calderón 1979; Villafuerte et al. 1997). However, high rainfall can make thermoregulation difficult, thereby increasing mortality rates in early winter (Rodel 2000). High rainfall can also lead to excessive soil moisture, which limits plant growth, leading to food shortages, and delaying the onset of the breeding period (Wood 1980; Bell and Webb 1991; Villafuerte et al. 1997; Trout et al. 2000). In the study area, the rabbit breeding season usually lasted from October to April, with the highest proportion of pregnant females from January to April (Calvete et al. 2002). Thus, the association found in our work may reflect the lower rabbit abundance in sites where high autumn rainfall causes a shortening of the breeding season. Conversely, an increase of rainfall in February and May, when rainfall is usually low, may be associated with an increase in suitable quality food for rabbits. This will extend the length of the breeding period and enhance the physical condition of young rabbits during the driest summer period (Richardson and Wood 1982; Peitz et al 1997). These effects could be related to the high rabbit abundance detected in our study in areas with high rainfall during February and May.

Influence of spatial structure of crops and cover on rabbit abundance

Vegetative cover has been positively associated with rabbit abundance in other studies (Rogers and Myers 1979; Papillon and Godron 1997; Fa et al. 1999). In Mediterranean agricultural landscapes, non-cultivated natural areas provide rabbits with refugia from predators. Thus, even when agricultural intensification has lead to a 35% decline in the area of naturally vegetated sites (Nadal et al. 1996), our results showed that scrub cover in naturally vegetated sites within agricultural landscapes is important in maintaining rabbit abundance. However, our study failed to detect any relationship between rabbit abundance and minimum distance to ecotone between crop and natural-vegetation area. We expected a negative correlation between this variable and rabbit abundance, since rabbits are typically more abundant at sites where foraging habitat exists as patches within refugia (Rogers and Myers 1979; Rogers 1981; Moreno and Villafuerte 1995; Virgós et al. 2003). This lack of association in our study was, probably, because transects were aligned along the ecotones between crops and natural vegetation, rather than being randomly located. When transects are established in random directions, rabbit abundance estimates are highly associated with the number of ecotones crossed by the sampling line, and therefore with density of ecotones (Fa et al 1999; Palomares 2001).

In extreme dry semiarid agricultural landscapes such as those of the Mediterranean, naturally-vegetated areas have lower plant productivity than cultivated soils. As a result, crops are the main food resource for rabbits. We found that rabbit abundance was related to type of crops. Studies on the diet and food habits of rabbits in agricultural landscapes have showed that they preferentially feed on cultivated Gramineas, such as wheat and barley, especially during the peak-growing season, which coincides with the rabbit breeding season (Homolka 1988; Chapuis and Gaudin 1995). Our results showed that rabbit abundance was highest in segments where the edge between alternate cereal crops was at most 50 m from the ecotone between natural cover and crop. Rabbits that inhabit sites where cover is close to this habitat component have relatively safe access to abundant, good quality food during the breeding season, in all years. As a result, they probably enjoy relatively high breeding success. At other sites, rabbits face two major obstacles. First, in alternate years, they can consume only wild plant species produced in resting crops. Resting crops are usually ploughed in the second half of the breeding season to eliminate weeds, probably causing a reduction in the length and intensity of rabbit reproduction. Second, they have to venture further into open crops, which increases their vulnerability to predation. The findings about the distance from cover to edge between alternate cereal crops associated with increases in rabbit abundance agree well with previous studies on rabbit use of prairies in SW Spain in relation to the decrease of the risk of predation (Moreno et al. 1996).

The dependence of rabbit abundance on crop productivity was also suggested in the marginally significant negative association of rabbit abundance with distance to cultivated trees, and the positive association with non-irrigated cereal crops. The ground around non-irrigated crops of trees such as olives and almonds is usually ploughed several times each year to eliminate weed competition with the cultivated trees. This regular ploughing permanently reduces the availability of high quality food to rabbits in these crops.

Conclusion

Since the arrival of Myxomatosis in the study area in the 1950s and the arrival of RHD in the 1990s a decrease in rabbit abundance has been recorded. However, agricultural landscape has also changed since then, with an increase in the mean area of crops, the decrease of ecotone density, and the number of edges between cereal crops with alternate yearly resting (Nadal et al. 1996; Tella et al. 1998). Our results demonstrate that, besides topography, soil hardness and climate, rabbit abundance is influenced by agricultural practices (types of crops), and by some agricultural landscape components that are affected by agricultural intensification (scrub structure of residual natural areas and edges between alternate cereal crops). Therefore, our results suggest that, besides both diseases, agricultural landscape changes have probably contributed to the decline of rabbit abundance during recent decades.

Similar to the findings reported by Fa et al. (1999) in Cadiz province, mean abundance of rabbit populations was very low, but exhibited a high variance. Many sites with little or no rabbit sign appeared to be as suitable as habitat for rabbits as other sites where rabbits were abundant. These findings suggest that, after the first negative impact of RHD, other factors could be hindering the repopulation of some suitable habitats, such as patch isolation, predation, disappearance of warrens or differential impact of RHD between populations (Calvete et al. 2002). Meanwhile, low density populations in marginal habitats could continue to have an increased risk of extinction, unless effective habitat management measures are established to increase habitat suitability and to connect isolated patches through adequate landscape features.

Our results provide policy makers, planners and land-managers with valuable information on the correlates between wild rabbit populations and the landscape spatial components in agricultural semiarid landscapes. The increase or conservation of scrub cover in natural-vegetation areas should increase habitat suitability for rabbits. In addition, implementing alternative patterns of agricultural use may be a powerful tool to manage rabbit populations. For example, the types of crops, and their spatial and temporal distribution could be chosen to provide more suitable rabbit habitat. The recovery by hunting associations of abandoned small crops to creation of alternate cereal crops, and the promotion, by government agencies in protected areas or by landowners interested in increasing small game in their properties, of traditional agricultural practices, with longer ecotones, smaller crops, and more edges between alternate cereal crops, may be sufficient to reverse the decline in rabbit densities and range, and therefore, to enhance populations of rabbit-dependent predators in Mediterranean landscapes.

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