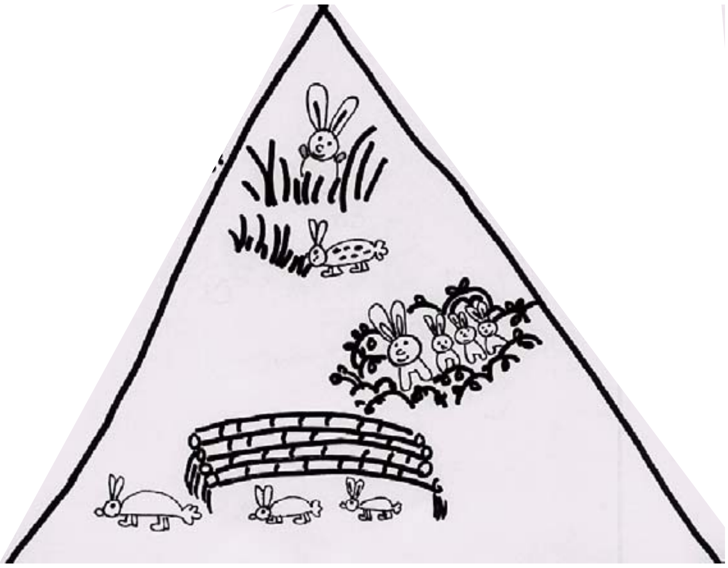

CAPÍTULO 1

Distribution and abundance of wild rabbitt populations: accounting the effects of historical variables versus traditional GIS variables

Influencia de las variables históricas y de las variables de paisaje sobre la distribución y abundancia de las poblaciones de conejo en Andalucía

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"El nombre latino de Hispania es, al parecer, de origen púnico; alude a la abundancia de conejos, que tanto sorprendió a los mismos griegos y romanos. La voz fenicia i-shepham-im, de la que se supone derivaría, pudo significar "costa o isla de los conejos". La H de Hispania es añadido romano, como lo es en Hiberia y en Hispalis."
Antonio García y Bellido. 1945. España y los Españoles hace dos mil años. Según la geografía de Strabon.

Resumen

El conejo, ampliamente distribuido por el Sudoeste de Europa, ha tenido una tendencia negativa en las últimas décadas, tanto en su distribución como en sus abundancias. Sería de esperar, por tanto, que la distribución actual reflejara el efecto de acontecimientos que ocurrieron en el pasado. El objetivo de este Capítulo es comprobar dicha cuestión y cuantificar si las poblaciones de conejos responden a estas características y propiedades del paisaje o, por el contrario responden a otros factores históricos que pudieran haber forzado su distribución o abundancias en el pasado. Para la consecución de dicho objetivo se han desarrollado modelos de regresión (modelos lineales generalizados) tomando como variable dependiente la presencia, en unos casos, y la abundancia, en otros, de conejo en 307 áreas andaluzas, y siendo las variables independientes, bien variables de paisaje (procedentes de sistemas de información geográfica, SIG), bien variables históricas (obtenidas mediante encuestas). A cada uno de estos cuatro modelos (presencia o abundancia con variables de paisaje o históricas) se le añadieron variables de autocorrelación espacial para comprobar la existencia de patrones espaciales. A través de estos modelos, se evaluó el uso de diferentes fuentes de información de las variables explicativas.

Las variables de SIG permitieron comprobar la influencia del paisaje (hábitat, clima, topografía, geología, efectos humanos y patrones espaciales) sobre la presencia y abundancia de conejo. La presencia de conejo presentó un patrón espacial, relacionado probablemente con las extinciones de conejo que ocurrieron en los hábitat menos adecuados para dicha especie.

Las variables de paisaje seleccionadas en los modelos de presencia de conejo fueron: los suelos más duros y pedregosos (que están relacionados con una menor probabilidad de encontrar una población de conejos), los climas más benignos para el conejo y la superficie cubierta por cultivos mixtos de secano (ambas aumentan la probabilidad de encontrar una población de conejos). Las variables de SIG seleccionadas en los modelos de abundancia mostraban que los climas benignos y la superficie cubierta por cultivos mixtos de secano también se asocian a mayores abundancias de conejo. Además la abundancia de conejo también se relacionó positivamente con una mayor superficie de ecotono, de cultivos mixtos en regadío y de cultivos homogéneos de secano, así como con la cantidad de superficie cubierta por vegetación natural.

Los mejores modelos de presencia de conejos se obtuvieron con las variables históricas, que parecen haber forzado su distribución o abundancias en el pasado: las enfermedades y los manejos. La presencia de conejos y su abundancia fueron explicadas en mayor grado por la intensidad de la recuperación de las poblaciones después de la entrada de la enfermedad hemorrágica durante la década de los 90 y en menor grado por la intensidad de la recuperación de las poblaciones después de la entrada de la mixomatosis durante los años 50. La presencia de la mixomatosis estuvo positivamente relacionada con la presencia de conejo pero negativamente relacionada con su abundancia. Esto se puede explicar, por un lado, por la relación existente entre la detección de la enfermedad y la densidad poblacional y, por otro lado, por el efecto obvio de la enfermedad en el incremento de la mortalidad en las poblaciones.

La presencia de conejo estuvo también relacionada con la intensidad de las estrategias de gestión desarrolladas a lo largo de los últimos 30 años. La presencia de conejos mostró una relación negativa con la intensidad de uso de las translocaciones y de las estrategias de prevención de enfermedades y parásitos. Esto se puede explicar porque dichas estrategias normalmente se aplican cuando la abundancia de conejo es muy baja.

Por último, el abandono del campo resultó inversamente relacionado con la presencia y la abundancia de conejo. Es más difícil encontrar una población de conejos en los lugares donde ha habido abandono del campo, y en el caso de encontrarla su abundancia es baja. Esta variable parece tener un componente espacial importante, posiblemente porque está asociada a un determinado tipo de paisaje.

Este Capítulo pone en evidencia la necesidad del uso de múltiples fuentes de información cuando se modela la distribución o abundancia de una especie silvestre. Esta aproximación es especialmente útil cuando las especies han sufrido cambios en cualquiera de estos dos parámetros, por lo que su distribución y abundancia puede venir influida por acontecimientos ocurridos en el pasado.

Distribution and abundance of wild-rabbit populations: accounting for the effects of historical variables versus traditional GIS variables

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ABSTRACT

Wild rabbit (*Oryctolagus cuniculus*) is widely distributed in southwestern Europe; however their population has declined over the past century both in terms of distribution and abundance, been expected that the current distribution reflects the effects of past factors. The aim of the present study was to test whether rabbits are responding to suitable and available landscape features, or to other factors that may have constrained their distribution or abundance in the past. To achieve this aim, we evaluated different sources of information to understand the present distribution and abundance of wild-rabbit populations.

We used GIS techniques to test the effects of landscape: habitat features, climate, topography, geology, hydrology, human presence, and spatial patterns. Rabbit presence was spatially segregated, which was probably related to population extinctions occurring in the least-preferred landscapes for rabbit, with these landscapes exhibiting an inherent spatial structure. Rabbit presence was explained to a high degree by variables related to the effects of past factors. However, rabbits avoided hard soils, preferring mixed non-irrigated cultures, their abundance being associated with the amount of the surface covered by these cultures. Rabbit abundance correlated also with the amount of ecotone, and with mixed irrigated cultures, homogeneous non-irrigated cultures, and other natural-vegetation habitats.

The best models for rabbit presence were those with factors that may have constrained rabbit populations in the past: rabbit diseases and historical management. Rabbit presence and abundance was related to the degree of recovery of the rabbit population after the first outbreaks of rabbit hemorrhagic disease and myxomatosis. The presence of myxomatosis was positively selected for rabbit presence, indicating the relationship between their detection and population density, and negatively selected for rabbit abundance, indicating the negative impact on rabbit populations. Rabbit presence was negatively related to the management strategies of rabbit translocations and the prevention of diseases and parasites, since these are normally applied when rabbit abundance is low.

Our paper provides new evidence that multiple information sources are required when modeling the distribution and abundance of wildlife species; especially historical information could be useful when the species is suspected to have suffered from changes in any of these two parameters and when the current distribution is the result of past situation effects.

INTRODUCTION

Most research into the factors affecting the distribution or abundance of wildlife populations and species has focused on the effects of habitat, microhabitat, or landscape structure (Mills and Gorman 1997; Henderson and Eason 2000). Recently, new GIS techniques have offered a wide variety of variables, such as those related to climate, human presence, or topography, for use in the study of the distribution and abundance of wild populations when habitat features provide insufficient information to answer a particular ecological question. For example, topographic characteristics have a strong influence on the selection of nesting and hunting areas by raptors (Bustamante et al. 1997; Martínez et al. 2003); climatic features and seasons regulate population growth of small birds (Bellamy et al. 1998); and human presence or activity limits species distribution (Smith et al. 1997; Harcourt et al. 2001).

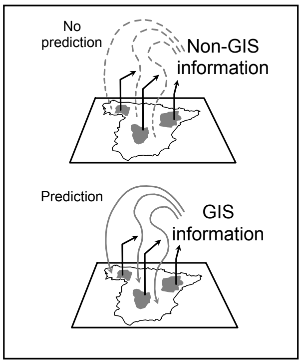

Figure 1. Schemes of two classes of wildlife model according to source of data and utility of the model. GIS information can be obtained for the whole area, and, once analyzed for the sample areas, abundance can be predicted for the whole area. Non-GIS information is not suitable for obtaining the whole surface because of the trade-off between costs and rate of change of the information produced; this can be obtained and analyzed for the sample area but is not suitable for a prediction covering the whole area

The models of wildlife species abundance developed to date search for the optimal habitat of a species without considering the effects of past events on the current abundance (Seoane and Bustamante 2001; Seoane 2002). Some authors have attempted to resolve this problem by combining information on population dynamics (when available) with GIS data or studying historical changes in the habitat (i.e., using satellite photographs) in order to explain historical trends (Silander 1983; Rushton et al. 1997; Kujawa 2002). However, in many cases habitat is not the main factor determining such trends since it remains available. There is considerable information, mostly derived from studies of endangered and pest species, showing that a wide variety of historical factors cause changes in wildlife abundance or distribution. For example, Milner-Gulland and Lhagvasuren (1998) showed the importance of historical hunting data in explaining the declines in numbers and distribution of the Mongolian gazelle *Procapra gutturosa*, an endangered ungulate. Swenson et al. (1995) showed the importance of political policies to the conservation of brown bear; and Hudson et al. 1992, Scott (1988), and Tompkins et al. (1999) showed the importance of infectious diseases and parasites to changes in wildlife abundance. However, such features – the effects of hunting or predator pressures, historical or current data on the management of wild populations, and historical information on diseases – have not been incorporated into global studies of the distribution of wild species. This may be attributable to the difficulty of making predictions based on such data as it is showed in the Figure 1. This difficulty has led to low interest in applying conservation measures over wide regions and the allocation of scant resources to the collection of such information.

There is therefore a need to evaluate whether historical and recent data on diseases, management strategies, predator pressure, and hunting pressure could be included in global studies when describing factors affecting the distribution of wild species, and whether their use could improve studies involving mainly habitat-availability models based on GIS techniques. We have studied these questions using the wild rabbit (*Oryctolagus cuniculus*) as an example. We selected this species because it is an important prey species and small-game species in Mediterranean ecosystems, it is widely distributed, there is considerable information on the factors affecting its abundance and distribution, and the species has suffered a steady decline in southwestern Europe since the 1950s (Delibes and Hiraldo 1981; Soriguer 1981; Villafuerte et al. 1998; Angulo and Cooke 2002).

Wild rabbits originated in southwestern Europe and have been dispersed worldwide for food or hunting (Monnerot et al. 1994). In many of the areas where it was introduced, such as Australasia and UK , it is a pest species. The need to control wild-rabbit populations meant that initial research on the distribution and abundance of wild rabbit focused on determining the factors limiting wild-rabbit populations. Experimental studies have shown how soil hardness, climate, and habitat can limit rabbit abundance. Soil hardness limits the abundance of rabbits by limiting their ability to dig warrens that are used for breeding (Kolb 1985; Trout and Smith 1995, 1998), as well as for refuge against predators (Kolb 1991, 1994) and refuge against extreme climate (Hayward 1961; Parer and Libke 1985). Climate regulates the breeding season by limiting the quality and quantity of food, and thus it regulates the potential for population growth (Wallage-Drees 1983; Bell and Webb 1991; Villafuerte et al. 1997). Many studies worldwide have shown that habitat structure plays a role in rabbit distribution (Jaksic et al., 1979; Soriguer and Rogers, 1979; Simonetti and Fuentes, 1982), with rabbits preferring to use an ecotone of scrub and pasture where they can optimise the relation between feeding and refuge (Rogers and Myers 1979; Kufner 1986; Moreno et al. 1996; Villafuerte et al. 1997).

In southwestern Europe, the climate, topography, and habitat are excellent for wild rabbit because it was in this region that they originally evolved. The main difference between the situation in this original range and that in countries where wild rabbit constitutes a pest is that population growth rates in southwestern Europe seem to have been limited historically by predator pressure (there are more than 29 different predators of rabbits) and hunting activity (almost 1.3 millions of hunters in Spain alone) (REGHAB 2002). However, the sharp decrease in wild rabbit numbers in southwestern Europe has been an important issue for national scientific, environmental, and hunting agencies. The main causes of this decrease are habitat loss and diseases (most importantly the arrival of myxomatosis in the 1950s and rabbit haemorrhagic disease (RHD) in the 1990s), which may be exacerbated by hunting and predator pressures (Villafuerte et al. 1997; see also Chapter 3). Management of wild rabbit populations has increased to conserve their populations, and the associated strategies are being continuously improved and optimised (Trout et al. 1992; Moreno and Villafuerte 1995; Calvete et al. 1997).

The most recent studies have investigated the decline of wild-rabbit populations, in particular the factors affecting fragmented populations. Some studies have focused on landscape analysis and habitat characteristics (Fa et al. 1999; Virgós et al. in press), while others have combined habitat information with climate and topography using GIS information (Trout et al. 2000; Calvete et al. in prep.). An attempt to introduce predator effects and the management of predators can be found in Trout et al. (2000). The results of these studies have brought to light the importance of other factors (not considered by these authors) that could provide an important source of variation, such as diseases, predator or hunting pressures, and direct management of rabbit populations, which are difficult to investigate in GIS or environmental studies. Some of these factors, such as diseases, definitely limit rabbit densities (Trout et al. 1992; Villafuerte et al. 1995; Trout et al. 1997; Marchandeau et al. 1998; Calvete et al. 2002). Diseases are one of the main control measures in areas in which rabbits constitute a pest (Kovaliski 1998; Fenner and Fantini 1999; O'Keefe et al. 1999).

In this paper we evaluate different sources of information in order to understand the present distribution and abundance of wild-rabbit populations in southwestern Europe. Two models were developed and tested. In the first one, GIS techniques were used to test the effects of habitat features, climate, topography, geology, hydrology, human presence, and spatial patterns on the distribution and abundance of wild rabbit in southern Spain. In the second model, we obtained historical and recent information on the management strategies applied to rabbit populations, on the presence and effects of diseases in these populations, and on hunting activity and related socioeconomic activities, and tested their effects on the distribution and abundance of wild rabbit in southern Spain. Both models were tested at two different levels: firstly, to analyse the variables related to the current distribution of the species; and secondly, to analyse the variables that are related to high or low wild-rabbit abundance in the areas where rabbit populations are present.

METHODS

Study area and sampling

To carry out the study we selected 307 locations in southern Spain (Fig. 2). The geographic coordinates of the survey points were selected using GIS via the software IDRISI (Eastman, 1997). Survey

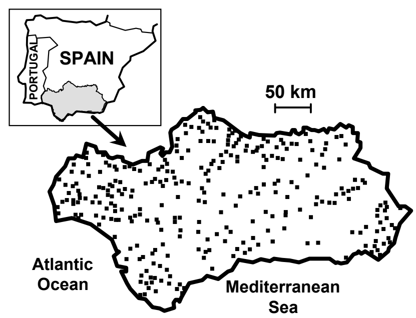

Figure 2. Study area. Sampled areas are represented by black squares.

points were selected based on a step-random sample design based on altitude and topography: areas lower than 1200 m in altitude and with slopes of less than 30% were favoured in the selection of study areas, in order to exclude mountain areas that are not suitable for wild rabbits. In addition, the locations were separated by at least 2 km.

Table 1. Final variables used in the model. a) Raw variables. b–f) Principal-component analysis (PCA) performed with groups of related raw variables. Factors of principal components extracted from original variables are in italics. Variables with the highest factor loading are indicated using boldface. Numbers in brackets are the PCA variances.
Sources: Mapa Digital de Elevaciones (MDT-20, Modelo Digital del Terreno, Consejería de Medio Ambiente de la Junta de Andalucía), Mapa Geológico Andaluz (SINAMBA, Consejería de Medio Ambiente de la Junta de Andalucía y SCIT, Universidad de Córdoba), Mapa Territorial de Andalucía, Mapa Hidrológico de Andalucía, y LandCover (SINAMBA, Consejería de Medio Ambiente de la Junta de Andalucía). We used southern Spain LandCover data for 1995 with a resolution of 50×50 m.

a) Raw variables

GIS variable	*Non-GIS variable*
Geographical coordinates, climate types	Hunting property and activities:
Land cover:	Hunting regime
Urban	Type of property
Non-irrigated homogenous herbaceous cultures	Free access
Non-irrigated homogenous cultures of trees	Rural abandonment
Irrigated homogenous cultures	Presence of livestock
Non-irrigated mixed cultures	Rabbit translocations in 1999
Irrigated mixed cultures	Reduction of hunting pressure in 1999
Mixed cultures and natural vegetation	Diseases:
Dense oak forest	Presence of RHD in 1999
Other dense forests	Presence of myxomatosis in 1999
Sparse scrub	Intensity of myxomatosis outbreaks
Dense scrub	Recovery degree after RH
Oak savanna (dehesa)	Recovery degree after myxomatosis
Pastures	

b) Topography PCA (95.59%)	***Altitude***	***Slope***	
Mean slope	0.23	**0.95**	
SD slope	0.09	**0.94**	
Mean altitude	**0.97**	0.21	
SD altitude	0.29	**0.90**	
Maximum altitude	**0.95**	0.31	
Minimum altitude	**0.99**	0.11	
c) Hydrology PCA (71.32%)	***Water***	***River veg.***	
Longitude of water	**0.69**	0.35	
Surface of water	**0.79**	–0.25	
River vegetation	–0.01	**0.92**	
c) Soil hardness cover PCA (79.26%)	***Hard soil***	***Soft soil***	***Sandy soil***
Sandy soils	0.02	0.00	**0.99**
Soft soils	0.08	**0.97**	–0.12
Compact soils	**0.82**	–0.53	–0.18
Stony soils	–0.00	0.14	0.02
Rocky soils	**–0.93**	–0.33	–0.15
d) Human effects PCA (87.54%)	***Road***	***Ecotone***	***Population***
Density of villages	–0.00	–0.03	**0.90**
Distance to nearest village	–0.19	–0.11	**–0.85**
Road density	**0.96**	0.05	0.13
Road length	**0.97**	0.05	0.06
Ecotone density	0.03	**0.94**	–0.01
Ecotone length	0.06	**0.93**	0.08
f) Hunting management intensity PCA(69.99%)	***Predator control***	***Habitat manag.***	***Disease manag.***
Current habitat management	0.16	**0.76**	0.14
Current predator control	**0.89**	0.07	0.09
Current disease management	0.18	–0.07	0.67
Habitat management 10 years ago	0.07	**0.90**	0.10
Predator control 10 years ago	**0.92**	0.13	0.09
Disease management 10 years ago	0.10	0.09	**0.80**
Habitat management 30 years ago	0.08	**0.82**	–0.00
Predator control 30 years ago	**0.87**	0.12	0.06
Disease management 30 years ago	–0.08	0.20	0.69

GIS variables

We quantify landscape composition within a 1-km^2 square centered on each sample point. In each of these squares we obtain a complete description of the area in terms of climatic, topographic, and habitat characteristics, and information on geological and hydrological data and human influences using available georeferenced data. We used ARC/INFO software (ESRI 1998) to analyse the data by assigning a spatial component, to obtain the variables of each sample square (Table 1). The initial 64 categories of soil were grouped into five types on the basis of soil hardness. The type of land cover was categorised into 16 groups on the basis of similarity of habitat characteristics for rabbits. Climate variables correspond to the classification made by Walter and Lieth (1960) based on climate diagrams of temperature and precipitation. In the study area seven climate sub-types corresponding to the Mediterranean climate (type IV) were present.

Interviews and field survey

People trained in wildlife surveys carried out interviews and rabbit surveys at the 307 selected points during June and July of 1998 and 1999. At each survey point, the interviewer identified the land and the hunting property in the area, and located an appropriate person to interview: a hunter, a landowner, or a conservation manager who knew management history of hunting in the area.

At each survey point, we conducted a census of rabbit abundance in June and July 1999. Rabbit abundance was estimated from faecal pellet counts. Such counts have been widely used and are particularly useful in areas where the rabbits themselves or other signs are difficult to detect, or where detection may be influenced by other factors such as soil or habitat type (Moreno and Villafuerte 1995; Palma et al. 1999). The counts were carried out at each survey point in 50 circular sampling units (0.5 m^2 per unit) randomly distributed over a 2-ha area selected as habitat being representative of the surrounding area. The rabbit abundance index at each survey point was computed on the basis of the mean number of faecal pellets in 0.5 m^2; a logarithmic transformation was necessary to prepare the data for statistical analysis.

Non-GIS variables used in the model

In each personal interview with the local hunter, landowner, or conservation manager, we wanted to obtain information on the main characteristics of the hunting area, including current and past rabbit management strategies, the effects of diseases on rabbit populations, and the history of diseases in the area (Table 1).

In the interview we asked about the type of property (private or public land), the hunting regime (private hunting area or social hunting area), access to the area (public or reserved), and information related to other socioeconomic activities: participants were asked whether there was livestock in the area and whether previously cultivated areas had been abandoned.

In regard to the effects of diseases on wild-rabbit populations, participants were asked to indicate the intensity of myxomatosis in the area, the degree of recovery of the rabbit population after the first epizootic of myxomatosis during the 1950s and after the first epizootic of RHD during the 1990s, and whether myxomatosis and RHD were detected in the area in 1999.

In regard to small-game management, participants were asked to indicate the intensity of use of a number of management strategies both at present as well as 10 and 30 years ago. The latter two of these historical periods correspond to the declines in rabbit abundance due to RHD and myxomatosis, respectively (Angulo and Cooke 2002). We distinguished nine management strategies that were grouped into habitat, predator control, and prevention of diseases and parasites (for more information on single management strategies, see chapter 2). We calculated a management intensity index based on the number of management strategies applied and the intensity of application of each one, for habitat, disease, and predation management strategies, and distinguished them into three periods: currently, and 10 and 30 years ago. We calculated the same index for the reduction in hunting pressure and for current translocations applied in the area during 1998-1999 hunting season.

Analytical procedures

There were many raw variables, and so we used exploratory correlation matrices to test the correlations between them. The correlation between pairs of continuous variables were determined using the Pearson correlation test; correlations between a continuous and a categorical variable were determined using ANOVA; and correlations between pairs of categorical variables were determined using cross-tabulation tables. Pairs of variables with Pearson *r* values, multiple *R* values, or phi-squared values higher than 0.4 were considered to be too highly correlated to both be used in regression analysis. In these cases, principal-component analyses (with a varimax rotated solution) were used and the original raw data set was reduced. To facilitate interpretation, principal-component analyses were performed within groups of related raw variables (i.e., topography, historical management, geology, human influence and fragmentation, and hydrology). The principal components obtained and the explained variance and final row variables are recorded in Table 1. Exploratory analyses were performed using STATISTICA software (STATISTICA 5.5, StatSoft, USA, 1999).

We built a generalised linear model (GLM) using the GENMOD procedure of the SAS package (SAS 1997) to fit explanatory variables to the observed data. GLMs allow the appropriate use of distribution errors and links for the dependent variable (Martínez et al. 2003). We constructed two separate models which used different explanatory variables: one using those obtained from GIS, the other using those obtained from interviews. Within each type of model we distinguished between a model for rabbit distribution (presence/absence) and a model for rabbit abundance (considering only areas where rabbits were present). We built a GLM for the presence/absence of rabbits in each sample area with binomial distribution errors and the logit link function. We decided to build a GLM for rabbit abundance [log(transformed pellets)/0.5 m^2] with normal distribution errors and an identity link, which minimized the deviance of the model, after considering other data distributions and links (gamma and negative binomial error distributions) (Herrera 2000). We started from a complete model on which we applied a backward elimination procedure to obtain the final model, using statistical criteria: the variable with the maximum non-significant probability was excluded in each step. The final model was attained when all variables retained were statistically significant ($P<0.005$). We corrected for overdispersion in the models of rabbit abundance. Finally, in order to account for spatial autocorrelation, we introduced spatial structures into the models that took the form of a second-degree polynomial of the X and Y geographic coordinates of the sampled sites (Legendre 1993).

Once we had finalised each model, we tested that the sign of the estimated coefficient for each independent variable retained in the final model was determined by the true correlation with independent variables and not by the sign of the coefficient of the other variables retained. We achieved this by exploring the relationship between every variable retained in the final model and the rabbit presence by fitting a new GLM (with the same error distribution and link) only with the variable under test. In addition, we used these models to obtain the percentage of deviance explained by each variable when compared to the null model (Martínez et al. 2003).

RESULTS

Study areas and rabbit abundance

Pellet counts could not be performed in some areas, thus resulting in a reduction in the sample number (to N=275). The data from some other areas were totally or partly invalidated because the interviewer could not find a suitable person to interview or the interviewed person did not answer all the questions. For this reason, the sample size of different analyses varied from 120 to 275.

Absence of rabbits was recorded in 57 areas, with rabbits present in 218. Rabbit abundance varied greatly, both spatially and numerically, with low abundance predominating (with 50% of data sampling units being under 0.5 pellets/0.5 m^2) (Fig. 3). The mean rabbit abundance was 1.37 pellets/0.5 m^2 (with an SD of 2.25 pellets/0.5 m^2) when including the absence areas, and 1.74 pellets/0.5 m^2 (SD 2.40 pellets/0.5 m^2) when considering only areas where rabbits were present. The maximum rabbit abundance in any sampled area was 12.2 pellets/0.5 m^2.

The sampled areas varied greatly in size, type of property, hunting regime, primary habitat type, level of wildlife conservation, and management strategies applied. Collectively, the sampled areas were representative of the whole of southern Spain, where the ecosystems predominately cover highly variable landscapes.

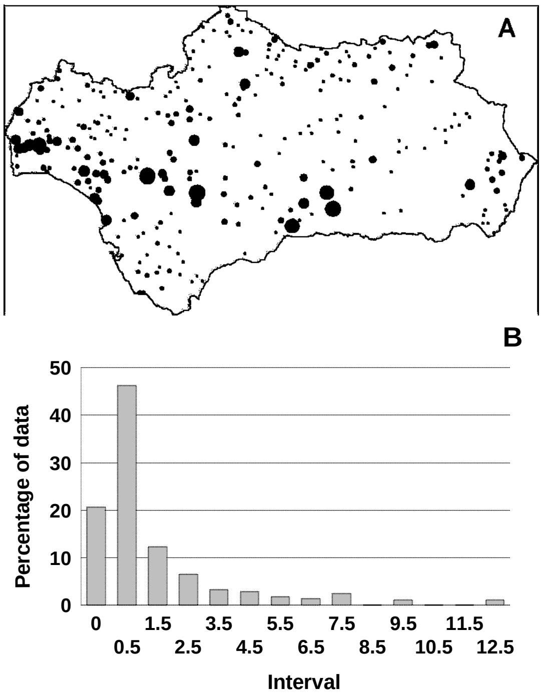

Figure 3. Rabbit abundance in the study area. (A) Map of rabbit abundance in southern Spain; each sampled point is represented by a circle whose size is directly related to rabbit abundance. (B) Histogram of the frequency of rabbit abundance. Number of cases is represented as a percentage of the total data (*N*=275), while intervals are based on the ranges of the values.

Models with variables obtained by GIS

The model for rabbit distribution (presence/absence) explained 13.5% of the original deviance (Fig. 4a). This model showed that the probability of finding a wild-rabbit population in a random area of southern Spain decreased with the amount of oak savanna cover (dehesa), with the amount of mosaics of natural vegetation and cultures, and with the amount of surface covered by mixed irrigated crops. The probability of finding a wild-rabbit population increased with arid climate (IV-III) and decreased with rainy climate (IV-4) (Table 2).

When geographic coordinates are introduced into the model, four variables of the polynomial performed with the geographic coordinates were selected (Table 2), indicating a spatial pattern in the rabbit distribution (Fig. 4a) . When the spatial autocorrelation is accounted for, some modification of the previous model appears: the probability of finding a wild-rabbit population

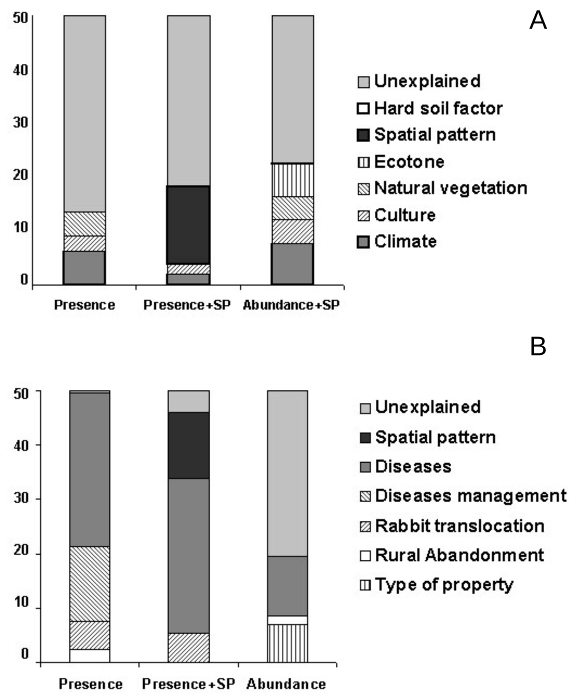

Figure 4. Percentage of deviance explained in models for rabbit presence and abundance, and when accounting for spatial pattern (SP). Independent variables have been grouped. (A) Models based on GIS variables. (B) Models based on historical variables.

in a random area increases with the amount of cover of non-irrigated mixed cultures, whereas it decreases with the amount of hard-soil cover and with the amount of cover of irrigated mixed cultures (Table 2). The amount of dehesa cover and mixed cultures of natural vegetation is substituted by the amount of non-irrigated mixed cultures and soil hardness when accounting for the spatial pattern. The most rainy climate is substitute by the coldest climate.

The two models for rabbit abundance produced similar results: the one excluding spatial autocorrelation explained 18.6% of the original deviation, while the one including spatial autocorrelation explained 22.6% of it. Therefore, we only show the results of the latter (Fig. 4a). The spatial pattern accounted for a small proportion of the total deviance explained by the model (Table 2). In areas where rabbit populations are present, many land-use variables modulate their abundance (Table 2). Rabbit abundance mainly increases with the amount of

Table 2. Generalised linear model (GLM) for the probability of presence and abundance of wild rabbits in southern Spain using GIS information. The percentages of deviance explained by each variable are shown (%). The sign of the single relationship is indicated in brackets when the sign in the whole model does not correspond to the sign of each single variable against the dependent variable. SP: spatial pattern considered.

Variable	*Parameter*	*Standard error*	X^2	*P*	*%*
PRESENCE without SP					
Intercept	25.4675	0.2690			
Climate (IV)iii	24.0774	0.0000	4.54	0.0331	16.0
Climate (IV)4	–0.9364	0.3356	7.97	0.0047	31.5
Irrigated mixed cultures	–0.0037	0.0016	4.73	0.0297	1.9
Mixed cultures and natural vegetation	–0.0022	0.0007	10.25	0.0014	18.1
Oak savanna (dehesa)	–0.0017	0.0005	10.82	0.0010	32.6
PRESENCE with SP					
Intercept	–2300.11	788.2802			
Climate (IV)iii	26.9889	0.0000	15.36	<0.0001	11.5
Climate (IV)3	(–)1.9444	0.7103	9.01	0.0027	0.3
Non-irrigated mixed cultures	0.0138	0.0116	4.07	0.0436	8.1
Irrigated mixed cultures	–0.0045	0.0018	5.92	0.0150	1.4
Hard-soil factor	–0.5039	0.1921	7.28	0.0070	1.1
Spatial pattern:					
X	–0.5168	0.1556	11.61	0.0007	4.2
Y	(–)1.1766	0.3857	8.98	0.0027	34.1
$X \times Y$	(–)1.2356	0.3729	11.56	0.0007	5.1
$Y \times Y$	–14.8093	4.7180	9.58	0.0020	34.3
ABUNDANCE with SP					
Intercept	–877.806	331.8696			
Climate (IV)iii	–1.0487	0.3796	7.63	0.0057	11.7
Climate (IV)1	–0.8212	0.3582	5.25	0.0219	6.2
Climate (IV)4	–0.5750	0.2100	7.50	0.0062	16.2
Non-irrigated homogenous herbaceous cultures	0.0014	0.0005	6.74	0.0095	10.2
Non-irrigated homogenous cultures of trees	0.0016	0.0005	8.21	0.0042	2.4
Non-irrigated mixed cultures	0.0035	0.0010	12.33	0.0004	1.4
Irrigated mixed cultures	0.0026	0.0010	6.80	0.0091	2.6
Mixed cultures and natural vegetation	0.0018	0.0007	7.08	0.0078	3.1
Dense oak forest	0.0023	0.0006	14.32	0.0002	15.2
Dense scrub	0.0019	0.0006	11.15	0.0008	0.5
Sparse scrub	0.0021	0.0005	15.55	<0.0001	0.2
Oak savanna (dehesa)	0.0020	0.0006	11.52	0.0007	2.3
Pastures	0.0021	0.0007	9.47	0.0021	0.7
Ecotone factor	0.1873	0.0858	4.76	0.0290	27.0
Spatial pattern:					
Y	(–)0.4209	0.1602	6.90	0.0086	0.02
$Y \times Y$	–5.0675	1.9332	6.87	0.0088	0.02

non-irrigated cultures or irrigated mixed cultures. Rabbit abundance decreases when climate is arid, rainy or cold (IV-III, IV-4, and IV-1 respectively).

Models with variables obtained by interviews

The model of rabbit distribution (presence/absence) accounted for 49.6% of the original deviance (Fig. 4b). Diseases and their management accounted for most of this deviance. The probability of finding a wild-rabbit population increases with a high degree of recovery after the first RHD outbreaks and when myxomatosis is present in the area, and decreases with the intensity of rabbit translocation and the intensity of disease management. Finally, the probability of finding a wild-rabbit population in a random area of southern Spain decreased when there is free access to the area or where there is rural abandonment.

Table 3. Generalised linear model (GLM) for the probability of the presence and abundance of wild rabbits in southern Spain using non-GIS information. The percentages of deviance explained by each variable are shown (%). The sign of the single relationship is indicated in brackets when the sign in the whole model does not correspond to the sign of each single variable against the dependent variable. SP: spatial pattern considered.

Variable	*Parameter*	*Standard error*	X^2	*P*	*%*
PRESENCE without SP					
Intercept	0.1846	0.8285			
Free access	–1.3611	0.7260	4.01	0.0453	<0.01
Rural abandonment	–1.26.3	0.6085	4.56	0.0327	5.0
Rabbit translocations in 1999	–0.7434	0.3115	6.24	0.0125	10.7
Disease management factor	–0.6300	0.2878	4.39	0.0362	27.2
Presence of myxomatosis in 1999	1.5284	0.6334	5.93	0.0149	7.1
Recovery degree after RHD	1.7805	0.5933	15.11	0.0001	50.0
PRESENCE with SP					
Intercept	238.784	116.2153			
Rabbit translocations in 1999	–0.7288	0.3758	4.74	0.0295	12.1
Recovery degree after RHD	1.5671	0.5403	14.07	0.0002	56.2
Recovery degree after myxomatosis	–0.9520	0.4107	5.40	0.0201	5.5
Spatial pattern:					
X	–0.6692	0.3284	5.07	0.0243	5.6
Y	–0.0542	0.0274	4.91	0.0268	10.8
X × *Y*	(–)1.4477	0.7673	4.19	0.0407	5.9
X × *X*	(–)0.0838	0.0308	10.14	0.0014	4.0
ABUNDANCE without SP					
Intercept	–0.7233	0.2625			
Type of property	0.9312	0.2868	10.54	0.0012	36.7
Rural abandonment	–0.5617	0.2381	5.57	0.0183	6.4
Presence of myxomatosis in 1999	–0.7813	0.3190	6.00	0.0143	7.8
Recovery degree after RHD	0.2626	0.1136	5.35	0.0208	49.0

When introducing spatial autocorrelation, the model obtained explained a lower percentage of the deviance (46.06%; Table 3). The spatial pattern accounted for almost 25% of the deviance explained by the model (Fig. 4b). The following variables were not selected when accounting for the spatial pattern: intensity of disease management, presence of myxomatosis in the area, and rural abandonment. Three explanatory variables obtained from the interviews had a significant effect on this model, predicting again high probabilities of presence of wild-rabbit populations with a high degree of recovery after the first RHD outbreaks and decreasing with a high intensity of rabbit translocations. A new variable is selected in this model, predicting high probabilities of finding rabbit populations with high recovery after the arrival of myxomatosis.

Models analysed to explain rabbit abundance in the areas where rabbit populations are present lead to identical results whether or not the spatial autocorrelation is accounted for. Any of the variables describing spatial structures were selected, while three variables from the interviews had a significant effect on the model (Table 3). In summary, the model for rabbit abundance explained 19.6% of the original deviance (Fig. 4b). Rabbit abundance increases with a higher degree of recovery after the first RHD outbreaks and decreases when myxomatosis was present in the area and with rural abandonment. Rabbit abundance was higher on public land than on private properties.

DISCUSSION

Wild rabbit has been an abundant species in the past, to the extent of being considered a pest species in many countries. It is widely distributed throughout southwestern Europe, where it originated from, occupying all landscapes at different abundance levels. However, in this region the populations of wild rabbits are currently the lowest recorded for centuries, in terms of both population abundance and species distribution (Villafuerte et al. 1995). This situation is reflected in our study area, where we observed that rabbit abundance was depleted, and is in agreement with previous studies (e.g., Fa et al. 1999).

Given the steady decline in rabbit numbers, it is expected that areas in which rabbits currently exist have special characteristics. In our paper, we have attempt to detect these characteristics by fitting models to rabbit presence. Although we have used a random sampling design, we show that spatial autocorrelation affects rabbit presence. This effect could be explained by the history of rabbit abundance, with local extinctions recorded in the last few decades occurring in the least-preferred landscapes for rabbits (Villafuerte et al. 1995; Palma et al. 1999). As most landscape structures are themselves spatially structured by their own generating processes (Legendre et al. 2002), rabbit preferences for particular landscapes may be the source of the spatial pattern detected in the current rabbit distribution.

The spatial pattern of rabbit presence was independent of the set of variables analysed, as it appears in the two models of rabbit distribution. However, the spatial pattern is much less important for modelling rabbit abundance than for modelling rabbit distribution. The rabbit distribution was explained to a lower degree by variables related to landscape availability, as obtained by GIS techniques, than by variables obtained from interviews related to the effects of past situations. However, landscape variables retained in the model are consistent with previous studies that found climatic, topographic, and habitat effects on wild-rabbit distribution (Fa et al. 1999; Trout et al. 2000; Virgós et al. in press). As previous studies, we showed that rabbit presence and abundance is limited by rainy and cold climate; rabbit presence was also favored by arid climate but rabbit abundance decreased when the aridity is high (Parer 1977; Richards 1979). Our results showed that soil hardness limits rabbit distribution, which is in agreement with previous works stating that soft soils are needed for the digging of warrens in order for the animals to reproduce and protect themselves from predators (Parer and Libke 1985; Trout and Smith 1995). However, although soil hardness is a significant variable in our model, habitat features remain more important.

Mediterranean landscapes mainly comprise a mosaic of cultures, situated in valleys where the most productive soils are located, and natural vegetation areas, situated in areas difficult to cultivate due to unfavorable orography. In the past 50 years, agricultural intensification has led to a reduction of natural vegetation, to an increase in the size of cultures, and to an increase in irrigated culture surfaces (Nadal et al. 1996; Tella et al. 1998). Our results show that rabbit populations are more likely to be found in mixed non-irrigated cultures, and that this type of culture is correlated with higher rabbit abundance. Studies on the diet and food habits of rabbits in agricultural landscapes have shown that cultivated Gramineas (e.g., wheat and barley) are positively selected, especially during the growing season, which coincides with the rabbit breeding period (Homolka 1988; Chapuis and Gaudin 1995). In fact, irrigated cultures are only positively related to rabbit abundance when different crops are mixed, which may represent an optimal food resource for rabbits. This idea is confirmed by the observation that the amount of ecotone is positively correlated with rabbit abundance: as cultures become more mixed, ecotone should increase. Ecotone between other types of landscape features has been shown to be essential for wild rabbits (Rogers and Myers 1979; Moreno et al. 1996). As a prey species, the wild rabbit is expected to optimise the time spent between refuge patches and food patches (Villafuerte and Moreno 1997).

Models analysed with variables not related to landscape availability remained those that most explained the current distribution of rabbit populations. However, information obtained from interviews reflects the perceptions of people regarding the evolution of rabbit abundance in the area. This is an assumption of the methods used in this paper, and should be taken into consideration in future studies. Variables selected in models analysed with interview information are related mainly to the evolution of rabbit populations in relation to diseases, to the pattern of rabbit diseases, and to historical management of rabbit populations. In addition, rural abandonment was negatively associated with rabbit presence. The probability of finding rabbit populations is higher in the absence of rural abandonment. Moreover, when a rabbit population is present, rabbit abundance is lower if rural abandonment has occurred. The variable of rural abandonment has an important spatial component, because it is not selected in models that account for spatial autocorrelation, which is probably explained by rural abandonment being associated with specific landscapes (Etienne et al. 1998; Schröder 1998).

Our results show that rabbit populations are most likely to be found – and at higher abundance – when the degree of recovery of the population after the first RHD outbreak was higher. This result corroborates previous studies which showed that the intensity of RHD recovery could be related to rabbit abundance: those areas with higher rabbit abundance were the ones that had recovered the most (Villafuerte et al. 1995). The same relationship appears to be present with myxomatosis, that is, in our model the intensity of recovery from myxomatosis is related to higher rabbit abundance. In fact, our results show also the importance of the detection of myxomatosis for wild-rabbit populations and its relationship with rabbit density. It is more likely to find rabbits in areas where myxomatosis is detected, but the presence of myxomatosis is related to lower rabbit abundance. The probability of encountering a sick rabbit in the field increases with the rabbit population density, because young myxomatous rabbits are easily seen . Thus, myxomatosis becomes a factor explaining rabbit distribution. However, it has an inherent negative effect on the population (Trout et al. 1992; Angulo and Cooke 2002), an effect reflected in our study by the negative relationship between myxomatosis detection and rabbit abundance. Both myxomatosis and RHD have been exposed as the main causes of the decline of wild-rabbit populations (Angulo and Cooke 2002). Firstly, the arrival of myxomatosis reduced the number of rabbits during the 1950s, and their populations – which could not recover to previous levels – were further reduced by the arrival of RHD during the 1990s; RHD had devastating effects on both wild-rabbit populations and on the populations of their predators, many of which are now endangered (Fernández 1993; Angulo 2001; Martínez and Calvo 2001; Martínez et al. 2003).

The decline in rabbit populations (and those of their predators) has led to management strategies in recent decades aimed at recovering their populations. Hunters, landowners, and conservation agencies are managing this process with different intensities, characterised by both the number of different strategies applied and by the frequency of their use. For example, the management of small game in an area is usually performed using multiple strategies (i.e. habitat and predator control, hunting reduction, translocations, and the prevention of parasites and diseases). Our data on the intensity of management strategies in southern Spain indicate that management intensity has increased during the past 30 years, with strategies related to wild-rabbit disease and parasite prevention (which are the most costly to implement) having increased in importance (see chapter 2 entitled “Multiple strategies for the management of small game: implications for wildlife conservation”). This paper shows that rabbit populations are found with a higher probability when the intensity of management applied to disease and parasite prevention is lower. This relationship may indicate either that disease management is mostly carried out when the populations are very low, or that the use of this type of management leads to the extinction of the populations. Although the effects of multiple strategies applied to wild-rabbit populations are not well understood, the effectiveness of individual measures has been assessed. In relation to disease and parasite management, some authors have successfully manipulated vectors of myxomatosis in the UK in order to reduce effects on populations, but Osácar et al. (1996) were unable to apply this procedure to Spain, probably because of the wider vector range present. However, no negative effects on population have been recorded when applying these measures. We can thus accept that disease management is mostly carried out when the populations are very low. In addition, if we distinguish between the three measures considered here – medication supply, disease vaccination, and deparasitations – the latter two are associated with rabbit translocations, as such animals should follow a sanitary protocol that includes vaccinations against myxomatosis and RHD, and deparasitation (Calvete et al. 1997). Our results show that rabbit translocations are also negatively related to rabbit presence; this indicates, as stated above, that these measures are applied when rabbit populations are scarce. C. Calvete (pers. comm.) maintain that rabbit translocations are carried out in Spain for hunting and conservation purposes in order to enhance rabbit populations when their abundance is low. This agrees well with our finding that rabbit populations are mostly absent when both measures – rabbit translocations and disease management – are carried out.

CONCLUSION

In this paper, we show that the current rabbit distribution is associated not only with the available landscape features, but also with factors that may have constrained their populations in the past: diseases and the management of their populations. This constitutes a good example of how research on factors affecting the current distribution of a wildlife species should include historical variables that might have previously constrained the distribution or abundance of the species.

When factors affecting wild species can be obtained by remote sensors, the information can be used to create easily updatable prediction maps (Seoane and Bustamante 2001; Seoane 2002). However, GIS data continue to be expensive and difficult to obtain. When it is necessary to obtain information through field surveys (which is not possible to obtain from any other sources), such as habitat features or land uses, it would be interesting to record information on historical, social, and disease events, as we have done in this paper for the wild rabbit. Models resulting from these factors would be useless as predictive models, because of the lack of information covering the whole area. However, these models are important for wildlife conservation when the goal is to identify the risk factors of endangered species, the variables that need to be improved, and the areas that need immediate attention (Seoane

2002). Moreover, they become very useful when the species population has decreased due to the effects of past situations. In these cases, which apply to most endangered species, suitable landscape features are available, and it is other factors that constrain their distribution.

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NOTES

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