

## Habitat factors related to wild rabbit population trends after the initial impact of rabbit haemorrhagic disease

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**Abstract.** The European wild rabbit (*Oryctolagus cuniculus*) is an introduced pest species in Australia and New Zealand. Rabbits have a devastating negative impact on agricultural production and biodiversity in these countries, and Rabbit Haemorrhagic Disease (RHD) is currently included in control strategies for rabbit populations. On the other hand, the European wild rabbit is a key native prey species in the Iberian Peninsula. Since the arrival of RHD, however, rabbit populations have undergone dramatic decreases and several predator species at risk of extinction are currently dependent on the rabbit population density. Therefore, from the point of view of biodiversity conservation, evaluating habitat correlates and trends of rabbit populations after the first RHD epizootic is of great interest to improve the long-term control or promotion of wild rabbit populations. We estimated the relationship between habitat factors and long-term population trends as well as the relationships between habitat factors and rabbit abundance 2 and 14 years after the arrival of RHD in several Iberian rabbit populations. We observed that only 26% of surveyed populations seemed to experience an increase in rabbit abundance over the last 12 years and that this increase was higher in the low-rabbit-abundance areas of 1992, leading to high rabbit abundance in 2004. Our results suggested that short- and long-term impacts of RHD were related to habitat quality. The initial impact of RHD was higher in more suitable habitats, but increasing long-term population trends were positively related to good habitat quality.

### Introduction

The European wild rabbit (*Oryctolagus cuniculus*) was introduced in Australia and New Zealand in 19th century, and was widely regarded as an agricultural pest and a threat to the conservation of native plants and wildlife. Rabbits cause erosion, land degradation and loss of native plants (Lange and Graham 1983; Myers *et al.* 1994) and the cost of rabbit control and agricultural losses are huge (Gibb and Williams 1994).

By 1988, Rabbit Haemorrhagic Disease (RHD) spread in Europe and caused a dramatic decline of the wild rabbit population, especially in the south-west of the continent. The impact of RHD on wild rabbit populations in Europe was followed with great interest in Australia and New Zealand, and the RHD-virus was imported into Australia to establish the efficacy of the virus as a biological control agent of Australian wild rabbit populations. In 1995 the RHD-virus spread into dense rabbit populations in inland Australia, and RHD was confirmed in New Zealand in 1997. Once it was proven that the virus was an extremely useful biological control agent, the Australian and New Zealand Governments legalised the use of RHD-virus for the long-term control of wild rabbit populations (Cooke and Fenner 2002).

On the other hand, the European wild rabbit is an important prey species for a large number of predators in the Iberian Peninsula. Several top predator species threatened with extinction, including the Iberian lynx (*Lynx pardinus*) and the imperial eagle (*Aquila adalberti*) depend on high rabbit densities (Delibes and Hiraldo 1981; Palomares 2001a). Following the arrival of RHD (Argüello *et al.* 1988), wild rabbit populations have been declining, leading to a pronounced decline in the threatened predator species (Ferrer and Negro 2004).

Recent surveys carried out in Spain have shown that, a decade after the spread of RHD, rabbit density is positively related to habitat suitability, including the presence of scrub cover as a refuge against predators, the presence of crops or suitable food, and the presence of soft soil in which rabbits can excavate warrens (Virgós *et al.* 2003; Calvete *et al.* 2004; Fernández 2005). In the same way, recent modelling approaches have suggested that the long-term impact of RHD on rabbit density may be mainly determined by rabbit population dynamics and, therefore, by habitat suitability (Calvete 2006). Consequently, the recovery of rabbit populations after RHD may be strongly associated with habitat structure and composition. Evaluating this association is

important, since it would enable the optimisation of resources used for long-term rabbit management in the presence of RHD, both in Europe and Australasia. Several studies have focused on short-term rabbit population trends after the first RHD epizootic (Lugton 1999; Marchandeu *et al.* 2000; Edwards *et al.* 2002; Parkes *et al.* 2002), but to date there have been no surveys of long-term rabbit population trends after the initial collapse caused by RHD and their association with habitat. In the present study, we sought to determine whether there was any change in the relationship between rabbit abundance and habitat structure and composition 2 and 14 years after the initial impact of RHD in several Spanish populations, and we identified the habitat factors associated with long-term rabbit population trends after the initial decay of populations caused by the disease.

## Methods

### *Sampling of rabbit populations*

The study area was Teruel province in the Aragón region, north-eastern Spain (Fig. 1). Rabbit abundance was estimated through latrine counts. In the spring and summer of 1992, two years after the first epizootic of RHD in the area, the Department of Environment of the Government of Aragón carried out a survey aimed at estimating the distribution and abundance of wild rabbit populations in the province (Pelayo and Sampietro 1993). In this survey, rabbit latrine counts were performed at 77 walked transects 1–1.6 km long and 2 m wide throughout the province. In summer 2004, one of the authors (CC) again sampled all of these transects using the same protocol. Both latrine counts were ultimately standardised to latrines per transect-kilometre and used as latrine abundance indexes, one per sampling period (hereafter latrine indexes).

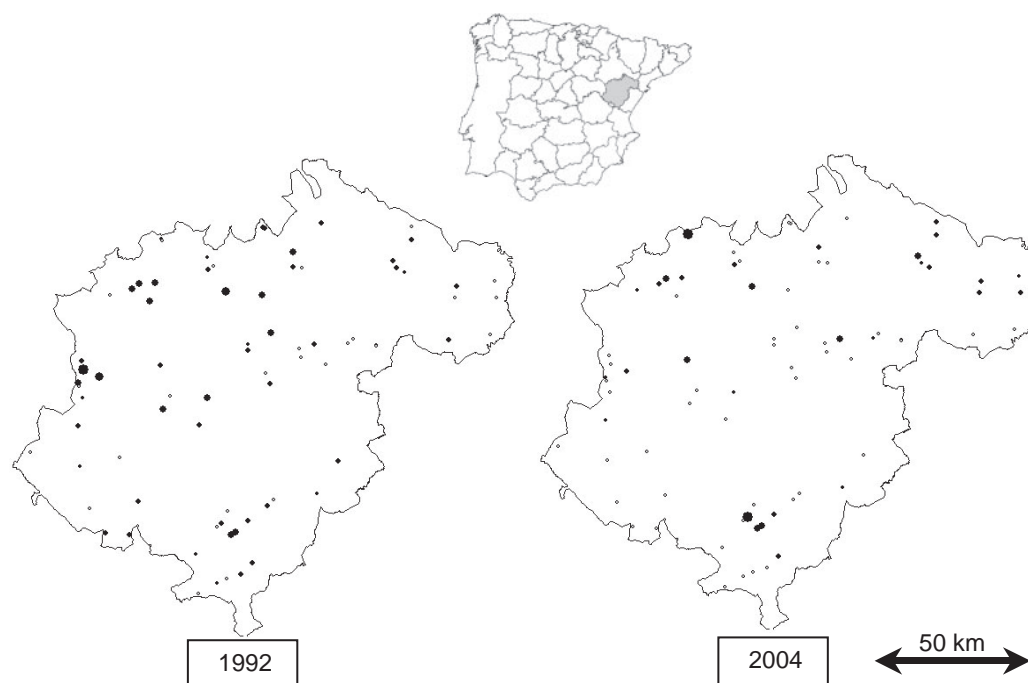
Latrine counts have already been used as an index to estimate rabbit abundance across different habitat conditions (Palma *et al.* 1999; Virgós *et al.* 2003; Calvete *et al.* 2004). Nevertheless, some previous works have shown that the rate of decay of rabbit pellets can be conditioned by habitat and rainfall (Taylor and Williams 1956; Simonetti 1989; Iborra and Lumaret 1997), suggesting that latrine counts should not be used to estimate rabbit abundance. Palomares (2001*b*), however, found no difference in the rate of decay of rabbit pellets among several Mediterranean habitats located in south-western Spain. In addition, a recent survey carried out in the Aragón region (north-eastern Spain) detected no significant influence of habitat and rainfall on the relationship between latrine counts and rabbit abundance or population trends, showing that, in addition to rabbit abundance in different habitats, latrine counts can also provide a useful estimation of between-year variation in rabbit abundance in large-scale studies, in spite of the potential problems with decay rates or age of rabbit pellets (Calvete *et al.* 2005*b*).

### *Environmental variables*

We recorded climatological variables, since they determine the distribution and density of rabbit populations at the macrohabitat level. We also recorded topography, soil hardness and landscape structure as variables associated with rabbit abundance at the meso- and microhabitat levels (Trout *et al.* 2000; Virgós *et al.* 2003).

Climatological variables were estimated from original data provided by the National Meteorological Institute. Mean annual rainfall (mm) and temperature (°C) for each transect were estimated from pluviometric and thermometric data recorded from 1992 to 2003 at weather stations. The distance from each transect to the nearest weather station was always <10 km for pluviometric data and <25 km for thermometric data. The mean annual temperature estimated for all transects was 11.9°C (range 9.1–15.2°C), and mean annual rainfall was 475 mm (range 300–1034 mm).

Topography was estimated from the percentage slope gradient, calculated in a 1 × 1 km square centred at the mid-point of each transect



**Fig. 1.** Location of sampled transects across Teruel province. Point size correlates with number of latrines  $\text{km}^{-1}$ . The maximum numbers of latrines  $\text{km}^{-1}$  counted in a transect was 20 and 19 in 1992 and 2004 respectively.

using geographical information systems software. Soil hardness was classified into four categories: soft, compact, hard and rocky, reflecting its relative suitability for burrow excavation (Calvete *et al.* 2004).

In the period between the two samplings, changes in landscape composition and/or configuration were known to have occurred in other sites of the province, especially changes in the distribution of crops and natural vegetation areas. Since this may have affected rabbit populations, we ascertained that no major landscape changes had occurred between the two samplings in the study sites. To do this, we delimited a 5 × 5 km area centred at the mid-point of each transect, and extracted this area from two Landsat satellite images obtained in 1990 and 2000 respectively (<https://zulu.ssc.nasa.gov>). For each image, we examined three spectral bands, comprising the mid-infrared, near-infrared and visible green light, and we assumed that these images were actual representations of landscape structure during both sampling periods. Due to the different resolutions and sensor characteristics used to obtain the two images, the two 5 × 5 km areas of each transect were compared by eye to confirm that no major changes in the distribution of crops and natural vegetation had occurred.

Characterisation of landscape structure was carried out on the satellite image obtained in 2000, since its resolution was higher than that of the image obtained in 1990. Using a supervised classification procedure implemented in the GIS-software Erdas-Imagine 9.0 (Leica Geosystems LLC, USA), we delimited areas of cultivation or natural vegetation with high or low scrub cover. This supervised classification procedure utilised as training and control points field data obtained in a survey by Calvete *et al.* (2004), which was carried out in Zaragoza province, adjacent to Teruel province. The best Kappa index of agreement (KIA = 0.66) was obtained when the cutting point between both cover categories was established at 30%. Thus, in addition to the cultivated areas, areas of natural vegetation were classified as having low (≤30%) or high (>30%) scrub cover.

Following supervised classification, the variables of landscape structure for each 5 × 5 km area were extracted from the 2000-image using Fragstats software (McGarigal and Marks 1995). Variables were designated according to the same nomenclature used in Fragstats. Due to the association of interspersed open/shelter areas with rabbit abundance (Villafuerte and Moreno 1997; Carvalho and Gomes 2004), we estimated, at the landscape level, the contrast-weighted edge density of the cultivated and cover areas, with the latter consisting of the high and low cover areas combined. At the patch level, we estimated the mean area for each kind of patch, i.e. cultivated (CAREAMN), high cover (HCAREAMN) and low cover patches (LCAREAMN), as well as the percentage of landscape surface occupied by cultivated (CPLAND) and high cover (HCPLAND) areas. In this case the percentage of landscape occupied by low cover areas was not estimated since it was a linear function of the former.

Given that it was not possible to accurately classify the type of crops using only satellite imagery, during the fieldwork carried out in 2004 we recorded the presence or absence of crops for 500 m from each transect. Crops recorded included unirrigated cereal (wheat or barley) and cultivated trees (almond orchard and/or olive grove). No more accurate estimations on crop distance or distribution were recorded since this was the sampling protocol followed in 1992.

#### Data analysis

Non-parametric analysis was used to test the correlation between the latrine indexes and between latrine indexes and population trends. Associations between rabbit latrine indexes performed during both sampling periods and environmental variables were tested by fitting generalised linear models to the data. Log-transformed latrine indexes ( $\log(x+1.1)$ ) were the dependent variables, and environmental factors the independent variables. Because 'latrine index' was an overdispersed and continuous variable, we used a gamma distribution with log-link function as the error distribution (McCullagh and Nelder 1997). For the

analysis of each sampling period, the presence or absence of different kinds of crops were included as dummy variables.

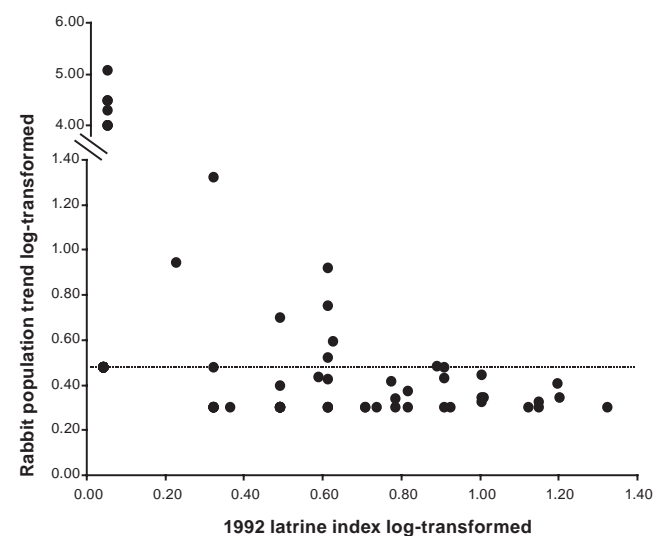
The association between rabbit population trends and environmental factors was also tested by adjusting a generalised linear model using the same error distribution. The trend for each transect was calculated as the growth rate of the latrine index from 1992 to 2004 ( $[(2004 \text{ latrine index} - 1992 \text{ latrine index}) / 1992 \text{ latrine index}]$ ). The estimated values were log-transformed in the same way as was values for latrine indexes and used as dependent variables. The variation in presence/absence of kinds of crops was included in the initial model as a dummy variable corresponding to the increase or decrease in each type of crop.

Since the selection of a unique final model is usually not the best solution, we used best-subset procedures to select the five best final models, as judged by the Akaike information criterion (McCullagh and Nelder 1997). Data were analysed using the SAS statistical package (Statistical Analysis Systems Institute 1990).

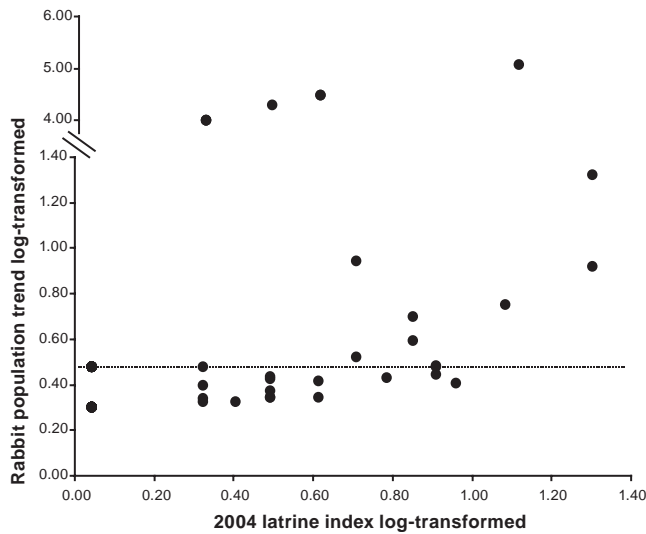
## Results

In total, 77 transects were sampled during 1992 and 2004. For both samplings, no latrines were found in 20 transects. In 26 transects, latrines were observed during the 1992 sampling but not during the 2004 sampling, whereas for 7 other transects latrines were found in 2004 but not in 1992. Thus, when we excluded the 20 transects that had no latrines at both times, 42 of 57 transects (74%) showed a decreasing (40 transects) or stable (2 transects) population trend, whereas only 15 (26%) showed an increasing trend. For all transects, there was a mean decrease in latrine index of 41% between 1992 and 2004.

Correlations between latrine indexes at both times and between latrine indexes and rabbit population trends were all significant (Figs 2–4). We found that increasing population trends (Fig. 2) were more frequent among transects with low 1992 latrine index values (Spearman's  $R = -0.6$ ,  $P < 0.001$ ),



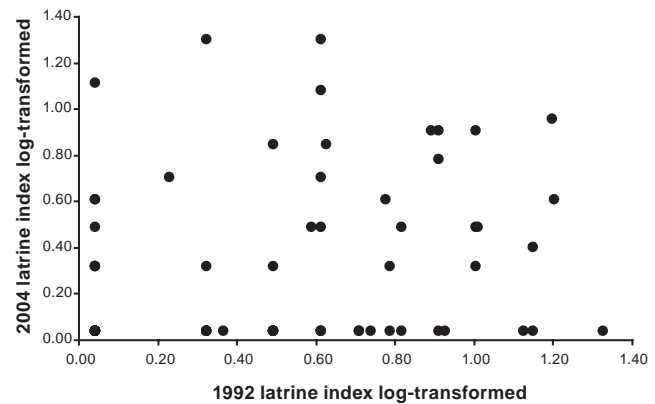
**Fig. 2.** Correlation between 1992 latrine index and rabbit population trend from 1992 to 2004. Values lower than the dashed line indicate decreasing population trends.



**Fig. 3.** Correlation between 2004 latrine index and rabbit population trend from 1992 to 2004. Values lower than the dashed line indicate decreasing population trends.

and that the highest 2000 latrine index values were positively correlated with the highest rabbit trend values (Fig. 3) (Spearman's  $R = 0.52$ ,  $P < 0.001$ ). The correlation between latrine indexes at both times was positive and significant (Fig. 4), but its correlation coefficient was low (Spearman's  $R = 0.31$ ,  $P < 0.001$ ).

We also attempted to determine the environmental variables associated with latrine index in both sampling years. Variables retained in selected models suggested different relationships between rabbit abundance and habitat in both samplings (Tables 1, 2). In general, models selected for the 1992 latrine index showed that rabbit abundance was negatively related to mean annual rainfall and the presence of cultivated areas, and positively related to soil hardness. In contrast, for 2004, rabbit abundance was positively associated with the presence of cultivated areas and negatively related to soil hardness. Only the mean area of high cover



**Fig. 4.** Correlation between log-transformed rabbit latrine indexes in 1992 and 2004.

patches (HCAREAMN) was negatively associated with rabbit abundance at both sampling times.

To test the association between rabbit population trends and environmental factors, we first excluded from the analysis data from all transects in which no latrine had been found in 1992. Among these were the 20 transects in which no latrine was found during both 1992 and 2004 and the 7 transects in which latrines were found in 2004 but not in 1992. In the latter, the population trend estimations were abnormally high when compared with those of the other transects. Thus, we considered these as outliers and excluded them from definitive analysis. We found that their exclusion did not change the pattern of the definitive models selected but did improve model fitting.

Analysis of rabbit population trends (Table 3) showed that changes in rabbit abundance between surveys were highly associated with climatic and geological factors of the habitat as well as with landscape structure. A favourable population trend was positively related to mean rainfall and negatively related to soil hardness. All populations with positive trends were located in areas with mean annual rainfall ranging from 360 to 617 mm. A favourable rabbit population trend was

**Table 1.** Coefficients of habitat variables retained in the five best final generalised linear models selected following the Akaike criterion for the analysis of latrine index estimated in 1992

HCAREAMN, mean area of high cover patches; CAREAMN, mean area of cultivated patches

Model	Selected variables, regression coefficients and ( $P$ )				AIC	$\chi^2$ (d.f.)	$P$	Explained deviance (%)
1	Cultivated trees	Mean rainfall	HCAREAMN		31.38	11.85 (3)	0.008	13.90
		-0.787 (0.021)	-0.024 (0.042)	-0.02 (0.01)				
2	Cultivated trees	HCAREAMN			32.65	8.58 (2)	0.014	10.67
		-0.713 (0.037)	-0.023 (0.004)					
3	Cultivated trees	Soil hardness	Mean rainfall	HCAREAMN	32.81	12.43 (4)	0.014	14.46
		-0.732 (0.032)	0.209 (0.398)	-0.024 (0.046)				
4	Cultivated trees	Mean rainfall	HCAREAMN	CAREAMN	33.04	12.20 (4)	0.016	14.24%
		-0.784 (0.021)	-0.027 (0.032)	-0.021 (0.008)				
5	Cultivated trees	Cereal crops	Mean rainfall	HCAREAMN	33.08	12.15 (4)	0.016	14.19%
		-0.784 (0.021)	-0.126 (0.586)	-0.025 (0.039)				

**Table 2. Coefficients of habitat variables retained in the five best final generalised linear models selected following the Akaike criterion for the analysis of latrine index estimated in 2004**

HCPLAND, % surface occupied by high-cover areas; CPLAND, % surface occupied by crops; LCAREAMN, mean area of low-cover patches; HCAREAMN, mean area of high-cover patches; CAREAMN, mean area of cultivated patches

Model	Selected variables, regression coefficients and ( <i>P</i> )						AIC	$\chi^2$ (d.f.)	<i>P</i>	Explained deviance (%)
1	Cultivated trees 0.487 (0.128)	HCPLAND 0.042 (0.002)	CPLAND 0.044 (0.002)	LCAREAMN 0.015 (<0.001)	HCAREAMN -0.023 (0.042)		-46.19	13.84 (5)	0.017	15.58
2	Cultivated trees 0.694 (0.03)	HCPLAND 0.028 (0.011)	LCAREAMN 0.01 (<0.001)	HCAREAMN -0.022 (0.05)	CAREAMN 0.08 (0.002)		-46.16	13.81 (5)	0.017	15.55
3	Soil hardness -0.464 (0.1)	Cultivated trees 0.636 (0.053)	HCPLAND 0.019 (0.034)	LCAREAMN 0.01 (0.001)	CAREAMN 0.072 (0.005)		-45.76	13.41 (5)	0.02	15.18
4	HCPLAND 0.041 (0.003)	CPLAND 0.047 (0.001)	LCAREAMN 0.016 (<0.001)	HCAREAMN -0.023 (0.039)			-45.72	11.37 (4)	0.023	13.27
5	Soil hardness -0.375 (0.197)	Cultivated trees 0.648 (0.047)	HCPLAND 0.026 (0.018)	LCAREAMN 0.01 (<0.001)	HCAREAMN -0.018 (0.114)	CAREAMN 0.076 (0.003)	-45.60	15.25 (6)	0.018	16.88

also positively associated with the proportion of land occupied by cultivated areas, especially with the increased presence of unirrigated cereal crops. A positive trend was also associated with the mean area of patches occupied by natural vegetation and the proportion of land occupied by areas of high scrub cover.

### Discussion

The results presented here indicate that, after the initial impact of RHD, most surveyed rabbit populations have exhibited a long-term decline, with some becoming extinct or having a high risk of extinction due to low population density. In contrast, some populations that had the lowest population abundances just after the arrival of RHD showed long-term positive trends, reaching the highest population abundance 14 years later. Although this pattern seems clear, its absolute magnitude should be interpreted carefully, since yearly variations in rabbit abundance may partially mask long-term trends.

Several studies have reported great differences in the initial impact of RHD among rabbit populations, with many of these differences being related to climatic conditions such

as temperature or rainfall (Henzell *et al.* 2002; Mutze *et al.* 2002; Bruce *et al.* 2004). Thus, the partial immunisation of populations against RHD using a pre-existing non-pathogenic rabbit calicivirus (RCV) in high-rainfall areas has been invoked as a putative cause of positive rabbit population trends in Australia (Cooke and Fenner 2002). However, the initial impact of RHD has frequently been associated with higher rabbit population densities before the arrival of the disease (Henzell *et al.* 2002; Parkes *et al.* 2002; Story *et al.* 2004), since high densities of susceptible rabbits favoured the transmission of the virus, increasing morbidity and therefore the overall initial mortality caused by RHD. Moreover, landscape structure has been reported to determine the spatial and social structure of wild rabbit populations, as well as habitat availability and use. Thus, in addition to pre-RHD rabbit density, landscape structure may modulate the transmission process of the RHD virus (Moriarty *et al.* 2000; White *et al.* 2003).

The selected models adjusted to our 1992 data showed negative relationships between rabbit abundance and habitat factors that traditionally have been positively associated with rabbit abundance. These include the presence of soft and

**Table 3. Coefficients of habitat variables retained in the five best final generalized linear models selected following the Akaike criterion for the analysis of rabbit population trends between 1992 and 2004**

CPLAND, % surface occupied by crops; HCPLAND, % surface occupied by high cover areas; LCAREAMN, mean area of low cover patches; HCAREAMN, mean area of high cover patches

Model	Selected variables, regression coefficients and ( <i>P</i> )						AIC	$\chi^2$ (d.f.)	<i>P</i>	Explained deviance (%)
1	Soil hardness -0.173 (0.058)	Mean rainfall 0.01 (0.08)	CPLAND 0.021 (<0.001)	LCAREAMN 0.007 (<0.001)	HCAREAMN 0.069 (<0.001)		-72.97	36.01 (5)	<0.001	50.87
2	Soil hardness -0.22 (0.021)	Cereal inc. 0.118 (0.189)	Mean rainfall 0.01 (0.071)	CPLAND 0.02 (<0.001)	LCAREAMN 0.006 (<0.001)	HCAREAMN 0.065 (<0.001)	-72.59	37.63 (6)	<0.001	52.42
3	Soil hardness -0.162 (0.084)	CPLAND 0.02 (<0.001)	LCAREAMN 0.007 (<0.001)	HCAREAMN 0.077 (<0.001)			-72.24	33.27 (4)	<0.001	48.14
4	Soil hardness -0.193 (0.047)	Cereal inc. 0.153 (0.088)	Mean rainfall 0.015 (0.007)	HCPLAND 0.02 (<0.001)	CPLAND 0.025 (<0.001)	LCAREAMN 0.007 (<0.001)	-72.23	37.27 (6)	<0.001	52.08
5	Soil hardness -0.152 (0.098)	Mean rainfall 0.011 (0.05)	HCPLAND 0.009 (0.291)	CPLAND 0.025 (<0.001)	LCAREAMN 0.007 (<0.001)	HCAREAMN 0.045 (0.11)	-72.10	37.14 (6)	<0.001	51.96

deep soils, the interspersed of refuge and open feeding areas (usually crops) and rainfall (Rogers and Myers 1979; Parer and Libke 1985; Boag 1987; Calvete *et al.* 2004). Since there is no evidence of existing non-pathogenic RCV in Iberian wild rabbit populations, our results are in agreement with findings showing an effect of pre-RHD population density on the initial impact of the disease and with the hypothetical influence of landscape structure on the transmission of the virus. Thus, our results suggested that the initial impact of the disease may have been proportionately stronger in good-quality habitats with higher rabbit densities, whereas less affected populations were those located in marginal habitats, in which rabbit densities were lower before the initial spread of the disease. In addition, the initial transmission of RHD virus may also have been enhanced in habitats with open feeding areas (crops), in which rabbits may have exhibited higher social interactions to decrease the risk of predation (Villafuerte and Moreno 1997).

Following the initial impact of RHD, habitat suitability was positively related to long-term increases in rabbit population trends, so that rabbit abundance 14 years after the arrival of RHD in the study areas was again positively related to habitat factors traditionally associated with it. An interesting possibility is the development of genetic resistance to the RHD virus in the rabbit populations, since this may have been most rapid in populations where mortality was initially highest, i.e. in populations located in high-suitability habitats.

On the other hand, lower mortality rates due to non-RHD causes (White *et al.* 2002) or higher production of offspring (Story *et al.* 2004) have been suggested as compensatory mechanisms that may decrease the impact of RHD on populations. Moreover, Calvete (2006) developed a model showing that the impact of RHD can be highly dependent on rabbit population dynamics and, therefore, on habitat carrying capacity, and that the presence of a unique, highly pathogenic RHD virus can be compatible with the existence of high-density populations at equilibrium with the disease, without the concurrence of genetic variations among rabbit populations or the presence of a protective, non-pathogenic RHD-like virus. Given that lethality of the RHD virus is lower in young rabbits (see review of Cooke and Fenner 2002), this model predicted the highest long-term impact of the disease in populations located in habitats with low to medium carrying capacity. In contrast, lower long-term impact of the disease was predicted in high-density populations in habitats with high carrying capacity, since in these populations mean age of infection was decreased, yielding a lower mortality from RHD. This type of habitat would include habitats containing cover as refuge against predators, soft soils for the excavation of breeding stops and warrens, and high-quality food provided by crops (unirrigated cereal crops in our survey) and natural vegetation in high-rainfall areas, thus increasing the positive trend of populations after the initial impact of disease. The outcomes of this model

have not been proven in a formal way to date, but our results, however, were in agreement with the predicted outcomes, suggesting the validity of this theoretical approach.

The high variability of long-term population trends and the initial impact of RHD in populations located in habitats with different suitabilities may have been combined with uncontrolled factors in our study, such as subsequent predation impact and hunting pressure (Trout and Tittensor 1989; Reddiex *et al.* 2002; Calvete *et al.* 2005a), or stochastic events such as flooding (Palomares 2003), to at least partially determine the current high variance in the distribution of the rabbit population in the Iberian Peninsula (Fa *et al.* 1999; Virgós *et al.* 2003; Calvete *et al.* 2004; Fernández 2005).

Our results showed that rabbit populations, in general, have decreased even more in the study area 14 years after the initial negative impact of RHD. However, long-term population trends in the presence of RHD were highly variable among populations and were associated with habitat structure and composition. This association suggested that, from the viewpoint of biodiversity conservation, the long-term management of rabbit populations in the presence of RHD should be based in habitat management, increasing or decreasing the impact of RHD by changing habitat suitability, and therefore by the subsequent changes in population dynamics. In addition, since these changes in habitat may affect the spatial and social organisation of rabbits, and therefore the transmission process of the RHD virus, we suggest that future research should be aimed at determining and quantifying the links between the habitat structure and composition and the transmission process of the RHD virus and how the latter varies according to habitat transformation (White *et al.* 2003).

### Acknowledgments

The main funding was provided by the Dirección General de Medio Natural (Gobierno de Aragón). Partial funding was provided by the Plan Andaluz de Investigación (RNM-118 research group). We thank E. Virgós, E. Angulo and two anonymous referees for their useful comments. We are indebted to E. Escudero, J. Guiral and R. Soriguer for their technical assistance. Special thanks go to R. Estrada and P. Calvete.

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Manuscript received 24 November 2005, accepted 8 August 2006