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Modeling the distribution of wild rabbits (*Oryctolagus cuniculus*) on a Mediterranean island

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Abstract The European rabbit (*Oryctolagus cuniculus*) is a widely distributed mammal with an often contradictory ecological role, imposing the need for population management. Sound management requires an in-depth understanding of the complex species–habitat relationships. In this study, CART analysis was employed to identify the most important environmental and anthropogenic factors affecting the spatial distribution of wild rabbit on Lemnos Island, northeastern Aegean Sea in Greece. On Lemnos, this species is considered an agricultural pest due to its overabundance resulting from the long-term absence of viral diseases, limited predation pressure, and lack of effective management. The study was carried out during the summer of 2008 by surveying rabbit densities in 181 2×2-km squares. Seven environmental and 14 anthropogenic variables, measured at two spatial scales, were used as explanatory variables. Soil hardness was the most influential variable, dividing the island into two distinct areas, namely the rabbit-poor areas with hard rocky soils and the rabbit-rich areas where soft soils prevail. In the former, the presence of a sharp relief can lead to complete absence of the species, while a combination of gentle relief, low altitudes, and low presence of arable land can lead to moderate rabbit density. In the latter, human-caused disturbance can reduce the number of rabbits, while a high density of ecotones and streams and a high presence of riparian vegetation can increase population densities to its highest levels observed. Our findings can formulate a scientific basis for the development of an effective management strategy for its population control.

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Introduction

The density and distribution of any animal population is often the result of complex interactions among environmental, anthropogenic, and biotic factors. The understanding of these interactions and their effects on species population distribution is of crucial importance to wildlife managers (Fisher et al. 2002; Gibson et al. 2004; Fernandez 2005; Anadon et al. 2009; Bakaloudis et al. 2009; Schaub et al. 2011), aiming either at the control, sustainable harvest, or conservation. Species distribution models constitute important tools for land managers and conservationists. They allow the in-depth understanding of the effect of landscape patterns on ecological processes and species distribution (Law and Dickman 1998; Morrison et al. 2006; Nabe-Nielsen et al. 2010), especially when they take into consideration the historical and contemporary role of human presence and the human-generated landscape configuration (Rushton et al. 1994; Bustamante 1997; Pearce and Ferrier 2001; Fernandez 2005). The latter is of particular importance in the northeast Mediterranean islands, where the long human presence and the associated land-use practices have shaped the landscape in an often distinctive way, compared to the continental Mediterranean region (Tzanopoulos and Vogiatzakis 2011).

The European wild rabbit (*Oryctolagus cuniculus*) is a highly successful colonizer due to its environmental adaptability and tolerance (Flux and Fullagar 1992). It plays a vital, multidimensional and often contradictory ecological role across its worldwide range (Thompson and King 1994; Devillard et al. 2008; Lees and Bell 2008). In many of the areas where it was introduced, the prevailing ecological conditions favored its rapid population increase, turning it into a pest. It often constitutes an important threat for biodiversity and human economy, destroying agricultural crops and native vegetation, competing with native species and livestock and causing severe ecological damage (Thompson and King 1994; Williams et al. 1995; Cooke 2008; Lees and Bell 2008). On the other hand, in the Iberian Peninsula, where the species is native, it is a key prey species with an important ecological and socioeconomic role (Serrano 2000; Delibes-Mateos et al. 2008a; Ferreras et al. 2011). However, a general concern has been expressed about the future of populations in these regions, as they have been declining during recent decades, mainly due to viral diseases, namely myxomatosis and rabbit hemorrhagic disease (RHD) (Alves and Ferreira 2002; Delibes-Mateos et al. 2008b). In both cases, its population management is an immediate priority in order to prevent, reduce, or avoid economic damage and negative ecological cascade effects.

At a regional level, a number of factors including landscape spatial pattern, human activities, predator pressure, and in some cases the long-term constant pressure caused by viral diseases (e.g., RHD and myxomatosis) can cause significant variations in population distribution and density with important implication on the control or conservation of the species population (Lombardi et al. 2003; Fernandez 2005; Williams et al. 2007; Delibes-Mateos et al. 2009a). On Lemnos Island, the wild rabbit was introduced several centuries ago (Flux and Fullagar 1992; Williams et al. 1995). However, its increased population over the last two decades has caused devastating effects on the rural economy (Kontsiotis 2011), turning it into an agricultural pest. It is worth mentioning that the total damage to agricultural crops for the year 2008 caused by the rabbit's grazing was estimated to be € 361,243 (€ 312,202 for cereals and € 49,041 for vineyards) (ELGA 2008). Additionally, the rabbits' grazing negatively affects natural habitats on the island by reducing the produced biomass (Kontsiotis 2011). Under this frame, the adoption and implementation of a sustainable and scientifically sound management plan for the species population control is imperative.

Many scientists have studied the effect of environmental heterogeneity on the abundance of wild rabbits at various spatial scales (Lombardi et al. 2003; Martins et al. 2003; Carvalho and Gomes 2004; Calvete et al. 2004; Fernandez 2005; Lombardi et al. 2007; Williams et al. 2007; Delibes-Mateos et al. 2009b). However, information concerning their distribution and ecological behavior in insular ecosystems is rather limited. At the same time, extrapolation of results achieved in continental areas is often risky because insular landscapes exhibit important peculiarities as a result of their limited size, resources, and geographic remoteness (Tzanopoulos and Vogiatzakis 2011).

The island of Lemnos demonstrates three important peculiarities in relation to the wild rabbit population, which makes it an attractive site for the investigation of the associations between its population and both environmental and anthropogenic patterns. Firstly, unlike the rest of the continental Mediterranean, where recurrent mortality from viral diseases caused significant fluctuations in population densities (Thompson and King 1994; Villafuerte et al. 1995), there are no records of similar events on the island yet. Lack of viral diseases possibly explains the increased rabbit population on the island. A second peculiarity is the rather limited predation pressure, as there are no mammalian predators that could affect prey numbers (Lima and Dill 1990; Newsome 1990; Kotler 1997; Banks 2000; Bos and Carthew 2003), and only the common buzzard (*Buteo buteo*) relies on rabbits in the study area. Finally, a third peculiarity is the absence of any effective wild rabbit management program, such as rabbit-proof fencing, habitat management, poisoning, ripping of warrens, fumigation, etc. (Williams et al. 1995), except of hunting, which could have influenced the natural distribution of rabbits causing a bias in the spatial distribution model.

The aim of the current study was twofold: firstly, to identify the combined effect of environmental and anthropogenic patterns on the density and distribution of wild rabbits population across the island, and secondly to assess the usefulness of these results in developing a sustainable and scientifically sound management plan for the control of the wild rabbit's population.

Methods

Study area

The study was carried out on Lemnos Island (39°46′–40°02′ N, 25°02′–25°26′ E), in the north Aegean Sea. The island covers an area of 475.6 km^2 and is inhabited by 18,100 people. It is dominated by plain areas, but low hills up to 430 m also exist in its western part. The climate is typical Mediterranean and it is characterized by very hot and dry summers and mild winters. The average annual precipitation is 474.4 mm and the average annual ambient temperature is 15.9 °C. The main habitat types in the island are scrublands and agricultural cultivations. Scrublands are mainly found in the western and southern parts of the island, composed primarily by *Sarcopoterium spinosum*, *Thymus capitatus*, *Centaurea spinosa*, *Genista acanthoclada*, and *Anthyllis hermanniae*. Agricultural cultivations occupy the flat parts of the island and the main crops are cereals and vineyards. Two general types of soil-depth environments are predominant in the island: (a) the shallow soils with phryganic vegetation, intense erosion, and relatively undulating terrain, and (b) the deep alluvial deposits with agricultural cultivations in relatively flat terrain.

Rabbit surveys

The island was divided into 181 2 × 2-km squares using a grid. Spotlight counts were undertaken from a four-wheel-drive vehicle using a spotlight with a light intensity of 3,000,000 candles. A transect, approximately 1.5 km long, was located within each grid cell and was surveyed for three consecutive nights. Transects were always placed at the center of each grid cell, but their direction was decided based on vehicle accessibility. Vehicle speed was generally 15 km h^{-1}, and counts were taken by two observers (Martins et al. 2003). The first observer was recording the wild rabbits in one side of the route, in a width of 50 m, and the second observer–driver was recording the rabbits that were crossing the road (see Katona et al. 2004). Mean relative density (population density hereafter) of grid cell *i* was defined as the mean number of rabbits per surveyed area counted during the three consecutive nights, and expressed as individuals ha^{-1}.

All counts were conducted during July and August 2008. This period was chosen because crops had been harvested, enabling easier field observations. In addition, the breeding season was at the end while the hunting season had not started, and thus the maximum number of individuals was recorded. Counts were avoided during inclement weather conditions (rainy days, strong winds, etc.) and during the dates close to the full moon (Fletcher et al. 1999).

Environmental and anthropogenic variables

A total of 21 environmental and anthropogenic variables were measured in two spatial scales; landscape and home range level (Dellafiore et al. 2008; López-Darias and Lobo 2009; Graf et al. 2005) (Table 1). We assumed that each cell represents the landscape, and a circular area with a radius of 100 m centered in each cell represents the average home range of the wild rabbit (Moseby et al. 2005). At the landscape level, variables were derived using geographic information system (GIS) archives (Arc Gis 9.2) and by satellite image analysis, while at the home-range level variables were estimated in situ by spot observations.

Environmental variables included mean slope (SLOP), mean altitude (ALT), density of streams (STRE), topographic index (TIND), density of ecotones (ECOT), and number of different land uses (LAND). The TIND was calculated for each cell from the formula: $(h_{max} - h_{min})/20$, where h_{max} is the maximum altitude in the cell, h_{min} is the minimum altitude in the cell, and 20 is the unit of the contour. The index had four categories: 1 = mild landscape, 2 = slightly alternating landscape, 3 = alternating landscape, and 4 = intense landscape relief. Soil hardness (SOIL) was estimated by spot observations in each circular plot by assessing the dominant soil within the plot as 1 = soft, 2 = compact, and 3 = hard-rocky, in order to reflect its relative suitability for burrow excavation. The number of different land uses (LAND) was measured at the landscape level with the use of the Corine Land Cover (2000) database.

Seven anthropogenic variables at landscape level were measured including: presence of human settlements (VILLPR, 0 = absence, 1 = presence), area of the village (VILLA), population of the village (VILLPOP), density of paved roads (PAVR), and density of dirty roads (DIR). The hunting status (HUNT) was recorded as a binary variable with 1 = hunting allowed and 2 = hunting prohibited. In addition, we measured the area of the wildlife refuge (WILDL). Seven further anthropogenic variables at the home range level were estimated. The vegetation types were subdivided into four categories and the percentage of each category was

Table 1 Variables used in CART

Mnemonic	Variable	Units	Scale level
Environmental			
SLOP	Mean slope	%	Landscape context
ALT	Mean altitude	m	Landscape context
TIND	Topographic index	Four-point scale	Landscape context
STRE	Streams density	m ha^{-1}	Landscape context
ECOT	Ecotone density	m ha^{-1}	Landscape context
LAND	Number of land uses	Individuals	Landscape context
SOIL	Soil hardness	Three-point scale	Home range
Anthropogenic			
VILLPR	Village presence	Two-point scale	Landscape context
VILLA	Village area	ha	Landscape context
VILLPOP	Village population	Individuals	Landscape context
PAVR	Paved roads density	m ha^{-1}	Landscape context
DIR	Dirty roads density	m ha^{-1}	Landscape context
HUNT	Hunting status	Two-point scale	Landscape context
WILDL	Wildlife refuge area	Ha	Landscape context
%PHRYG	Phrygana	% cover	Home range
%AGR	Agricultural land	% cover	Home range
%HERB	Herbaceous vegetation	% cover	Home range
%RIP	Riparian vegetation	% cover	Home range
%BAR	Bare land	% cover	Home range
FOOD	Index of food availability	Five-point scale	Home range
PATCH	Number of patches	Individuals	Home range

estimated for phrygana (%PHRYG), agricultural cultivation (%AGR), herbaceous vegetation (%HERB), and riparian vegetation (%RIP). Also, the areas without vegetation (%BAR) were recorded. We further estimated an index of food availability (FOOD). We considered that lower availability of food exists in areas without vegetation (0 = bare ground) following with ascending order the areas occupied by 1 = phrygana, 2 = herbaceous vegetation, 3 = riparian vegetation, and 4 = agricultural cultivations. Finally, in each circular plot, we counted the number of patches (PATCH) by using satellite images.

Data analysis

Classification and regression trees (CART) analysis (Breiman et al. 1984; Witten and Frank 2000) was employed for the identification of the main factors determining the population density of the wild rabbit on Lemnos Island. A classification tree (employed when categorical response variables are used) is a powerful, non-parametric method that can effectively manage the complexity often inherent in ecological data (De'ath and Fabricius 2000). Classification trees repeatedly divide the data into two mutually exclusive groups on the basis of a single explanatory variable until a set of homogenous groups, in terms of the response variable, is achieved (De'ath and Fabricius 2000), or until the data cannot be divided any further based on the used explanatory variables. At each division, the variable that best divides the data is used. The most important advantages of classification trees, which make them suitable for the current study, are: (a) they can handle both continuous and categorical explanatory variables, (b) they can deal with nonlinear and high-order relationships between explanatory and the response variable, they can be represented graphically making their interpretation and conceptualization easier (De'ath and Fabricius 2000; Lawer and Edwards 2002; Mitchley and Xofis 2005).

Population densities were ranked in ascending order from 0 to 22.6 ind. ha^{-1} and then they were summed. Each density was divided by the grand total and a cumulative sum of quotients of densities was created. Then, the cumulative sum of quotients was divided into four equal classes, while a fifth class was assessed when rabbits were absent. Therefore, the five population density classes, which were used as the response variable in the CART analysis, were: absent, 0.1–6.89, 6.9–8.83, 8.84–10.9, and >11 ind. ha^{-1}.

The analysis was performed using the Statistica 8 statistical package (StatSoft Inc. 2007) under the General Classification and Regression Tree Model. The "Gini" measure of nodes impurity was employed as the splitting index and "Prune on Misclassification error" was selected for pruning branches from the complete classification tree. The minimum number of instances in a terminal node was set at 2 with an unlimited number of tree levels. The right tree size selection was assisted by the results of a fivefold cross validation (CV) which were also used for estimating models accuracy. The right tree size was the one with the smallest CV-cost and among trees with similar CV-costs the one which was the less complicated and more ecologically meaningful was selected. Furthermore, two additional criteria were employed for optimal tree selection. Firstly, the overall classification accuracy of the selected tree had to sufficiently exceed the classification accuracy of the "null model", which in this case was 40.5 %. Secondly the kappa statistics of the selected classification tree had to exceed 0.4, which according to Fielding and Bell (1997), is an indication of a good model. The overall performance of the model was assessed using an error matrix based on the fivefold CV results.

Results

The overall mean population density of rabbits was estimated at 4.28 ind. ha^{-1}, ranging between 0 and 22.6 ind. ha^{-1} (Fig. 1). Rabbits were distributed on almost the whole island (Fig. 1), and a distinct spatial pattern of their density was observed. High densities were observed in the northern, northeastern, and eastern parts of the island, while low densities were found in the southwest.

The CART analysis resulted in a tree with 15 terminal and 14 nonterminal nodes (Fig. 2). The overall correct classification rate was 75.9 %, sufficiently higher than the 40.5 % of the null model, while the kappa statistic was 0.66, well above the lowest acceptable limit of 0.4, indicating a good model.

A number of different environmental and anthropogenic factors, measured at both landscape and home-range scale, are involved in determining the population density of wild rabbits. Soil hardness clearly divides the island into two distinct areas; those where hard soils dominate, having generally low densities, ranging between presence and 6.9 ind. ha^{-1}, while in areas with moderately hard or soft soils density can exceed 17 ind. ha^{-1}.

In the low-density areas, slope seems to have an unfavorable effect on population, leading to complete absence in areas where it exceeds 22 %. On the other hand, in areas with less steep slopes, the population density ranges between presence and 6.9 ind. ha^{-1}, and only in extremely favorable conditions, defined by a high ecotone length, relatively lower presence of paved roads and agricultural land and in altitudes not exceeding 169 m it can reach up to 8.84 ind. ha^{-1}.

In areas where moderately hard or soft soils dominate, which have a higher potential for high densities, the interactions between the various factors in determining population densities are much more complicated. Perhaps the clearer effect is the one of settlement presence, which leads to low densities, ranging from just presence to 6.9 ind. ha^{-1}, when it exceeds 9.84 % cover.

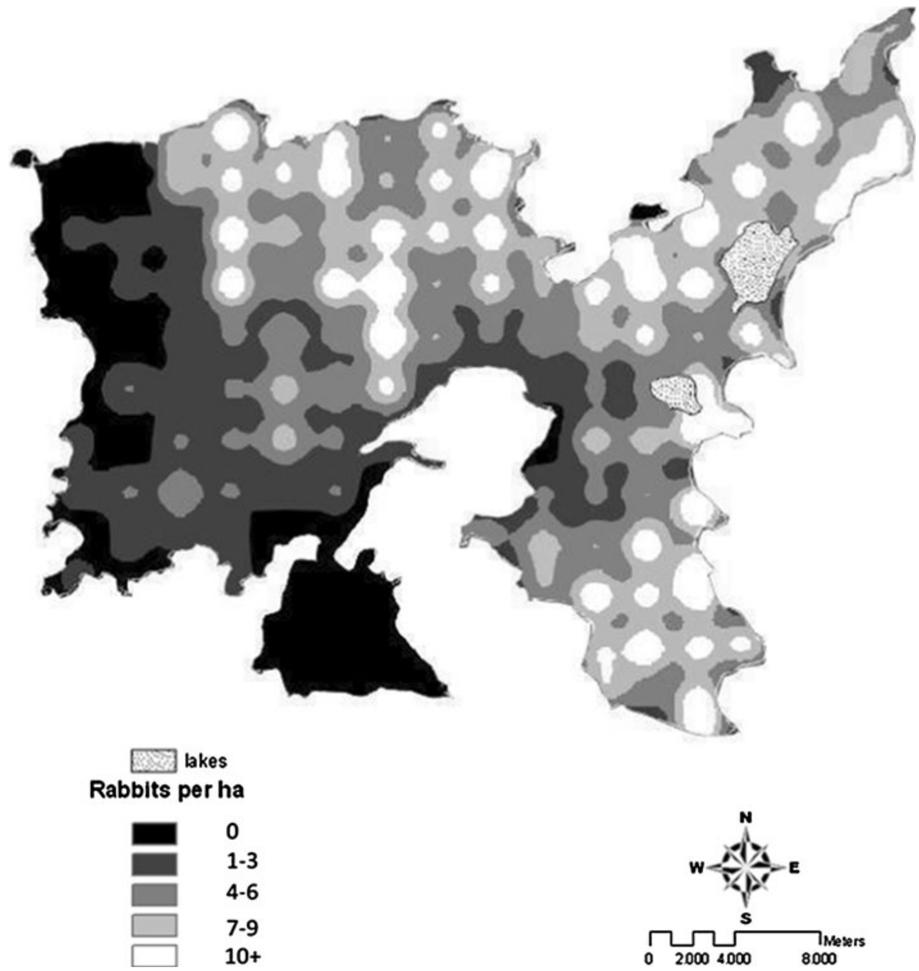

Fig. 1 Spatial population density (ind. ha^{-1}) of the wild rabbit in Lemnos Island, during 2008

In the rest of the areas, a positive effect of riparian vegetation and ecotone length is demonstrated, forming the best conditions for the species with population density exceeding 11 ind. ha^{-1}, reaching occasionally more than 17 ind. ha^{-1}, when riparian vegetation exceeds 2.5 % cover or ecotone length exceeds 15.79 m ha^{-1}. When neither of these two parameters is met, then population densities are moderate and under specific conditions it can be low, despite the positive effect of non-hard soils. The diversity and type of land uses also plays a significant role in the species' population distribution. In areas where up to two land uses are found, the population density varies between 6.9 and 8.84 ind. ha^{-1}, while the same density is observed in areas with more than two land uses and where the agricultural land occupies less than 37.5 %. The negative role of slope steepness is also observed in the non-hard soil areas, restricting population density to their lowest limits. On the other hand, the positive role of ecotone length and streams, accompanied possibly by riparian vegetation, is also observed, with population density ranging between 8.84 and 11 ind. ha^{-1} when ecotone exceed 7.84 m ha^{-1} or between 6.9 and 8.84 ind. ha^{-1} when stream length exceeds 11.04 m ha^{-1}.

Discussion

The model demonstrates a relationship between rabbit density and both environmental and anthropogenic factors. Approximately half of the measured variables were identified as significant in the model, resulting in a complex relationship between landscape pattern, human activities, and rabbit density. Variables measured at both spatial scales were found to have a significant effect on the distribution of the species. This justifies the need for combining different scales to adequately describe the wild rabbit's responses to habitat heterogeneity (Fernandez 2005). However, a distinctive pattern with one particular scale being associated with some particular category of needs could not be identified, as variables from both scales are related to the same species requirements for suitable refugees and available food resources. The understanding of the complex species–habitat relation-

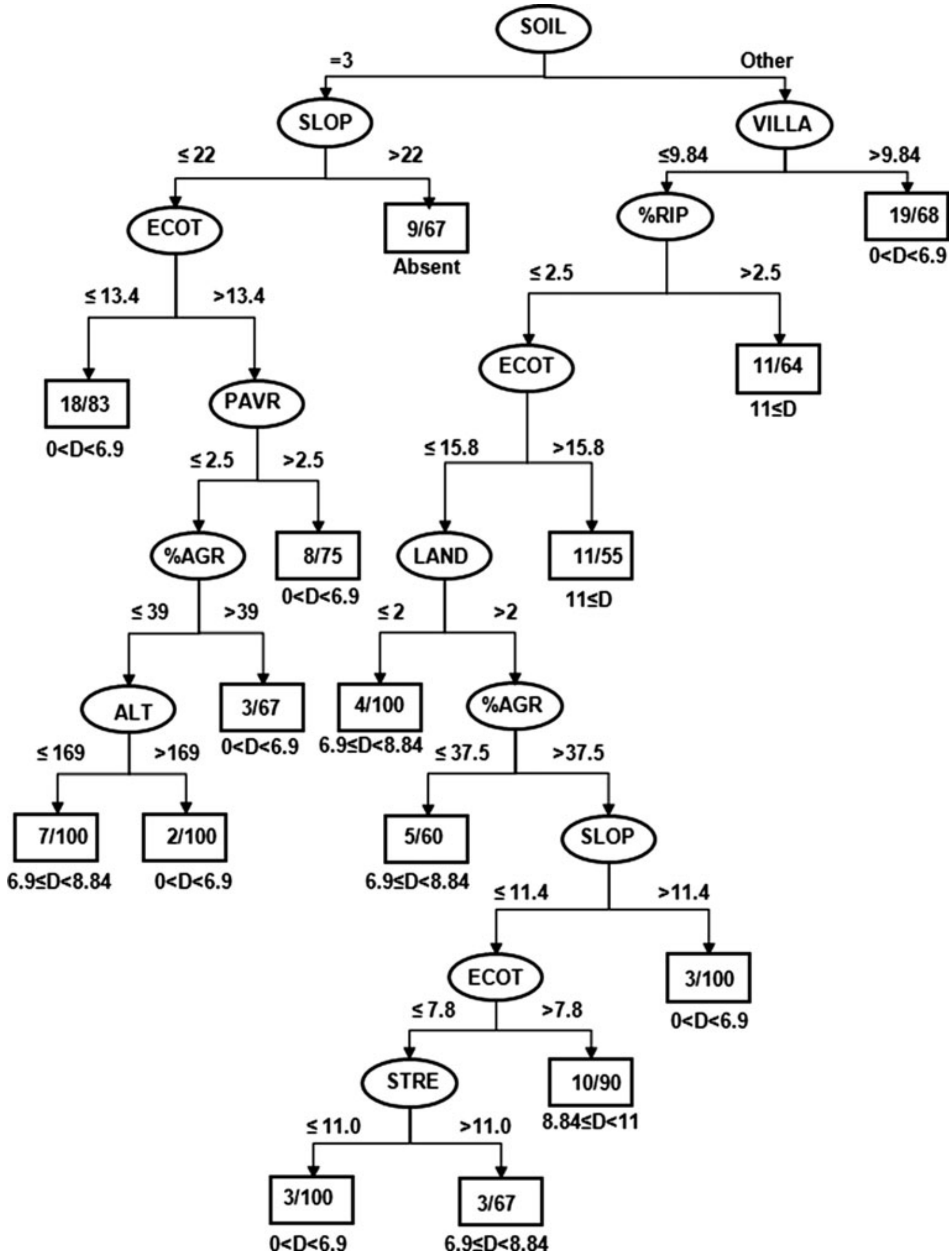

Fig. 2 Classification tree model depicting habitat relationships of wild rabbits on Lemnos Island during 2008. Inside each terminal node (*rectangular block*) is shown the number of instances in this branch and the percentage correctly classified. Its respective relative population density class is shown below each terminal node. Inside each non-terminal node (*oval*), the variable used to divide the data with their thresholds along the branches are shown

ships will form the basis for a targeted, site-specific management for the effective control of wild rabbit's population, both in agricultural and semi-natural areas.

Soil hardness was identified as one of the most important factors affecting population density, as the presence of hard-rocky soils constitutes a restricting factor for high rabbit densities. Soil hardness and depth are key factors for the relative suitability for warren excavation by rabbits (Parer and Libke 1985; Calvete et al. 2004; Williams et al. 2007). Soft and sandy soils are preferred because they are dug more easily and have an increased permeability to water (Myers and Parker 1975; Rogers and Myers 1979; Rogers 1981). On the other hand, in hard-rocky soils, the digging is difficult or even impossible, forcing the rabbits to live, in some cases, in surface shelters (Williams et al. 1995). However, the mean terrain slope will ultimately determine the existence of the species in areas dominated by hard-rocky soils, as steep slopes increase the probability of the rabbit's absence. The negative impact of intense topography (slope and altitude) on wild rabbit's distribution has also been reported by others (Williams et al. 1995; Calvete et al. 2004; Farfán et al. 2008), since these areas are less productive and less suitable for wild rabbits. This is probably due to the increased rates of soil erosion, associated with steeper slopes, which minimizes the presence of microhabitats suitable for rabbit's excavation. On the other hand, even under the hostile conditions caused by the presence of hard-rocky soils, gentle slopes can lead to the local deposition of soil, providing conditions suitable for warren excavation, and the subsequent development of small populations.

Human presence and the associated activities have been reported to have negative effects on wildlife by acting directly on the physiology, behavior, and mortality of wildlife, or indirectly by causing alterations to wildlife habitat (Cole et al. 1997; Cline et al. 2007; Guillemain et al. 2007). Similar results were obtained here, with the negative effect of human presence being expressed by the low population densities observed in areas with a high density of paved roads, and in areas with a high presence of settlements, even if soil conditions are favorable. This is probably the result of increased mortality on paved roads, conflicts between wild rabbits and domestic carnivores, as well as the alteration of habitats suitable for the species. Hunting was introduced as a binary explanatory variable in the analysis dividing the island into areas where hunting is allowed and areas where it is prohibited (refugees), but no significant effect was identified. This (rather surprising) result can be attributed to two primary reasons. Firstly, to the illegal hunting and secondly, to the periodic nighttime shooting, introduced since November of 2005 for population control, which are both practiced in the entire region. Those two factors probably balance the hunting status across the island and subsequently the distinction between refugees and hunting areas fail to depict a possible variation in hunting intensity.

A positive effect of some linear features, including ecotones, streams, and riparian vegetation, was clearly observed in the current study. Those features determine, to a large extent, habitat suitability at both home range and landscape scale. The high presence of riparian vegetation or ecotones resulted in the most favorable conditions for the species, where densities exceeded 11 ind. ha^{-1}. Even in areas where hard soils prevail, a high presence of ecotones can compensate for the hostile conditions, and under specific circumstances can lead to moderate population densities. The presence of particularly favorable soil conditions on the stream banks and the increased biomass and resources, both in ecotones and riparian vegetation, were probably the main reasons for the higher densities observed in these areas, by providing rabbits with a combination of increased food availability and shelter. In southwestern Spain, Fernandez (2005) reports that rabbits were most abundant near streams because there was plenty of quality food due to the existence of water even in dry seasons. Also, many researchers have emphasized the higher abundance of rabbits in the edges, as a result of the increased animals' mobility and diversity of resources offered in those places (Rogers and Myers 1979; Palomares 2001; Lombardi et al. 2003; Carvalho and Gomes 2004; Fernandez 2005).

Land-use diversity seems to positively affect the density of rabbits, particularly when favorable soil conditions occur. Similar results have been reported in other studies, which pointed out the preference of the species for a diverse habitat mosaic, providing shelter and food availability (Rogers and Myers 1979; Villafuerte and Moreno 1997; Fa et al. 1999), as well as the positive effect of crops in wild rabbits density under such circumstances (Boag 1987; Virgos et al. 2003; Calvete et al. 2004).

The effect of arable land on population density depends on the general conditions of the site and especially on the soil type. In hard-rocky soils, a high percentage of arable land limits the population to low densities, because in these agriculturally marginal sites the coverage and protection of rabbits is mainly dependent on the high presence of shrubby vegetation (Williams et al. 1995). In soft soils, by contrast, areas with relatively low proportion of arable land support low to moderate rabbit densities, while areas with a relatively high proportion of arable land are often associated with moderate to high rabbit densities (Calvete et al. 2004), especially when it is combined with elongated ecotones and streams.

Implications for management

The wild rabbit's population in Lemnos has reached high numbers and it currently constitutes an environmental and agricultural threat, justifying the need for the adoption of appropriate management measures. The present study provides useful insights on the characteristics determining population density, which can be managed for population control.

Population density mapping at an appropriate spatial scale is a necessary first step for the determination of priority areas, where the application of suitable management measures should reduce wildlife-rural economies conflicts. Furthermore, it is a useful tool for the division of large areas into smaller management units, according to geomorphologic characteristics; making the management both cost- and time-effective and efficient (see Williams et al. 1995). The presence of urban areas and other anthropogenic elements (i.e., paved roads) will also be taken into account for the designation of management units, because they are functioning as barriers preventing the colonization of wild rabbits.

A sound management scheme should aim at the dramatic reduction of population numbers in agricultural areas while at the same time maintain viable and sustainable populations in natural areas. Ecotones and riparian vegetation were found to be associated with high population density and their reduction is necessary if population is to be controlled in agricultural areas. In those areas, ecotones are often formed between cultivated and abandoned fields, while the latter are also important warren sites. Cultivation of abandoned fields will lead in more homogenous mosaic with reduced length of ecotones and subsequently reduced wild rabbit numbers. Furthermore, in the absence of warren sites, wild rabbits will be concentrated in field margins where warren ripping could be effectively applied (Barrio et al. 2011). Warren destruction could also be applied on stream banks crossing agricultural areas. The periodic application of the aforementioned measures will significantly reduce habitat suitability for wild rabbits. Those actions should be combined with measures that increase mortality, such as intensive shooting at the appropriate time (i.e., before the onset of breeding season). On the other hand, intensive shooting alone should be practiced in natural areas, both for maintaining the population at desirable levels and for ensuring a significant income for local communities.

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