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Micro-scale distribution of rabbits on Fuerteventura Island

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Abstract The European rabbit (*Oryctolagus cuniculus*) is a conservation and social dilemma in the Canary Islands. It is the main prey of endangered species, it causes severe impacts on vegetation, as well as has a considerable hunting economic value but damages agriculture. We assessed drivers of European rabbit habitat selection on Fuerteventura Island (Canary Islands, Spain) in order to understand the ecology and to contribute with data for managing this introduced species. To measure rabbit abundance, we counted the total number of fresh pellets and latrines. We used Generalized Linear Models (GLMs) to analyze the relationship between rabbit abundance and four groups of variables that represented the biological requirements of the species (environmental, food resources, refuges/shelters, and biological interactions). Hierarchical partitioning techniques were used to estimate the explanatory capacity of these different groups of variables. Our model better explained fresh pellet abundance (89% of total deviance) than latrine abundance (57%). Variables related to food resources best explained the abundance of both latrines and pellets. We identified a set of plant species highly correlated with rabbit abundance, which probably makes up the species' diet. Variables relating to refuge/shelter and the environmental were also relevant. Interactions with other mammals did not strongly affect rabbit abundance on Fuerteventura Island. Mean annual precipitation and temperature were variables that individually best explained abundance, although half of their relevance is shared with others non-environmental variables. Our results provide policy makers and land-managers with applied information on the relationship between rabbit populations and micro-scale components of Fuerteventura.

Keywords Abundance relevant factors · Canary Islands · Distribution models · European rabbit · Habitat selection · Invasive species · *Oryctolagus cuniculus*

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Introduction

In the Mediterranean ecosystems of the Iberian Peninsula, where rabbits declined dramatically (see Calvete et al. 2004a), several threatened species are highly dependent on the abundance of this species (Delibes and Hiraldo 1981; Ferrer and Negro 2004; Delibes-Mateos et al. 2008). Thus, numerous efforts have been made to enhance wild populations for conservation and hunting purposes (Moreno and Villafuerte 1995; Moreno et al. 2004; Calvete and Estrada 2004; Calvete et al. 2004b), as well as much data has been compiled on factors affecting its abundance (e.g., Fa et al. 1999; Palomares 2003; Virgós et al. 2003; Calvete et al. 2004a).

A separate source of concern stems from the fact that rabbits have been transported to many other places in the world (Thompson and King 1994; Long 2003; Lees and Bell 2008). They are reported in more than 800 islands (Flux and Fullagar 1992) and are among the world's worst invasive species (Lowe et al. 2000). Rabbits are included in a small group of species responsible for the most damage to invaded islands ecosystems (Courchamp et al. 2003). Impacts of feral rabbits on the islands in which they have been introduced are severe (see Lees and Bell 2008). Among the effects attributed to them are drastic damage to seabirds colonies (e.g., Bell 1995; McChesney and Tershy 1998), alteration of vertebrate populations through modification of food webs (e.g., Courchamp et al. 2000; Norbury 2001), impoverishment of vegetation (e.g., Chapuis et al. 1995), extinction of some vertebrate species (e.g., North et al. 1994), and dramatic effects on agriculture (e.g., Sumption and Flowedew 1985; see Scanlan et al. 2006). Many technical and economic efforts have been attempted to minimize these effects on islands (Tomlinson and Gooding 1970; Chapuis et al. 2001; Veitch and Clout 2002; Parkes and Murphy 2003; Donlan et al. 2003; Genovesi 2005). Thus, the eradication of this species is one of the most urgent management priorities for conservation in many archipelagos (e.g., Genovesi 2000; VanderWerf et al. 2007).

The introduction of the European rabbit into the Canary Islands dates back to the fifteenth century (De Abreu 1977). It is currently present on all the islands and islets and in almost all types of ecosystems, with the exception of the islet of Montaña Clara, from where it was eradicated (Martín et al. 2002). Rabbits are embedded in the ecosystems and the human economy of the Canary Islands. From an ecological point of view, they are considered among the main causes of the decline of numerous endemic plants (see Beltrán et al. 1999) but, on the other hand, rabbits help to maintain populations of threatened endemic scavengers and avian predators (e.g., Gangoso et al. 2006), but also introduced carnivores (for example feral domestic cats Nogales and Medina 1996).

From a social perspective, rabbits are the major small game species of the Canaries and an important source of revenue (Gobierno de Canarias 1998), but they negative impact agriculture in a significant way (Hernández 1986). Hence, annually, the government of each island makes important efforts to manage the species. Ideally, management strategies should be directed to promote rabbit eradication from the Canary Islands. However, a probably unaffordable eradication campaign, in conjunction with the clear trade-off that exists between rabbit's negative and positive ecological impacts and its social and economical role, favors government actions directed to control population increases.

Despite these complications, quantitative information on the ecological role of the species and its distribution are lacking in the Canary Islands, from either the ecological or conservation points of view. This is in spite of the fact that designing appropriate conservation plans implies proper monitoring of the ecology and distribution patterns of invasive species (Genovesi and Shine 2003). There are a number of studies of diet (Martín 1999; Martín and Marrero 1999; Marrero and Martín 2000; Martín et al. 2003), and there is some knowledge of its consumption of endemic and introduced plants fruits (Nogales et al. 1995, 2005; López-Darias and Nogales 2008). Other studies have explored factors affecting rabbit abundance in La Palma Island and Alegranza, a small islet of the archipelago (Cabrera-Rodríguez 1998, 2006; Martín et al. 2003).

The aim of this contribution is to provide the first basic quantitative information on variables currently influencing the abundance of this invasive mammal in Fuerteventura Island. We examined the species distribution at a fine scale, processing an exhaustive compilation of field sampling variables with Generalized Linear Models and hierarchical partitioning techniques, in order to estimate the relevance of groups of explanatory variables and as individual variables. Our results provide comprehensive information for understanding the prevalence of rabbits on the Canary Islands. This information is essential for managing the species in Fuerteventura Island and fundamental to interpret its current occurrence in the whole archipelago.

Materials and methods

Study area

Fuerteventura Island is the second largest island (approximately 1,660 km^2), the second lowest in altitude (807 m a.s.l), and the closest to Africa (approximately 115 km) of the Canary Islands (27°–29°N, 13°–18°W; Fig. 1). The island climate is arid, and habitats are semi-desertic, with mean annual temperatures around 20°C (Dorta 2005) and annual precipitation below 100 mm.m^{-2}. Fuerteventura Island is the oldest island of the archipelago (20.4 ± 0.4 Ma; Carracedo et al. 2005; Criado 2005) and severe erosion is apparent. Large extensions of biogenic sand, called "jable", a few "malpaís" (hereafter

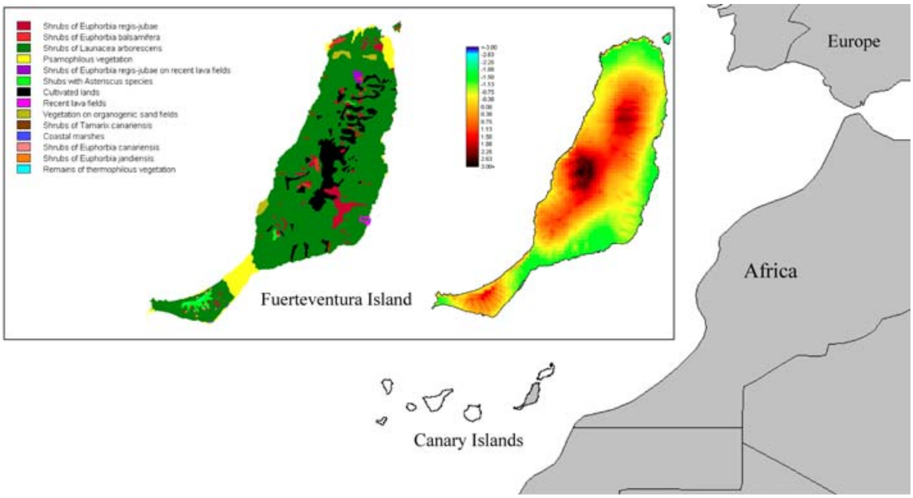

Fig. 1 Geographic location of Fuerteventura Island within the Canary Islands, showing their position with respect to the African continent and mainland Iberian Peninsula. On Fuerteventura, the location of sampling plots (*dots*) within different vegetation types (*left*; vegetation categories following Ruiz 1980) and across the principal component dimension that covers the climatic and altitudinal variation of the island are shown (*right*; *blue* = lower altitudes and mean annual precipitations and *red* = higher altitudes and mean annual precipitations; see text) (Color figure online)

lava fields; a large extension of recent volcanism), and numerous stone walls, characterize the landscape (Rodríguez 2005). The island flora has been altered by the exploitation of wood resources, intensive livestock grazing and the introduction of exotic herbivores. Thus, the landscape is dominated by substitution vegetation, the native vegetation being relegated to small patches in inaccessible or unfavorable areas (Rodríguez 2005). Rabbits are a controversial species in Fuerteventura: they are abundant and are probably one of the main reasons why some threatened predator populations are maintained in Fuerteventura (some extinct in the rest of the Canaries), while they are likely also the cause of the decrease of numerous endemic plant populations (Gangoso et al. 2006).

Plot location selection

To ensure reliability of species distribution models, it is essential to sample a significant number of sample points that are representative of the environmental and vegetation variability of the studied area (Hortal and Lobo 2005). Consequently, to describe environmental variation of Fuerteventura Island and prior to the selection of sampling plots, we conducted a Principal Component Analysis (PCA), using four climate variables (annual precipitation, mean annual temperature, minimum winter temperature and maximum summer temperature) and altitude at 100×100 m UTM squares resolution. The climate variables were extracted from the digital cartography of the Spanish Instituto Nacional de Meteorología (http://www.inm.es/), whereas altitude was extracted from an available DEM. We identified a unique factor with an eigenvalue greater than 1 (4.24), which explained 84.75% of total environmental variability. Factor scores were positively related to annual precipitation and altitude, but negatively related to the three temperature variables. Then, we divided the island in 100×100 m UTM squares and calculated the number of squares within each one of the 14 vegetation categories described for Fuerteventura (adapted from Ruiz 1980; Fig. 1). The number of UTM squares per vegetation category varied between 3 and 121 (mean $\pm$ SD; 27 $\pm$ 33). In order to carry out a proportionally lower sampling effort in the most common vegetation categories and, alternatively, to obtain a representation of the rarest ones, we estimate the square root of the number of 100×100 UTM squares for each vegetation category to subsequently calculate the proportion of UTM squares in each vegetation category.

In a next step, we established the number of plots that one person could feasibly sample ($n = 300$), dividing this number according to the formerly established proportions in order to estimate the number of sampling plots in each vegetation category. To specifically select the location of plots in each vegetation category, we considered the scores of the formerly PCA factor. Thus, the range of values of this PCA factor in each vegetation category was divided in a number of regularly distanced fragments equal to the previously estimated number of sampling plots, guaranteeing the representation of all climate and habitat diversity variability.

Subplot selection and area characterization

Seventy-one plots (100×100 UTM squares) were eliminated because they were located in urban, or very disturbed, areas. Thus, we only analyzed 229 plots (Fig. 1) out of the 300 originally selected. We located each plot using a Garmin III Plus GPS. Subsequently, in each plot, we placed 21 subplots separated by 5 m distance (5 subplots towards each one of the cardinal directions, established with a Suunto compass, and an additional subplot in the central point; Fig. 2). In each subplot we established a 1.5×1.5 m area, laid out perpendicular to the axis of each direction (Fig. 2), within which we measured four groups of

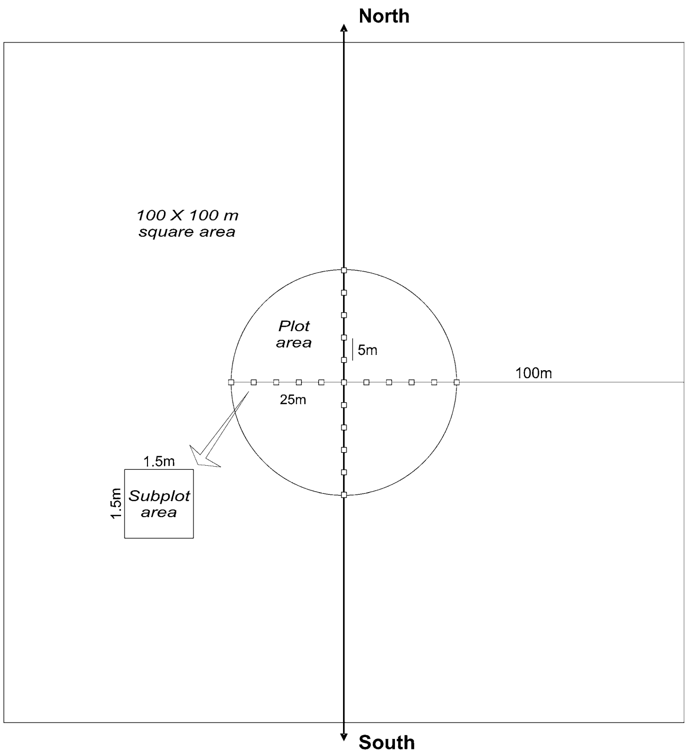

Fig. 2 Schematic representation of the subplot selection in each plot

variables which are selected to account for previously known biological requirements of the species: environmental data, food resources, refuges/shelter, and biological interactions.

Environmental variables

The extracted climatic variables (annual precipitation, mean annual temperature, minimum winter temperature and maximum summer temperature) and topographic variable (altitude), used previously for the selection of sampling plots, were also used at the same resolution (100 × 100 UTM square) in order to provide the individual environmental variables for each plot. The environmental factor previously extracted by PCA was also used as an explanatory variable. Locally, we measured the most representative slope and aspect (across the highest slope) of each plot using a Suunto compass and clinometer. As rabbit abundance could be influenced by the type of landscape, we assigned a categorical variable to each plot, which identified the primary landscapes of the island: lava field, town, "jable", stony slope, flat area, abandoned cultivation, cultivation, ravine, or abandoned cultivation terrace (see "Annex 1").

Food resources variables

As vegetation data are a good proxy measure of potential food resources, we recorded data on the herbaceous cover (%) and maximum and minimum plant height (cm) for each 2.25 m^2 subplot. We also noted the cover percentage in each plot of 111 plant species, as well as the distance to cultivated areas and to rural houses or farmhouses (m) as a measure of food availability, since rabbits take advantage of crops.

Refuge/shelters variables

In each subplot we recorded the total number, maximum height and width of stone heaps (cm), the total stone cover (%), and scrub and tree cover (%). We also noted partial stone cover (%) of four sizes (smaller than 10 cm, between 10 and 30 cm, between 30 and 50 cm and larger than 50 cm). In addition, we counted stone walls in each subplot and assigned another categorical variable to reflect the number of potential rabbits' shelters in each subplot: none, some, few or many. We categorized the soil penetrability of each subplot (sandy, clay, sandy-clay, "jable", rocky, "rocky-jable", pyroclastic, pyroclastic-sandy and cultivated), taking into account the presence of rabbit burrows in the soil.

In addition to these data, we also compiled general information on refuge/shelter at a bigger scale: the surrounding 50-m diameter plot and the surrounding 100-m radius of each plot. Using the same group of variables as those used to describe the subplots, we recorded the abundance of shelters, the number of abandoned houses, stone walls, ravines, stony ground, and the maximum height, width and number of stone heaps in the local area, as potential sources of shelters for rabbits. We divided ravines into three categories: small, medium and large, as a cline of shelters is available according to ravine size. We classified stone walls into long (>100 m) or short (<100 m) so as to further understand their possible association between rabbits and stone walls.

Biological interactions variables

To examine positive or negative interactions between rabbits and the most abundant mammals in the island, we counted the number of dung pellets of feral goat/sheep and introduced ground squirrel droppings in each subplot. Sheep and feral goat dung pellets, which were virtually indistinguishable, were counted together, while fresh droppings (more strongly colored and harder) were recorded separately as a measure of recent presence of goats/sheep and ground squirrels.

For subsequent analysis, plots were considered as the sample unit and, depending on each variable nature, subplot measures were averaged or summed, as well as some were transformed to dummy variables (see "Annex 1").

Rabbit abundance data

Between July and October 2005, we counted the number of fresh rabbit pellets and latrines in each subplot. Both measures have been described as good indices of rabbit abundance (Taylor and Williams 1956; Iborra and Lumaret 1997; Palomares 2001). A latrine was considered when there was accumulation of at least 50 pellets. We recorded the total number of pellets and latrines in each plot as the dependent variable for regression analysis.

Statistical analyses

We used Generalized Linear Models (GLM) to summarize the relationship between the abundance of rabbit pellets/latrines and explanatory variables (see McCullagh and Nelder 1989). We assumed a logarithmic relationship between the dependent and the explanatory variables (the link function), and a Poisson error distribution of the dependent variable. As a first step, the dependent variable (number of fresh rabbit pellets or latrines) was regressed individually against all explanatory variables. In order to account for non-linear relationships between the predictors and the rabbit abundance, we examined whether linear, quadratic or cubic functions of each continuous variables were statistical significant. Next, we selected a partial complete model based on those variables belonging to the same group (environmental, food resources, refuges/shelters, and biological interactions) that were previously determined as significant using the Akaike criteria to select the best model. Finally, a measure of the whole explanatory capacity of the variables was obtained by including all the formerly statistically significant variables at the same time. All the models obtained were checked for overdispersion (when the observed variance is higher than the variance of a theoretical model), computing parameter estimates and related statistics taking this overdispersion into account. As a last step, we backward-stepwise regressed the residuals of the complete models with the nine terms of a third-degree polynomial of central latitude (Lat) and longitude (Lon) of each 100×100 m UTM cell (Trend Surface Analysis; Legendre and Legendre 1998) to examine the existence of a possible unexplained spatial pattern in the dependent variable (rabbit pellets/latrines). We verified these residuals for autocorrelation, since one or several important spatially structured explanatory variables may have been left out if they are spatially autocorrelated (Cliff and Ord 1981; Legendre and Legendre 1998; Keitt et al. 2002).

The explanatory variables used in multiple regression models are often correlated. Although determination of causal factors using correlative techniques is always a delicate task (MacNally 2000), correlations can constitute a key material and the basis for more sophisticated experimental proposals. When one is interested in forecasting the dependent variable, this collinearity is not a great concern because the objective is to maximize the explanatory variability of the model (Legendre and Legendre 1998). This strategy was followed by us in the former analyses, carried out only to obtain a measure of the explanatory variability accounted for each group of variables and not to estimate correctly model parameters. Conversely, if we aim to correctly estimate the regression coefficients (the independent contributions of each explanatory variable on the dependent one), this collinearity forces us to discriminate the pure effect of one variable when the effect of the others has been taken into account. Hierarchical partitioning (MacNally 2000, 2002) allows us to measure the amount of variation attributed exclusively to each variable, and the variation that may be attributed to a group of explanatory variables by calculating the average effect of inclusion of each group of variable. Thus, this technique has been applied for rabbit pellets in order to estimate the unique contribution of the main groups of explanatory variables (environmental, food resources, refuge/shelters). The STATISTICA 6.0 package (StatSoft Inc 2001) was used for all statistical computations.

Results

Influence of environmental variables

After regressing the number of fresh rabbit pellets and latrines against all explanatory variables individually, six environmental variables were statistically significant for fresh pellets and latrines, respectively (Table 1). Environmental PCA factor, mean annual temperature and precipitation were the most relevant ones. The partial complete model explained 45.4 and 21.3% of total variability for fresh pellets and latrines, respectively (Table 1).

Table 1 Explanatory variables accounting for the highest percentage of total variability in the abundance of rabbit pellets and latrines

		Dev	%Dev	Sign		Dev	%Dev	Sign
Rabbit pellets model					*Rabbit latrines model*			
Environmental variables	Null model for pellets	27,845			Null model for latrines	186		
	Environmental PCA factor	17,451	37.3	++	Mean annual temperature	125	32.7	−+
	Mean annual temperature	17,929	35.6	−+	Mean annual precipitation	129	30.7	++
	Mean annual precipitation	18,202	34.6	++	Environmental PCA factor	131	29.3	++
	Altitude	20,251	27.3	+−+	Altitude	150	19.4	+
	Slope	22,492	19.2	+++	Slope	160	13.7	−
	Aspect	24,538	11.9	+−	Aspect	171	8.1	+−
	Partial complete model	15,215	45.4		**Partial complete model**	164	21.3	
Food resources variables	*Fagonia cretica*	19,366	30.4	+−+	Type of cultivation	120	35.4	
	Anagallis arvensis	19,716	29.2	+−+	*Phagnalon saxatile*	130	30.2	+−
	Scorpiurus sulcatus	20,035	28.0	+−+	*Anagallis arvensis*	131	29.4	+
	Atractylis cancellata	20,460	26.5	+−	Asteracea	144	22.5	+
	Carrichtera annua	20,883	25.0	+−+	*Scorpiurus sulcatus*	145	21.7	+
	Wahlenbergia lobelioides	20,990	24.6	+−+	*Fagonia cretica*	145	21.6	+−
	Hedypnois cretica	22,022	20.9	+−+	*Atractylis cancellata*	146	21.2	+−
	Asteraceae	22,246	20.1	+−+	*Convolvulus althaeoides*	147	20.7	+−
	Graminea	22,661	18.6	+−+	*Phagnalon saxatile*	147	20.6	+
	Helianthemum ledifolium	22,677	18.6	+−+	*Micromeria varia*	153	17.4	+−
	Phagnalon saxatile	22,808	18.1	+−+	*Plantago amplexicaulis*	154	17.1	+
	Silene sp.	23,118	17.0	++−	Herbaceous plant cover	158	14.8	+
	Carrichtera annua	23,358	16.1	+−+	*Asparagus pastorianus*	159	14.3	+−+
	Ajuga iva	23,506	15.6	+−+	Soil without vegetation	160	13.8	−
	Partial complete model	6,406	77.0		**Partial complete model**	82	55.6	

Table 1 continued

		Dev	%Dev	Sign		Dev	%Dev	Sign
Refuges/shelters variables	Maximum plant height	23,029	17.3	+−	Short stone walls	155	16.4	+
	Sandy-clay soil	24,915	10.5	+−+	Number of stone walls	161	13.0	+
	Short stone walls	25,494	8.4	+−+	Maximum plant height	162	12.0	+
	Stones cover	26,030	6.5	++−	Number of stone heaps	165	11.1	+−
	Number of stone walls	26,326	5.5	++−	Maximum stone heaps height	169	8.7	+−
	Partial complete model	13,652	51.0		**Partial complete model**	129	30.4	
Biological interaction variables	Fresh squirrel droppings	25,134	9.7	+−+	Goats/sheep dung pellets	178	4.1	−
	Dry squirrel droppings	25,929	6.9	+−+	Goats/sheep dung pellets	179	3.8	−
	Partial complete model	23,410	15.9		**Partial complete model**	178	4.1	
	Complete pellets model	3,081	88.9		**Complete latrines model**	82	55.6	

Variables are shown according to their group. We noted the deviance and the percentage of explained deviance of each variable regressed individually. The type of significant function (linear, quadratic or cubic) as well as the sign of each term is included in the case of continuous variables. Plant species are preceded by a “d” when they dominated sample plots. The percentage of deviance accounted for partial completed (with explanatory variables of the same group selected after applying the Akaike criterion) and complete models are also included

Influence of food resource variables

More than a 90 variables were statistically significant and accounted for more than 2% of total variability of pellets (see Table 1 for the most explicative ones). Of these, several plant species explained more than 10% of total variability. A partial complete model of this group of variables accounted for 77% of total variability of fresh rabbit pellets (Table 1), including 29 variables. More than 60 food resource variables accounted for more than 2% of total variability in rabbit's latrines, with several plant species also being the most explicative variables (accounted for more than 10% of total variability; Table 1). The partial complete model of food resources variables explained 55.6% of total variability for latrines including seven variables (Table 1).

Influence of refuges/shelters variables

Quantitative variables representing the number of shelters should be highlighted, particularly maximum plant height in the case of fresh pellets (Table 1). For latrines, short stone walls and the number of them were also highly relevant. The complete model with the significant refuge variables explained 51% of total variability in fresh pellets and 30.4% in the case of latrines (Table 1).

Influence of biological interaction variables

This group of variables was the less relevant for both fresh pellets and latrines. The cubic functions of the fresh and dry Barbary ground squirrel droppings were the most significant variables for rabbit fresh pellets (Table 1). In the case of rabbit latrines only fresh and dry goat/sheep dung pellets were statistically significant (Table 1). A complete partial model for rabbit pellets and latrines accounted for 15.9 and 4.1% of total variability, respectively (Table 1).

All significant variables modeled together accounted for 88.9 and 55.6% of total variability of rabbits' fresh pellets and latrines, respectively (Table 1). The addition of spatial variables did not improve any of the two models, and residual autocorrelation was not significant at any lag distance. Hierarchical partitioning was only assessed for pellets as this model had the highest explanatory capacity. The mean percentage of variation accounted for by environmental, refuges/shelters, food resources and biological interactions was 21.0, 24.4, 42.8 and 8.9%, respectively. Geographical variation in the number of rabbits' fresh pellets predicted according to the complete model is shown in Fig. 3.

Discussion

Our results show that food resources, refuge availability, environmental variables and biological interactions followed a cline from the least to the most important in explaining the abundance of *Oryctolagus cuniculus* on Fuerteventura Island. The predictive capacity of our model for rabbit pellets was significantly high, probably due to the wide spectrum of species requirements that were considered. The model results for latrines were not so accurate, possibly because latrine abundance has a crucial relationship with the species' behavior (Sneddon 1991). This model may also have been influenced by other factors. However, there is a high concordance between significant variables explaining pellets and latrines, with both models sharing the majority of those variables.

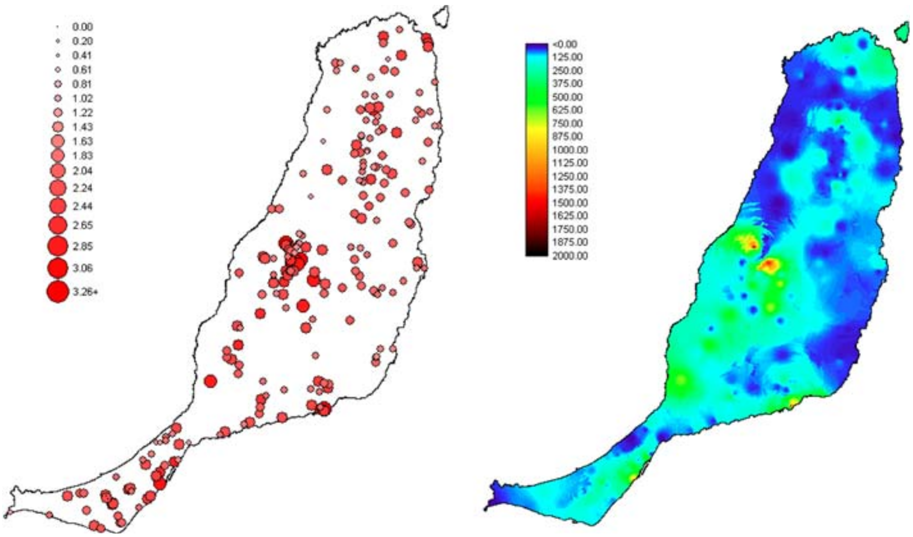

Fig. 3 Geographical variation in the number of rabbits' fresh pellets (in a log scale) predicted according to the complete model (Table 1) for the 229 sampling plots (*left*), and interpolated map (*right*) generated with the simple-mean mobile techniques in Idrisi 32 (Clark Labs 2001)

Resources best explained rabbit abundance. Rabbit populations undergo abundance oscillations because of seasonality in reproduction (Delibes and Calderon 1979), which is affected by food availability (Villafuerte et al. 1997). Grass is considered an essential food source for rabbits (Hulbert et al. 1996), and the majority of significant variables in our model are related to the abundance of numerous grass species. If these plant species are food resources, we should expect them to be part of rabbits' diet in the archipelago. In the semiarid small islet of Alegranza, rabbits consume at least 12 plants species (Martín et al. 2003). Numerous dry or fleshy-fruited seeds in their pellets indicate that they also eat reproductive parts of many plants species in other islands (Nogales et al. 1995, 2005; López-Darias and Nogales 2008). According to our results, 90 different plants species were shown to be significant in explaining rabbit abundance. Surprisingly, 46 species among these have been recently shown to be part of rabbit diet in Fuerteventura Island (López-Darias and Nogales 2008). One of the main results of our work is that our final model includes all these 46 plant species as significant variables. Our results suggest that the rabbit diet in Fuerteventura could be composed of an even higher number of plant species, most of them grasses. Nevertheless, rabbit diet must be studied in Fuerteventura Island to explore this supposedly wide trophic niche.

Refuge variables were the next most explicative ones. Maximum vegetation height was one of the most relevant variables, highly correlated with shrub cover. Previous studies have emphasized the preference of rabbits for high scrub and grass cover, as sources of shelter and food, respectively (Moreno et al. 1996; Villafuerte and Moreno 1997; Fa et al. 1999; Virgós et al. 2003). A trade-off also exists between these requirements. Depending on the type of predation risk (Kolb 1994; Palomares et al. 1996; Lombardi et al. 2003), rabbits may be forced to use areas with greater protection (Jaksic and Soriguer 1981; Palomares and Delibes 1997). Our models fit these results, as food and refuges affected the species abundance in Fuerteventura. Fuerteventura is a semiarid island, where rainfall is scarce and concentrated in short periods each year.

Vegetation is therefore adapted to rainfall, and is a limiting factor for the abundance of strict herbivores. Moreover, variables such as the number of stone walls or the presence of big stones with refuges are positively related to rabbit abundance. On the island, rabbits are known to use these structures as refuges or to build up their warrens. Refuges, on the other hand, might be essential for maintaining populations on the island and for escaping from enemies. The species suffers from high human hunting pressure, and also it constitutes the main part of the diet of all the island predators (avian predators, Gangoso et al. 2006; feral cats, Medina et al. 2008).

Environmental variables were less relevant. However, annual precipitation, temperature, and the scores of the PCA factor were the variables that individually best explained rabbit abundance. These three variables might control vegetation availability in such a xeric island, thus influencing rabbit abundance. Moreover, the inherent correlation among naturally occurring variables hinders our search for causal relationships (MacNally 2000). Our hierarchical partitioning analysis highlights the difficulty of distinguishing between the four groups of variables, and that almost half of the variability explained by only one group of variables can be also accounted for by other correlated variables from another group.

Biological interactions with other herbivores seem not to be highly relevant. In fact, a negative relationship between squirrel and rabbit abundance was detected. Barbary Ground Squirrel (*Atlantoxerus getulus*; Linnaeus, 1758) is an invasive ground squirrel introduced to Fuerteventura from Morocco in 1965 (Machado and Domínguez 1982). Although a wide set of impacts has been described for this species (Gangoso and López-Darias 2004; Nogales et al. 2005; López-Darias and Nogales 2008), potential interactions with rabbits are unknown. Squirrel density is highly dependent on the abundance of rocky shelters, stone walls or stone heaps (López-Darias and Lobo 2008). Rabbits also used these structures on the island and may be competing for refuges. It would be worthwhile to further examine this negative interaction between squirrel and rabbit abundance.

Our analysis also suggests that some variables explained rabbit abundance at a coarser scale. Landscape type is correlated with the species' abundance, possibly because of cultivations patterns. Our results support the findings of Calvete et al. (2004a), who explored the relationship between cereal crops and rabbit abundance. Although quantitative studies are lacking, rabbits are known to take advantage of cereal crops in Fuerteventura. Government management strategies (especially during dry seasons or years) in this semiarid island include campaigns promoting cultivation of cereals (wheat, barley or oats) in public or private areas all around the island. These campaigns aim to maintain high rabbit densities for hunting purposes. Only the large expanses of flat areas of Fuerteventura had unsuitable habitats for high rabbit densities.

Our results provide policy makers and land-managers with valuable information on the relationship between rabbit populations and micro-scale variables in Fuerteventura. Due to the importance of vegetation for rabbit abundance, we suggest that increasing of both scrub and grass cover should increase habitat suitability for rabbits. Moreover, cultivation of food sources may be a useful tool for increasing rabbit populations. Nevertheless, rabbits also negatively affect natural ecosystems, so further investigations are necessary to develop an optimal management strategy that resolves this conservation dilemma, in which rabbits, by one side, constitute an essential prey species for threatened endemic scavenger and avian predators but also cause impacts on native vegetation, and by another side, present a considerable economic value for hunting but negatively affect agriculture.

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Annex 1

See Table 2.

Table 2 Variables measured, grouped according to the four groups considered (environment, food resources, biological interactions and refuge/shelter)

Types of variables	Scale	Variable names	Variable nature	Measurement method	Categories/(units)
Environment	P	Slope	1		(%)
		PCA factor	1		
		Mean annual temperature	1		(mm/m^2)
		Mean annual precipitation	1		(mm/m^2)
		Altitude	1		(m)
		Aspect	2		North, south, east and west
	L	Landscape type	2		Badland, town, “jable”, stony slope, flat area, abandoned cultivation, cultivation, ravine, and abandoned cultivation terrace
Food resources	S	Herbaceous cover	1	A	(%)
		Scrub cover	1	A	(%)
		Tree cover	1	A	(%)
		Soil without vegetation	1	A	(%)
		Maximum plant height	1	A	(cm)
		Species of maximum height	2	D	Name of the species
		Minimum plant height	1	A	(cm)
		Species of minimum height	2	D	Name of the species
		All plant species present	2	D	Names of all species present
		Dominant plant species	2	D	Name of the dominant species
	P/L	*Distance to cultivations*	1		(m)
		Distance to roads	1		(m)
		Distance to rural houses or farmhouses	1		(m)
		Distance to isolated houses	1		(m)
		Type of vegetation	2		14 different categories (see Ruiz 1980)

Table 2 continued

Types of variables	Scale	Variable names	Variable nature	Measurement method	Categories/(units)
Refuges/ shelters	S	Number of stone heaps	1	S	
		Maximum height of stone heaps	1	A	(cm)
		Maximum width of stone heaps	1	A	(cm)
		Stone cover	1	A	(%)
		Stones smaller than 10 cm	1	A	(%)
		Stones between 10 and 30 cm	1	A	(%)
		Stones between 30 and 50 cm	1	A	(%)
		Stones larger than 50 cm	1	A	(%)
		Number of stone walls	1	A	
		Occurrence of potential shelters for rabbits	2	D	None, some, few, many
		Type of soil (penetrability)	2	D	Sandy, clay, sandy-clay, “jable”, rocky, rocky-”jable”, pyroclastic, pyroclastic-sandy and cultivated
	P	Number of potential shelters for rabbits	2		None, some, few and many
		Number of stone walls	1		
		Type of stone walls	2		Long, short
		Number of ravines	1		
		Types of ravines	2		Small, medium, large
		Number of stone heaps	1		
		Maximum height of stone heaps	1		(cm)
		Maximum width of stone heaps	1		(cm)
	L	Occurrence of stone heaps	1/2	D	None, some, few and many
		Number of abandoned housings	1		
Biological interactions	S	Number of squirrel old droppings	1	S	
		Number of fresh droppings of squirrel	1	S	
		Number of old goat/sheep dung pellets	1	S	
		Number of fresh goat/ sheep dung pellets	1	S	

The scale at which each variable was measured is shown by *S* subplot, *P* plot, *L* landscape. Variables types are indicated by 1 (quantitative) or 2 (categorical), showing each category for categorical variables and units for quantitative ones. Procedure followed to measure subplot variables is indicated by A (when subplots data were averaged for posterior analysis), S (when data were summed) or D (when variables where transformed to dummy ones). Italicized variables correspond to those used both as continuous and dummy binary ones

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