Capítulo 3

Cambios estacionales en el uso del hábitat por herbívoros de diferente tamaño en un ecosistema semiárido mediterráneo

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

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Resumen

En general, se asume que a la escala de paisaje la selección de hábitat por los herbívoros está directamente influida por la abundancia y calidad del alimento, así como por la presencia de agua y refugio. A esta escala, la topografía influye en la distribución de estos factores a través del flujo de agua y nutrientes, afectando indirectamente a la abundancia y distribución de los herbívoros. Diversas investigaciones han demostrado que las diferencias en el tamaño de los herbívoros y en la morfología de sus sistemas digestivos pueden explicar divergencias en la eficacia y selectividad mientras comen y en la forma de evitar a los depredadores, lo que probablemente lleva a que herbívoros de diferente tamaño usen de manera diferente el hábitat. Utilizando un modelo causal apriorístico, testamos las hipótesis a cerca del papel de los factores directos e indirectos que pueden afectar al uso del hábitat por un herbívoro grande rumiante (ovejas en régimen extensivo) y un herbívoro pequeño no rumiante (conejo europeo) en un ecosistema de dehesa de la Península Ibérica. Los datos se recogieron durante tres estaciones: primavera, verano e invierno y se analizaron mediante modelos de ecuaciones estructurales (SEM). Los resultados muestran que el uso del hábitat por los herbívoros estuvo, durante las tres estaciones, indirectamente influido por la humedad y concentración de nitrógeno del suelo, a través de sus efectos sobre la abundancia y distribución del alimento. Respecto a la influencia de los factores directos, el uso del hábitat de ambos herbívoros resultó opuesto en primavera y en invierno; en primavera, las ovejas estuvieron principalmente limitadas por la abundancia de comida, y los conejos por el riesgo de depredación; en invierno, las ovejas se vieron influidas de manera similar por la abundancia de alimento y por la distancia al refugio, mientras que los conejos estuvieron más limitados por la abundancia de alimento. Este patrón cambió en verano cuando la vegetación herbácea se secó y fue insuficiente para mantener a las ovejas, las cuales fueron conducidas fuera del ecosistema (trashumancia). En esta estación, los conejos cambiaron su modelo de uso de hábitat ajustándose a la disminución de comida, pero a expensas de aumentar su vulnerabilidad frente a los depredadores. El agua no influyó como factor en ningún caso. La alta heterogeneidad de hábitats, generados por la topografía y una gestión extensiva del suelo, es un factor determinante en la coexistencia de herbívoros grandes y pequeños.

Seasonal shifts in habitat use by different-sized herbivores in a semi-arid Mediterranean ecosystem

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Abstract

It is generally assumed that at the landscape scale herbivore habitat selection is directly influenced by the relative abundance and quality of food, water and refuge. At this scale, topography determines the distribution of these factors through water and nutrient dynamics, indirectly affecting herbivore abundances. Additionally, research has demonstrated that differences in herbivore body size and digestive system morphology may account for divergences in foraging efficiency and predator avoidance, which probably lead to different habitat use. By means of an aprioristic causal model, we tested hypotheses about the role of direct and indirect factors affecting habitat use by a large ruminant (free-ranging sheep) and a small hindgut fermentor (wild rabbit) in a Mediterranean ecosystem (dehesa) of the Iberian Peninsula. We collected a large dataset during three contrasting seasons: winter, spring and summer, which was analysed using structural equation modelling (SEM). In these seasons, herbivore habitat use was indirectly influenced by soil moisture and nitrogen through their effect on food abundance and distribution. Regarding direct factors, habitat use by both herbivores resulted opposite in spring and winter; in spring, sheep were limited by food quantity and rabbits mainly constrained by predation risk; in winter, sheep were influenced similarly by food abundance and refuge distance, whereas rabbits were principally influenced by food abundance. The pattern changed in summer when herbaceous vegetation dried up and food was insufficient to support sheep which were driven away from the ecosystem (transhumance). In this season, rabbits shifted their pattern of habitat use as an adjustment to food shortage, but at the expense of increasing their vulnerability to predation. Water did not influence as factor in any case. High habitat heterogeneity, maintained by topography and a low intensity land uses, is a determinant aspect which allowed the coexistence of large and small herbivores.

Keywords: Dehesa ecosystem, different-sized herbivores, foraging habitat use, *Oryctolagus cuniculus*, path model, structural equation modelling, transhumance.

1. Introduction

Herbivores have a strong influence on the function and dynamics of most terrestrial biomes (Huntly 1991). In turn, the spatial pattern and abundance of resources and plant communities determines foraging habitat selection by grazers (Cougenhour 1991; Gross *et al.* 1995). Feeding site selection is controlled by a complex set of factors. First it depends on herbivore body size, mouth morphology and digestive system (Gordon 1989). Small animals have low total metabolic requirements and are able to subsist on scarce but high quality foods. Contrarily, large herbivores have higher total metabolic requirements and need abundant food that can be of lower quality (Demment and Van Soest 1985). Second, selection of feeding habitats by herbivores will also depend on vulnerability to predators, since different-sized herbivores differ in their predation risk whilst foraging (Olff and Ritchie 1998). Large mammals usually suffer low predation risk because they assume active defence or are simply too large to be captured or disturbed by predators. Consequently, they are mainly limited by food availability. However, small herbivores such as rodents and small burrowing mammals are not only limited by food supply but also by high predation risk (Krebs *et al.* 1999). Vulnerability to predators often means that small herbivores are confined to the proximity of cover and burrows (Kotler *et al.* 1991; Palomares and Delibes 1997). Third, foraging habitats can also be conditioned by the availability of water over time and space (Barnes *et al.* 1991).

Mediterranean man-made savannahs from former oak woodlands (dehesas) are one of the most important ecosystems of the Iberian Peninsula and occupy more than 3.000.000 ha (Campos 1993). The characteristic undulating topography of dehesa ecosystems results in an alternance of smooth slopes and valley floors. This implies that water and nutrient run-off from upper to lower zones leads to the differential distribution of edaphic fertility and productivity among different zones of the territory. Distribution of resources determines grassland species composition, primary productivity and quality. Slope soils are poor with a low content in nitrogen and organic matter (Figueroa and Davy 1991), while lowland soils are richer in nutrients and water, resulting in relatively high quality herbaceous communities (Vázquez-de-Aldana *et al.* 2002). In general, dehesas are under the influence of Mediterranean type climate, which is characterised by a marked seasonality with two unfavourable seasons for vegetation growth: hot, dry summers and cool, erratically moist winters. Summer drought determines the dominance of annual species in Mediterranean grasslands, whose vital cycle is comprehended between the first autumn rains and the beginning of the summer. Water shortage in summer, both free and in green food, highlights the importance of water requirements as a factor influencing herbivore distribution and survival throughout this season. In these systems, where food and water dynamics are subjected to strong spatial and temporal variations, herbivore habitat selection needs to be interpreted within a seasonal context.

In this study, we investigated the nature and relative importance of factors that determine foraging habitat utilisation by different-sized herbivores in a semi-arid dehesa ecosystem, by means of structural equation modelling (SEM). The study was carried out during three seasons (spring, summer and winter) which differ in herbivore densities, environmental conditions and resource availability. Two herbivores of contrasting size, social behaviour and foraging strategy were selected: wild rabbits and free-ranging sheep. Sheep are ruminant and have been classified as generalist herbivores (Schwartz and Ellis 1981), whereas rabbits are hindgut-fermentors (Hintz 1969) and have been classified as selective herbivores (Bhadresa 1977). We developed two a-priori models, one for each herbivore, composed by direct and indirect cau-

sal factors influencing herbivore abundance. The aim was to assess whether the influence of seasonal changes in causal relationships between different factors could be determining herbivore habitat selection. We hypothesised that herbivore abundances are directly influenced by a set of environmental factors associated with food and water availability and refuge, and indirectly by several soil variables. We addressed the following questions: (1) What are the differences in foraging habitat choices between small and large herbivores? (2) What is the relative role of food, water and refuge in herbivore habitat selection throughout different seasons? and (3) How do geomorphology and soil characteristics finally influence factors conditioning habitat selection by herbivores?

2. Material and methods

Study area

Research was conducted in the "Dehesa of Chapinería", a 330 ha dehesa located in the south-west of Madrid, Central Spain (40º 23´ N, 4º 12´ W) between spring 2002 and winter 2003. Mean elevation is 690 m. Climate is semi-arid Continental-Mediterranean. Mean annual temperature and precipitation are 12.6º C and 432.6 mm, respectively. During the study period, mean annual temperature and precipitation were 12.1º C and 671.2 mm. The substrate is sandy to sandy-loamed, upon a fractured bedrock of granite, which outcrops all over the territory. Geomorphology is conditioned by a gentle undulating topography. Vegetation physiognomy is typical of a dehesa system, with small woodland patches and sparsely punctuated holm oak trees (*Quercus ilex* spp. *rotundifolia*) in a pasture matrix. There are also extensive areas of Mediterranean scrub dominated by *Lavandula stoechas* L. and *Retama sphaerocarpa* Boiss. The herbaceous layer is very rich and mainly composed of annual grasses, legumes and composites that germinate after the first heavy autumn rains, flower during the spring, die at the beginning of summer and pass

the unfavourable season (summer) as dormant seeds in the soil (Fernandez-Alès *et al.* 1993). There is a sharp gradient in composition and plant functional structure in pasture communities. In slopes and uplands the herbaceous community consists of short annual plants with low biomass, whereas in lowlands, the vegetation is dominated by taller species and abundant perennial grasses.

The dehesa is managed for small game hunting as well as livestock grazing. The main wild herbivore is a dense population of European rabbits (*Oryctolagus cuniculus* (L.)). The area is also grazed by a transhumant flock of 600 free-ranging sheep (about 2 sheep/ha), from December until the end of June. In summer, when most above ground herbaceous biomass is dry, sheep are moved to nearby mountain pastures. Traditional ploughing and mowing are also carried out. Ploughing is performed in uplands and slopes in order to eliminate thickets and encourage pasture growth. In favourable years, lowland areas are mowed at the end of spring, when grasses have flowered.

The proposed models

We developed two a-priori models, one for each herbivore, composed by direct and indirect causal factors influencing herbivore abundance as a surrogate of habitat selection. We hypothesised that herbivore abundance is directly influenced by a set of environmental factors associated with food and water availability and refuge, and indirectly by several soil variables (which control food abundance and quality, water and refuge). Obvious differences between both species suggest that the direct and indirect causal factors must be substantially different. We also expected shifts in the causal relationships governing herbivore abundance because conditions like food, water abundance and risk of predation may experience intense changes between seasons. Therefore, we tested our model in three different seasons: spring summer and winter. In general, both herbivore models are identical but in the sheep model the number of

warren entrances is substituted by sheepfold distance and consequently several links disappear. All the links and hypotheses are shown in **Table 3.1**.

Specifically, the models assume that soil fertility and soil moisture positively affect both food abundance and food quality. In contrast, soil stoniness is a negative predictor of food abundance. We hypothesized that food abundance and food quality influence rabbit and sheep abundances positively, and that herbivore abundances will be higher closer to drinking water sources. We assumed that the relationship between soil moisture and distance to drinking water sources would be positively correlated.

Rabbits are often restricted to the proximity of warrens and areas of dense scrub, where they avoid predators more efficiently than in open areas (Palomares and Delibes 1997). Also, when herbaceous biomass availability is low, consumption of holm oak sprouts, leaves and acorns is a common practice in rabbits (Martins

et al. 2002). Thus, we hypothesized that rabbit abundance would be positively affected by woody vegetation cover and warren abundance. Rabbit warren building is limited by the presence of soils suitable for excavation, dense scrub vegetation and low flooding risk (Parer and Libke 1985, Martins *et al.* 2002, Palomares 2003). The model considers that soil stoniness and soil moisture negatively affect warren abundances, but woody vegetation cover will affect this factor positively.

Sheep also browse on holm oak when herbaceous food resources are scarce (Bartolomé *et al.* 1998), and use trees as shade (pers. obs.). Additionally, sheep behave as central place foragers, being the sheepfold the central point of their home range (Lynch *et al.* 1992). Thus, the models consider that sheep will be positively influenced by woody vegetation but constrained by sheepfold distance in such way that the further away from the sheepfold, the fewer sheep.

Table 3.1: Paths and hypotheses for rabbit and sheep abundance models. In summer, the model for sheep was not tested because sheep were absent from the system. Results contrasting the hypothesized effects are marked in bold. Three paths (soil stoniness - warren entrances, woody vegetation - warren entrances, soil fertility - food quality) remained constant in the three seasons.

	Hypothesized effects	Spring	Summer	Winter
Links for rabbit -only model				
Food abundance - Rabbit abundance	Positive	**No effect**	Positive	Positive
Food quality - Rabbit abundance	Positive	**Negative**	Positive	**Negative**
Water distance - Rabbit abundance	Positive	**No effect**	**No effect**	**No effect**
Woody vegetation - Rabbit abundance	Positive	**No effect**	Positive	**No effect**
Warren entrances - Rabbit abundance	Positive	Positive	**No effect**	Positive
Soil moisture - Warren entrances	Negative	Negative	Negative	Negative
Soil stoniness - Warren entrances	Negative	Negative	Negative	Negative
Woody vegetation - Warren entrances	Positive	**No effect**	**No effect**	**No effect**
Links for sheep -only model				
Food abundance - Sheep abundance	Positive	Positive	Not estimated	Positive
Food quality - Sheep abundance	Positive	**Negative**	Not estimated	**No effect**
Water distance - Sheep abundance	Positive	**No effect**	Not estimated	**No effect**
Woody vegetation - Sheep abundance	Positive	**No effect**	Not estimated	**No effect**
Sheepfold distance - Sheep abundance	Negative	Negative	Not estimated	Negative
Common links for both models				
Soil fertility - Food abundance	Positive	Positive	**No effect**	**No effect**
Soil fertility - Food quality	Positive	Positive	Positive	Positive
Soil moisture - Food abundance	Positive	Positive	Positive	Positive
Soil moisture - Food quality	Positive	Positive	Positive	Positive
Soil moisture - Water distance	Negative	Negative	Negative	Negative
Soil stoniness - Food abundance	Negative	**No effect**	**No effect**	Negative

Sampling design and measurements

We randomly selected 220 points from a total of 350 intersections of a 50 m regular grid placed on an aerial photograph of the study area. Each of the 220 points were surveyed in the field for herbivore abundance and habitat variables in spring (April-June), summer (July-September) and winter (January-March).

Sheep and rabbit abundances were described on the basis of pellet counts in permanent clearance plots. Two rabbit dung plots of 0.5 x 0.5 m and one sheep dung plot of 0.5 x 5 m were laid out, avoiding woody vegetation and rabbit latrines. All pellets were cleared from the dung plots when first established and then revisited six weeks later, when accumulated pellets were removed and counted. Pellet counting has been widely used to estimate the abundance of lagomorphs and ungulates (Wood 1988, Bailey and Putman 1981). Pellet persistence can differ between habitats and seasons (Taylor and Williams 1956). Thus, we estimated "pellet decay rates" in the three seasons and in lowland and upland zones in order to ensure that the period between pellet clearance and count was adequate.

Regarding habitat variables influencing herbivore abundance, we measured food abundance, distance to water and soil moisture in each season. Food quality, sheepfold distance, woody vegetation cover, warren entrances, soil stoniness and fertility were measured only in spring, since they remain relatively unchanged throughout the seasons. How each of these variables was quantified and measured is explained hereafter.

In order to quantify seasonal food abundance, visual basal green cover was measured in two permanent 0.5 x 0.5 m quadrats. To obtain a measure of "food quality", the cover of each plant species was also visually estimated in two 0.2 x 0.2 m quadrats in spring. This quadrat size has been commonly used to study Mediterranean annual herbaceous communities

(Montalvo *et al.* 1993). In Mediterranean dehesas, species composition largely determines sward quality (Vázquez-de-Aldana *et al.* 2000). Following this criteria, we obtained the synthetic variable "food quality" represented by the first axis of a Detrended Correspondence Analysis (DCA) performed on species cover data recorded at the 220 points.

Water distance was considered as the shortest distance to surface water from every sampling point. Woody vegetation cover was assessed as percentage cover in a 10 m radius circular plot around each point. Number of rabbit warren entrances was recorded as the number of entrances in a 50 m radius around each point, since the feeding range of rabbits is restricted to about 100 m from warrens (Chapuis 1990). Sheepfold distance was measured as the shortest distance to the sheepfold from each sampling point.

To estimate soil parameters, four randomly 10-cm deep soil samples were randomly collected at each of the 220 points. This soil depth was selected because most root biomass is concentrated in the uppermost 7 cm of soil in intensively grazed communities (Rodriguez *et al.* 1995), and the effects of soil components on herbaceous plants are more evident within this fraction. Soil samples were air-dried and passed through a 2-mm sieve to separate stones and litter. We used the weight of stones larger than 2 mm as a measure of soil stoniness. To obtain soil fertility we developed a bioassay experiment. Barley seeds were sown on the sieved soil samples, maintained under greenhouse conditions and kept at constant humidity. Barley seedlings were harvested when maximum growth had been achieved and the first signs of senescence were observed in some leaves. Shoots were oven-dried at 70º C and weighed (see Moro *et al.* 1997 for methodology). To discern which soil components were mainly responsible for soil fertility, we carried out soil analyses on 100 of the 220 samples. Twelve variables related to soil texture and soil chemical properties were measured. Soil texture (per-

cent sand, silt and clay content) was determined using Bouyoucos method (Bouyoucos 1936). Available phosphorus was determined using Burriel-Hernando method (Burriel and Hernando 1950). Analyses of organic matter, carbon, total nitrogen, pH, and available macronutrients (K, Ca, Na and Mg) followed M.A.P.A. (1994). Finally, we collected four additional soil samples at each point in spring, summer and winter. Samples were oven-dried at 100º C and weighed before and after drying. The difference in weight was considered a measure of soil moisture.

To assess the influence of the geomorphology on herbivore choices and soil properties (fertility, moisture and stoniness) we categorised the study area into large-scale geomorphologic classes by means of a Geographic Information System. Five distinct classes were obtained: Highlands, slopes, flat areas in mid-slope, lowlands and wet lowlands (**Fig. 3.1**). They represent a gradient from highlands to wet lowlands of increasing herbaceous cover, primary productivity, perennial herbaceous cover and decreasing woody vegetation. Approximately percentage of land occupied for each topographic position was: highlands: 7.72%; slopes: 41.81%; flat areas in mid-slope: 6.36%; lowlands: 21.81%; wet lowlands: 21.36%.

Data analyses

Structural equation modelling (SEM) was used to test how well the data support a set of hypothesized relationships among the variables (Hayduk 1987, Mitchell 1992). SEM is a powerful statistical technique when a prioristic causal model is specified and the model, including direct and indirect effects, results in a complex system (Mitchell 1992).

The maximum likelihood method was used to estimate standardised path coefficients. The model was evaluated separately in each season and for each herbivore. Food abundance, woody vegetation cover, number of warren

entrances, soil fertility and sheep abundance were log transformed to meet the assumption of multivariate normality. SEM allows assessment of the degree of fit between the observed and expected covariance, expressed as goodness-of-fit χ^2. The test statistic is asymptotically distributed as χ^2 under the assumption of multivariate normality. Deviation from multivariate normality (for which univariate normality is a prerequisite) may affect goodness-of-fit test. A significant χ^2 indicates that the model does not fit the data. However, it is generally accepted that this χ^2 test should be interpreted with caution and supplemented with other goodness of fit indices as χ^2 can also result from violation of several assumptions whereas failure to reject a model (a non significant χ^2) may result from inadequate statistical power (Bentler 1989, Mitchell 1993). Thus, we also used the Normed Fit Index (NFI) (Bentler and Bonnet, 1980), which is based on the model χ^2 relative to that of a model that assumes independence of all variables, and the Goodness-of-Fit Index (GFI) (Tanaka 1987), which is not affected by the methods of estimation. GFI and NFI range between 0 and 1, with values > 0.90 indicating a good fit (Bentler 1989). We used multivariate Wald tests to assess the significance of individual path coefficients. This test locates the set of path coefficients that can be considered zero without worsening the fit of the model (Bentler 1989). The coefficient of determination R^2 indicates the proportion of observed variance explained by each equation. The effect of unexplained causes on each dependent variable (U_i) was measured as $(1-R_i^2)^{1/2}$. Low R^2 values (high U) for a variable suggest that the equation for this variable may be omitting relevant explanatory variables (Mitchell 1993). SEM analysis was performed with the CALIS procedure of the SAS statistical software package (SAS Institute 1990).

Edaphic components determining soil fertility

To assess the physical and chemical soil variables which explain soil fertility, a stepwise multiple regression was used. Previously, we perfor-
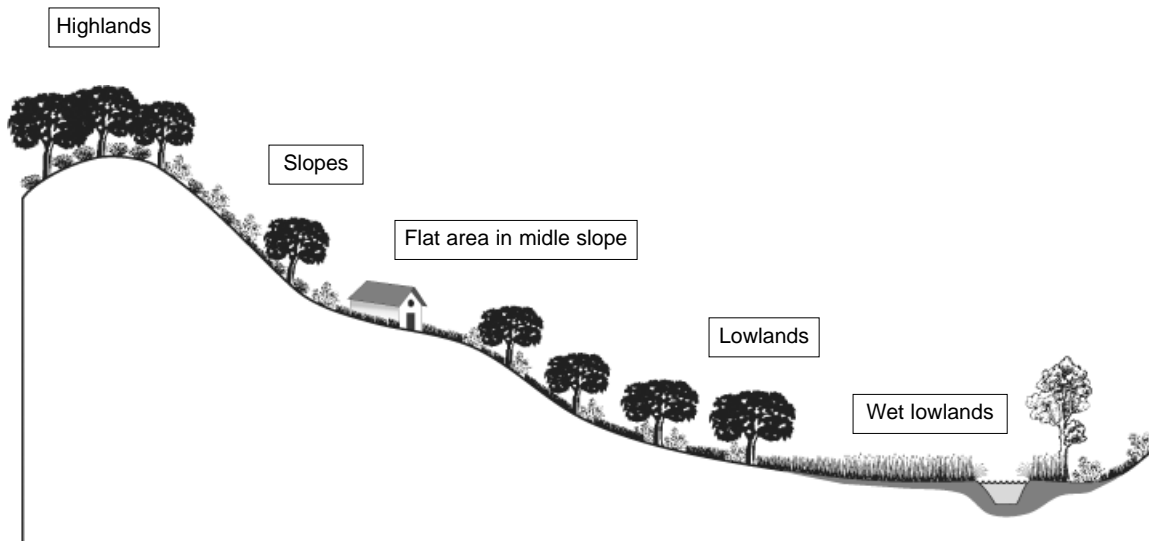
Fig. 3.1: Characteristic undulating topography and land management determines spatial variability from highlands to lowlands in dehesa ecosystems. Highlands are characterised by woody vegetation patches with sparse pastures, whereas slopes are dominated by abundant scrub. Flat areas in mid-slope are represented by a mosaic of scrub and pasture patches with relatively abundant herbaceous vegetation. The sheepfold is located in this area. Lowlands are characterised by plain open dehesa (savannah-like) habitats with productive pastures punctuated by trees and shrubs. Wet lowlands are located close to a temporal bed stream (normally dry in summer) and are dominated by open, highly productive grasslands with tall perennial grass species and little presence of woody vegetation.

med a correlation analysis to test for collinearity among all 12 soil variables to eliminate those that were highly correlated (**Table 3.2**). When variables were highly correlated ($r > 0.70$) (Fowler and Cohen 1992) we deleted the variable we judged to be more difficult to accurately interpret. Finally, five soil variables: clay, nitrogen, potassium, phosphorus and pH, were included in the analysis. A forward stepwise procedure was used to identify the main explanatory soil variables. The dependent variable, soil fertility (from the bioassay experiment), was squared-root transformed in order to attain normality and homocedasticity.

Geomorphology

Differences in soil properties and rabbit and sheep abundances between the five geomorphologic classes were assessed with one-way ANOVAs. All variables were tested for normality and homogeneity of variances. Log or square-root transformations were performed where necessary. Post-hoc tests (Tukey-test, $p < 0.05$) were used to test which groups differed significantly.

Table 3.2: Selected variables included in the stepwise analyses and the variables highly correlated with them ($r > 0.70$). Average r is the mean value of each group correlation coefficients.

Highly correlated groups	Selected variable	Averaged r
Sand, clay and silt	Clay	0.868
Nitrogen, organic matter and carbon	Nitrogen	0.986
Magnesium, potassium, and sodium	Potassium	0.869
Phosphorus and calcium	Phosphorus	0.998
pH	pH	-

3. Results

Path analysis

Model fit.- Models for rabbits and sheep in spring and winter had Bentler-Bonett GFIs and NFIs >0.90, indicating a good fit compared to a null model that assumes independence between variables. In summer, the rabbit model had relatively poor GFIs and NFIs but close to 0.90 (**Table 3.3**), suggesting a reasonable adjustment. Soil fertility, soil moisture and soil stoniness presented a similar pattern within the three seasons in the rabbit and sheep model. Their effects were consistent with our hypotheses (**Table 3.1**) except for soil fertility in spring, which only had a significant effect on food abundance; and for soil stoniness in winter, which showed a significant path on food abundance. Food abundance and food quality were strongly predicted by soil moisture in every season.

Table 3.3: Model fit parameters: Normed Fit Index (NFI), Goodness of Fit Index (GFI) and Chi-squared test.

	GFI	NFI	χ^2	df	p
Rabbit spring	0.93	0.93	65.4	13	0.0001
Rabbit summer	0.89	0.85	127.6	13	0.0001
Rabbit winter	0.92	0.91	90.1	13	0.0001
Sheep spring	0.93	0.93	87.2	11	0.0001
Sheep winter	0.90	0.91	97.6	11	0.0001

Rabbit abundance.- Consistently with our hypotheses, food abundance had a positive effect on rabbit abundance in summer and winter (**Fig. 3.2** and **Table 3.1**). Also, food quality and woody vegetation cover had positive effects on rabbit abundance in summer. As we expected, warren entrances positively influenced rabbit abundances in spring and winter. Soil moisture and soil stoniness had a negative influence on warren entrances, whilst woody vegetation cover had no effect on abundance. Surprisingly and contrary to our expectations, distance to drinking water did not affect rabbit abundance in any season.

Sheep abundance.- As we hypothesized, food abundance positively influenced sheep abundance and sheepfold distance had a negative influence (**Fig. 3.3** and **Table 3.1**). In contrast to what we expected, food quality had a negative effect on sheep abundance in spring and no effect in winter. Also, distance to the nearest drinking water point and woody vegetation cover had not effect on sheep abundance.

Edaphic components and geomorphology

The stepwise multiple regression analysis indicated that soil fertility was explained by nitrogen and clay (R^2 = 0.686, df = 2, F = 101.56, p = 0.000). Soil fertility, moisture and stoniness strongly varied between the five geomorphologic areas (Soil fertility: F = 29.35, p = 0.000; Soil moisture: F spring = 27.57, p = 0.000, F summer = 58.34, p = 0.000, F winter = 63, p = 0.000; Soil stoniness: F = 25.09, p = 0.000). Soil fertility and moisture reached the highest values in lowlands soil stoniness had the lowest values in these areas (**Fig. 3.4 a-b-c**). In spring and winter, rabbits were significantly less abundant in these relatively wet lowlands (**Fig. 3.5**). However in summer, rabbits were more abundant in flat areas in mid-slope and lowlands than in highlands and slopes (Fspring = 11.62 , p = 0.000; Fsummer = 2.88 , p = 0.023; Fwinter = 20.4, p = 0.000). Sheep were always more abundant in flat areas in mid-slope and lowland areas than in uplands, slopes and wet lowlands (Fspring = 9.74, p = 0.000; Fwinter = 12.35, p = 0.000) (**Fig. 3.5**).

4. Discussion

Soil moisture was the most important predictor of food abundance and quality throughout the year. This highlights the importance of water dynamics over soil fertility for primary production, and consequently determines the availability of food resources in these semi-arid ecosystems. The highest soil moisture levels were found in wet lowlands, areas of water and nutrient accumulation. In these areas, soil fertility, mainly explained by nitrogen and clay, was

also highest. Wet lowlands are highly productive, supporting abundant, high quality swards. Values of soil fertility also were higher in flat areas in mid-slope with respect to surrounding upland areas. This could be because water and nutrients being transported downslope are temporally collected in these relatively flat areas. Moreover, as the sheepfold is located in such an area, high concentrations of livestock dejections could be increasing soil fertility (e.g. Gómez-Sal *et al.* 1992). Soil moisture was the most influential parameter on warren locations, probably because warren building in flood-prone areas is disadvantageous for rabbits (Palomares 2003).

For rabbits, selection of foraging areas was mainly driven by predation risk minimisation and food availability. Rabbits foraged close to warrens in spring and winter. Warrens are used as refuge, being also critical structures for breeding (Myers and Poole 1961). In Mediterranean type climates, the rabbit breeding period extends from the beginning of the first autumn rains until the beginning of the summer drought (Gonçalves *et al.* 2002). Therefore, the significant relationship of warrens and rabbit abundance during winter and spring is in concordance with our expectations related to predation risk and breeding needs. In general, the areas where warrens are located are sites with low quantity and quality of food. Throughout the system we found that slopes contained more and larger warrens (8.88 warrens/ha and 83.43 warren entrances/ha in slopes contrasting with 2.20 warrens/ha and 13.84 warren entrances/ha in wet lowlands). Rabbit dependence on warrens generates a conflict between the need for high quality foraging conditions and a good breeding environment and protection. Warren locations can also explain why rabbits do not use wet lowland areas, since these areas are relatively far away from warrens and are more frequently inundated, particularly in winter and early spring. Additionally, vegetation in wet lowlands reaches a considerable height in spring. It has been suggested that rabbits tend to avoid dense and high standing pastures, selecting areas with shorter and sparser cover of herbaceous vegetation (Williams *et al.* 1974, Iason *et al.* 2002). In spring, food is not a limiting resource, as it is relatively abundant throughout the system, and this can explain the absence of a relationship between food and rabbit abundance. However, in winter, when food is more limited, this path is reinforced. In both seasons, food quality negatively affects rabbit abundance as wet lowlands are places with the highest values of food quality.

In summer this pattern is notoriously different. Lack of water constrains environmental suitability, most of the vegetation is dry and food becomes a limiting and extremely scarce resource. In addition, competition for food increases, as the rabbit population has grown rapidly as a consequence of reproduction. The link between food and rabbit abundance acquires a positive significance. In the absence of water, rabbits need to forage green food to survive (Hayward 1961). Therefore, they are forced to venture further away from warrens, towards lowlands, where some vegetation remains green. As Jarman and Sinclair (1979) indicated, grazing species actively select green parts of grasses from a relatively dry sward during the dry season. Since lowland areas are traditionally mown at the beginning of the summer, at least during favourable years, the reduction of vegetation height and biomass can facilitate the entry of rabbits in these zones. However, the abundance of green perennial species in summer does not seem enough to support the high rabbit densities found in our study area. Pastures usually become dry long before the first autumn rains. Consequently, rabbits are able to consume woody twigs and bark which may be moist enough to meet their water requirements, but contain too little digestive energy for maintenance (Cooke 1982). This apparent drawback may be overcome by rabbits through caecotrophy, which consists in the reingestion of soft faeces containing concentrated proteins and minerals (Hirakawa 2001). This is a valuable selective

a) Rabbits in spring
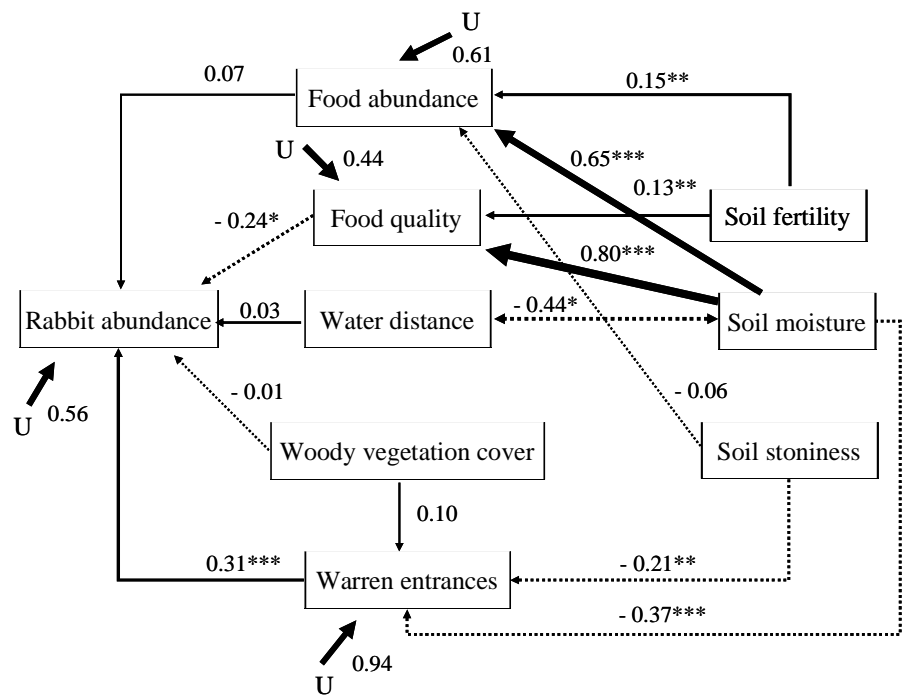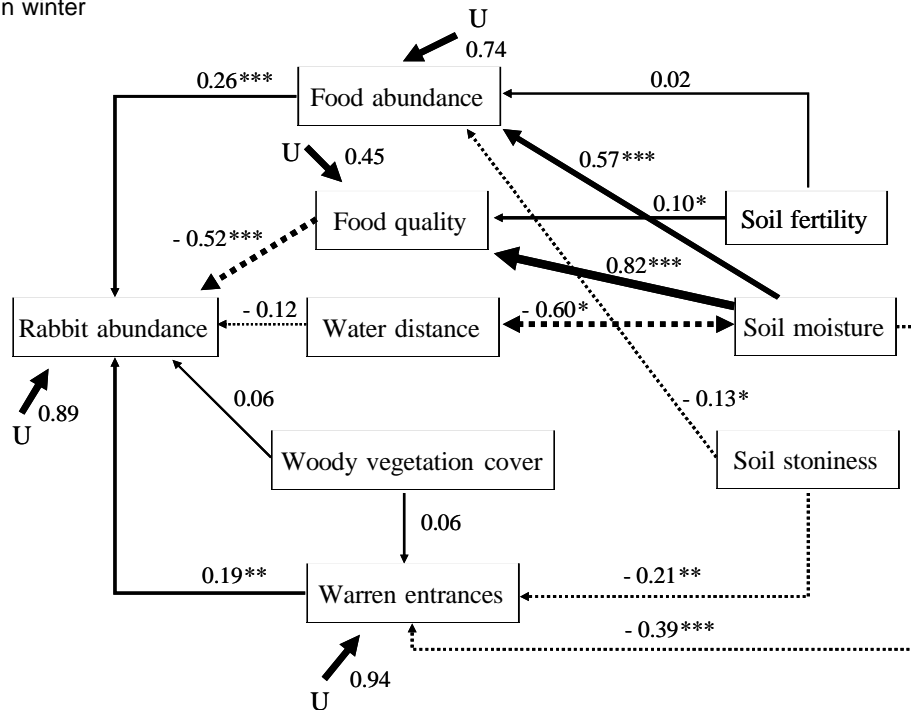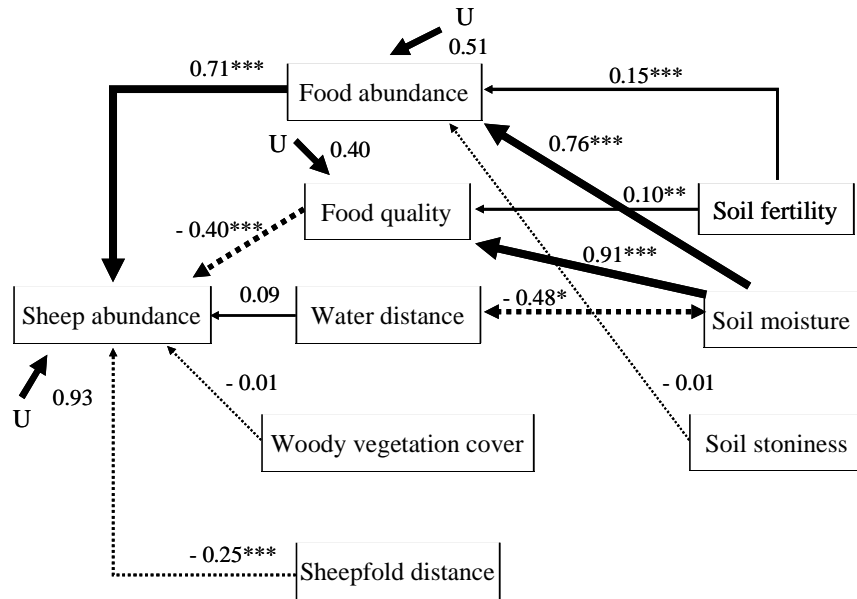

b) Rabbits in summer
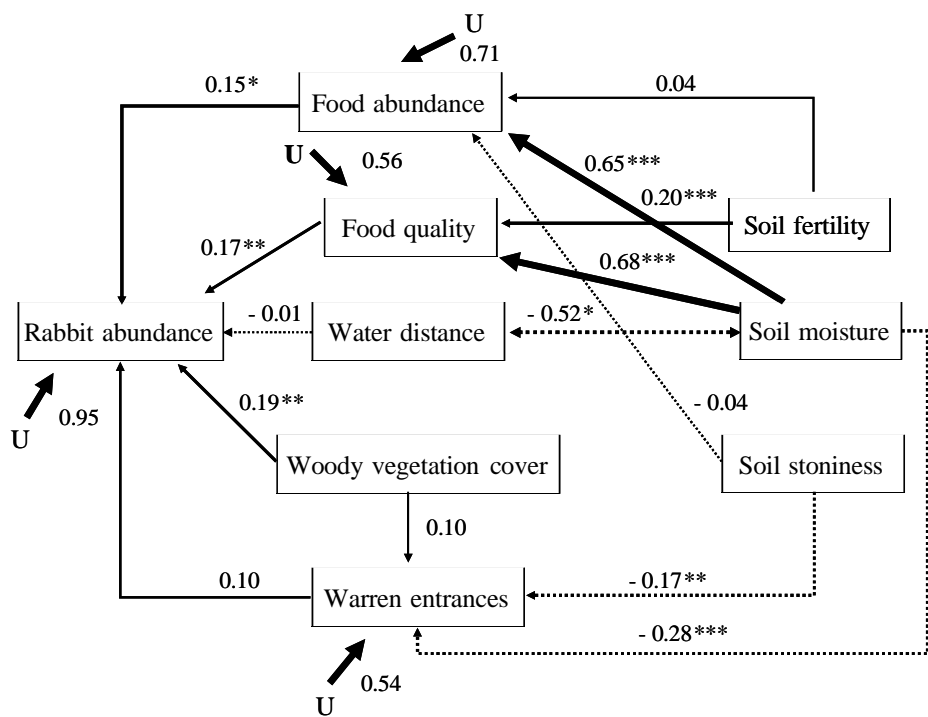
c) Rabbits in winter

Fig. 3.2: Path model representations for factor determinants of seasonal rabbit abundances (a) in spring, (b) in summer and (c) in winter. One-headed arrows represent causal relationships while two-headed arrows represent correlations. Positive effects are indicated by solid lines, and negative effects by broken lines. Arrow widths are proportional to path coefficient magnitude. Standardised path coefficients significantly different from 0 are marked with asterisks (* P < 0.05, ** P < 0.01, *** P < 0.001). U represents the unexplained variance of dependent variables. Models fit parameters are indicated in the Table 3.3.

trait under Mediterranean semi-arid conditions of food shortages or low quality pastures. Additionally, rabbits show a high capacity to optimise the use of hydric resources, economising water by concentrating their urine (Hayward 1961) and reducing the water content of faecal pellets (Verdú and Galante 2004). Summer is a critical period for rabbits. Use of open wet lowlands in summer implies a higher predation risk. Nutritional needs seem to be shifting this balance during this resource-limited period. The significance of warrens in our model is lost, and a stronger path with woody vegetation appears, well to be used as refuge, shade or as an alternative source of food.

For sheep, the selection of foraging areas was mainly controlled by food abundance and sheepfold vicinity. Domestic sheep are considered generalist herbivores, and this explains the strong relationship with food abundance. Surprisingly, sheep did not preferentially select highly productive wet lowland areas, preferring dry lowlands and flat areas in mid-slope (**Fig. 3.3**). In our study, the sheepfold (located in flat areas in mid-slope) acted both as nocturnal refuge and as the main water source. Free-standing water is the principal focus around which most of the larger ungulates orientate their foraging strategies (Coleman *et al.* 1989) and grazing intensity is reduced with longer distances to water points (Stuth 1991). Additionally, although wet lowlands may be suitable for grazing, they are further away from the sheepfold (mean: 840 m) than other areas. It has been shown that grazing pressure is significantly reduced at distances greater than 500 m from
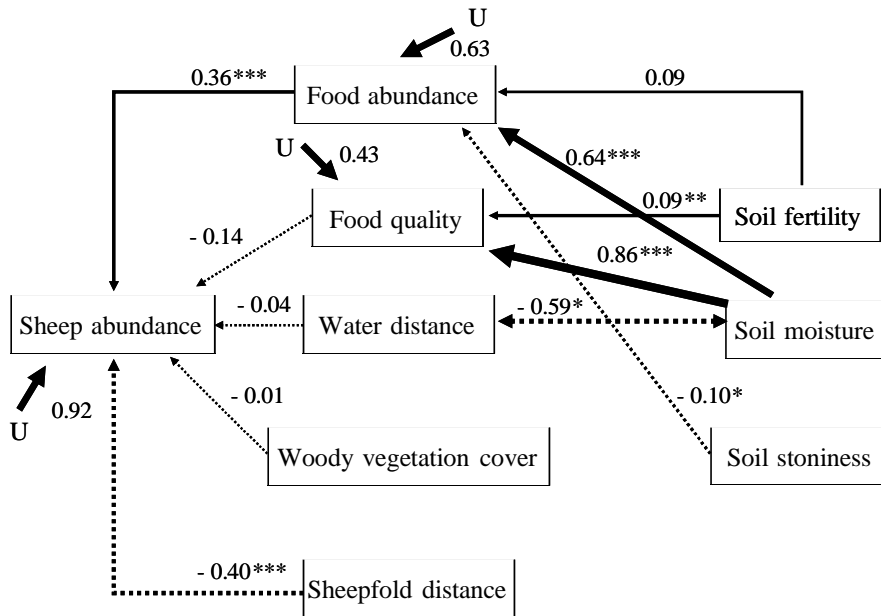
a) Sheep in spring

b) Sheep in winter

Fig. 3.3: Path model representations for factor determinants of seasonal sheep abundances (a) in spring and (b) in winter. Model for sheep abundances in summer was not tested because sheep were not present in the system in summer. One-headed arrows represent causal relationships while two-headed arrows represent correlations. Specifications as in Fig. 3.2.

the sheepfold (Rebollo 1996). Also, it is probable that sheep avoid foraging in the most productive areas since grazing becomes less efficient when vegetation reaches its highest standing crop (van de Koppel *et al.* 1996). On the other hand, as the study period was wetter than usual, areas close to the sheepfold were probably productive enough to support sheep grazing. In any case, given the strong bond of sheep with the sheepfold in terms of refuge, and the fact that it presents a secure and reliable source of water, it is likely that this result would have also been observed during a drier year. Probably, the lack of relationship between sheep abundance, food quality and woody vegetation was due to the absence of sheep in the area during the "critical" summer period. The absence of a relationship between sheep and water distance can be obscured by their strong bond with the sheepfold.

In general, our results suggest that large herbivores (sheep) were limited by food availability whereas the small ones (rabbits) were constrained mainly by antipredatory considerations and food abundance. These conclusions are in agreement with other authors (Owen-Smith 1988, Krebs *et al.* 1999). However, other factors can be important enough to influence foraging decisions. Refuge, in this case nocturnal refuge, influenced large herbivore foraging decisions. On the other hand, antipredator/forage trade-offs suffer deep changes, in the case of small herbivores, with the arrival of the resource-limited period.

We conclude that the distribution of both herbivores was not stable and reflected a response to seasonal and spatial variation in foraging resources. Factors influencing rabbit and sheep abundances were relatively constant in spring and winter, shifting in summer. Large species are the first to move away from swards as they die off during the dry season (Senft *et al.* 1987). A management decision (transhumance) drives sheep away from the ecosystem precisely when it becomes unsustainable, during the summer drought. The complete absence of sheep sug-

gests that available biomass is insufficient to support them during the summer months on a sustained basis. Rabbits were able to use all the areas throughout the year, from highlands to wet lowlands, adjusting their selectivity to seasonal food changes. Rabbit adaptations, such
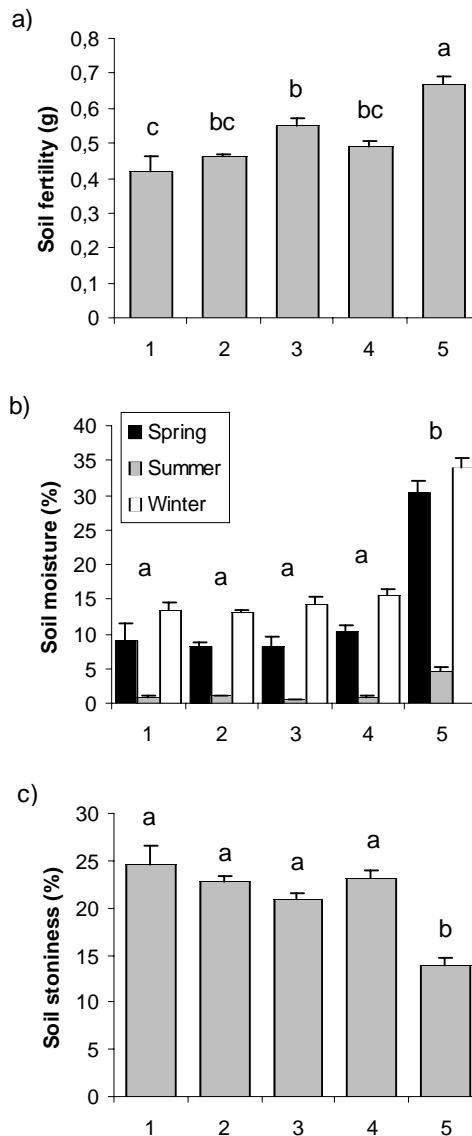

Fig. 3.4: Differences in indirect soil factors between the five topographic positions (1 = highlands; 2 = slopes; 3 = flat areas in mid-slope; 4 = lowland; 5 = wet lowlands) in spring, summer and winter. a) Mean (± SE) soil fertility (g barley); b) Mean (± SE) soil moisture (%); c) Mean (± SE) soil stoniness (%). Different letters indicate statistical differences (Tukey-test, $P < 0.05$).
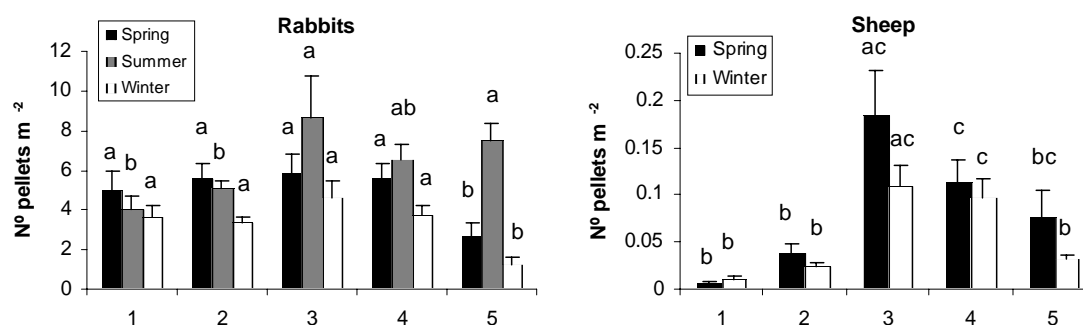
Fig. 3.5: Differences in rabbit and sheep pellet densities (mean no. pellets/m2/month) between the five topographic positions (1 = highlands; 2 = slopes; 3 = flat areas in mid-slope; 4 = lowland; 5 = wet lowlands) in spring, summer and winter (rabbits) and spring and winter (sheep). Summer is not represented in the sheep figure since they were absent from the system in this season. Different letters indicate statistical differences (Tukey-test, P < 0.05).

as caecotrophy, may enable them to compensate for the low quality resources found, for instance, near warrens. This reflects a strong ability to cope with arid and semiarid climate fluctuations and face shortages in resource availability. This plasticity may have enhanced the colonisation ability of rabbits in different parts of the world (Thompson and King 1994).

Traditional land management of dehesas shapes vegetation distribution in these ecosystems, which is characterised by a high degree of patchiness and high pasture species richness (Diaz *et al*. 1997, Marañon 1985). These characteristics favour a variety of vertebrate herbivores, generalists and specialists, independent of each other. However, as rabbits and sheep in our study overlapped in two areas (flat areas in mid-slope and dry lowlands) during spring and winter, could they be competing for the same foraging resources? The European rabbit is indigenous to the Iberian Peninsula (Cox and Moore 1973, Di Castri 1991), being the most abundant and widely distributed vertebrate (Muñoz-Goyanes 1960). However, habitat loss and the introduction of diseases, such as Myxomatosis and rabbit haemorrhagic disease (RHD), have caused a strong decline in European rabbit populations in their native habitat (Moreno and Villafuerte 1995, Moreno *et al*. 1996). This decline has had devastating conse-

quences as rabbits are a keystone element of Mediterranean food webs, where at least 39 predator species, some of them endemic, prey on rabbits (Delibes and Hiraldo 1981). Therefore, livestock management and rabbit conservation strategies would be in conflict if both herbivores compete for food. Differences in body size, digestive system and the influence of dental arcade morphology on feeding efficiency (Demment and Van Soest 1985) are adaptations that may lead rabbits and sheep to use different food resources although foraging in similar areas. However, diet selection studies would be necessary to confirm this. Anatomical differences allow each species to exploit different habitats only if ecosystems are highly heterogeneous.

The promotion of traditional land management, including moderate livestock grazing, in dehesa ecosystems is essential to maintain a mosaic of pastures and scrub, preferred rabbit habitats. Dehesa heterogeneity, promoted by low intensity traditional land uses, allows rabbits to adapt to seasonal changes in resources. For instance, mowing in the early summer enables rabbit use of lowland areas at the time of lowest food availability. Periodical, moderate scrub clearance promotes the maintenance of open areas where herbaceous vegetation cover can increase. Transhumant practices remove a large propor-

tion of livestock from pastures during the summer months, eliminating livestock competition for food resources during the resource-limited period. The extended intensification of farming systems, combined with abandonment of certain traditional practices such as transhumance, is causing a loss of natural values in dehesas (Beaufoy 1998). Traditional practices have allowed coexistence of rabbits and livestock but if they are not maintained the future of rabbits in dehesas is unsure.

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