Capítulo 4

Uso del hábitat por conejos (*Oryctolagus cuniculus*) adultos y juveniles en un ecosistema mediterráneo semiárido heterogéneo

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Rueda, M., Rebollo, S. & Gálvez, L. *In preparation*. Habitat use by adult and juvenile wild rabbits (*Oryctolagus cuniculus*) in a heterogeneous Mediterranean semi-arid ecosystem.

Resumen

Conocer los factores que determinan las preferencias de hábitat de las diferentes clases de edad de una población es fundamental para la conservación de especies y ecosistemas. Este conocimiento es especialmente importante para herbívoros que viven en climas mediterráneos, ya que a menudo cada clase de edad tiene que enfrentarse a la escasez de agua y alimento propias del verano. En este trabajo estudiamos la abundancia de conejos (*Oryctolagus cuniculus*) adultos y juveniles en un ecosistema mediterráneo (dehesa) de la Península Ibérica durante primavera, verano e invierno y su relación con las diferencias estacionales en la disponibilidad de recursos (agua y alimento) y densidad de refugios (madrigueras y vegetación leñosa). Las abundancias de conejo se estimaron mediante conteo de heces y se consideró que las más pequeñas de 6 mm pertenecían a individuos juveniles. Los datos fueron analizados mediante modelos de regresión múltiple. Los resultados muestran que los conejos adultos y juveniles tuvieron diferentes preferencias de hábitat a lo largo del año, dándose cambios estacionales en el uso del hábitat dependiendo del riesgo de depredación y las necesidades energéticas. Los juveniles seleccionaron para alimentarse áreas cercanas a las madrigueras o con una alta densidad de entradas a éstas, mientras que los adultos seleccionaron lugares con vegetación herbácea corta, asegurándose así una facil detección de los depredadores. Tanto adultos como juveniles ajustaron su selectividad de alimento a los cambios estacionales en la composición florística de una manera similar. Sin embargo, con la llegada del verano y la desaparición de alimento, los adultos se vieron forzados a moverse hacia áreas más productivas, generalmente zonas abiertas y desprotegidas, donde la vegetación herbácea permanece verde más tiempo, pero a expensas de aumentar su riesgo de depredación. Las diferencias en los requerimientos de hábitat entre conejos adultos y juveniles a lo largo de las estaciones sugiere que la heterogeneidad del hábitat es necesaria para mantener a ambas clases de edad y, por tanto, poblaciones viables de conejo.

Habitat use by adult and juvenile wild rabbits (*Oryctolagus cuniculus*) in a heterogeneous Mediterranean semi-arid ecosystem

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Abstract

Knowledge about the factors determining habitat preferences by different-aged individuals within a population is of interest for ecosystem and species conservation. This is especially important for herbivores living under Mediterranean climatic conditions, as they often have to deal with food and water shortages during the summer season. We investigated seasonal differences in resource availability (water and food), refuge density (warrens and woody vegetation) and adult and juvenile rabbit (*Oryctolagus cuniculus*) abundances in a Mediterranean ecosystem (dehesa) of the Iberian Peninsula during spring, summer and winter. Rabbit abundances were estimated by means of faecal pellet counts, where pellets smaller than 6 mm were considered to belong to juvenile rabbits. Data were analysed using multiple regression models. Results showed that adult and juvenile rabbits had different habitat preferences throughout the year and showed seasonal shifts in habitat use depending on predation risk and energy needs. Juveniles preferred to forage in areas close to warrens or with high warren entrance density in all seasons; whereas adults preferred to forage in short standing swards, ensuring a wide sensory range for the detection of approaching predators. Both juveniles and adults adjusted their foraging selectivity to plant community seasonal changes in a similar way. However, with the arrival of summer and its associated food depletion, adult rabbits were forced to shift towards more open productive areas where green vegetation persists, but at the expense of higher predation risk. Differences in habitat requirements between adult and juvenile rabbits through the seasons suggest that habitat heterogeneity at the local, within-habitat scale is necessary to support both rabbit age classes and maintain viable populations.

Keywords: Dehesa ecosystems, different-aged herbivores, *Oryctolagus cuniculus*, habitat preferences.

1. Introduction

An understanding of the habitat requirements of a species is essential for effective conservation (Putman 1996). For this reason, knowledge about the preferences of different groups within a population is desirable, since habitat selection can vary between ages and sexes (e.g. Kamler and Gipson 2003, Kokurewicz 2004). Age can influence the interaction of an organism with abiotic (e.g. thermoregulation, water intake needs) and biotic factors (e.g. type of food, vulnerability to predators, ability to use different types of refuge), which often results in habitat preference shifts between adult and juvenile individuals (Heatwole 1977). Diverse studies have presented evidence of differential habitat use by adults and juveniles in fish (Davey *et al*. 2005), reptiles (Shine *et al*. 2002), birds (Nijman and van Balen 2003) and mammals (Apollonio *et al*. 1998).

In mammals, age-related differences in habitat use are commonly linked to foraging demands, trade-offs between the risk of predation and starvation, and experience (Carey and Moore 1986). Nutritional and energy requirements may be different for adults and juveniles since adults must obtain energy and nutrients for maintenance and reproduction, whilst juveniles need extra nutrients for growth (Arenz and Leger 2000). Additionally, juvenile animals often experience higher mortality rates than adults (Sibly *et al*. 1997), mainly due to predation (e.g. Rongstand 1965). This difference in mortality risk results in divergences in behaviour such as the time spent on vigilance (Arenz and Leger 1997). Vigilance/foraging trade-off adjustments in response to predation risk and energy needs may therefore lead to different habitat preferences between adults and juveniles.

The European wild rabbit (*Oryctolagus cuniculus*) is native to the Iberian Peninsula (Cheylan 1991), being the most abundant and widely distributed vertebrate in the semi-arid ecosystems of Spain and Portugal (Muñoz-Goyanes 1960). A mosaic of scrub and pastures, which provide suitable food and cover for protection, and adequate soil conditions for burrowing, are the main rabbit habitat requirements (Rogers and Myers 1979). These elements are often found in dehesa ecosystems, since traditional land management practices create a mosaic of pasture, scrub and woodland, which can be considered a mixture of different habitat-types (Díaz *et al*. 1997). Dehesas generally support high rabbit densities (Blanco 1998). In these ecosystems, wild rabbits are under a high predation pressure, as they are the main food item for many predators (Delibes and Hiraldo 1981). As a prey species, rabbits forage in the proximity of warrens and scrub where they avoid predators more efficiently than in open areas (Palomares and Delibes 1997) maximizing the time spent between refuge and food patches (Villafuerte and Moreno 1997). Young rabbits are much more predated than adults, and up to 75 % of young inexperienced rabbits are killed by predators (Angulo 2004). Also, probably, they are more vulnerable to adverse weather conditions than adults (e.g. for young hares Hackländer *et al*. 2002). Thus, habitats with a high availability of shelter (warrens and scrub cover) should be more valuable for juveniles than for adults. Additionally, dehesas are under the influence of Mediterranean type climate, which is characterised by a marked seasonality, with a severe drought in summer. Water shortage in summer causes the death of annual herbaceous vegetation and a hard limitation in resource availability. This spatial and seasonal change of resources critical to rabbit survival may condition vigilance/foraging decisions and play a role in determining seasonal movements and pattern of adult and juvenile rabbits. However, to our knowledge, no research has identified this possibility for rabbits in the Iberian Peninsula.

Taking into account habitat requirements such as refuge and food availability, we aimed to identify whether adult and juvenile wild rabbits have distinct preferences and select different habitats in dehesa ecosystems. We carried out an one-year study during three seasons, spring, summer and winter, which differ in resource availability. We addressed the following questions: (1) what are the seasonal changes in adult and juvenile rabbit abundances? (2) what are the main differences in habitat preferences between adult and juvenile rabbits and do these preferences change seasonally? We hypothesised that spatial and temporal change in resource availability would determine differences in habitat preferences of adult and juvenile rabbits. Juveniles would be more constrained by predation risk and therefore be more abundant in habitats with high refuge availability.

2. Material and Methods

Study area

Research was conducted in the "Dehesa of Chapinería", a 330 ha area located in the southwest 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. The substrate is sandy to sandy-loamed, upon a fractured bedrock of granite, which outcrops all over the territory. Geomorphology is conditioned by a typical gently undulating topography which promotes water and soil fertility gradients from highlands to lowlands. This results in variations in nutrient quality of the herbaceous vegetation, higher quality forage being found in lowlands (Vázquez-de-Aldana *et al*. 2000). Vegetation physiognomy is typical of a dehesa system, with small woodland patches and sparsely punctuated holm oak trees (*Querqus ilex* spp. *rotundifolia*) in a pasture matrix. There are also extensive areas of Mediterranean scrub species dominated by *Lavandula stoechas* L. and *Retama sphaerocarpa* Boiss. The herbaceous layer is composed of a diverse array of annual grasses, legumes and composites. They germinate after the first heavy autumn rains, flower during spring, die at the beginning of summer and pass this unfavourable season as seeds in the soil (Fernández-Alés *et al*. 1993). There is a sharp gradient in composition and plant functional structure in pasture communities. In slopes and uplands the herbaceous community mainly consists of short annuals 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 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.

Taking into account geomorphology and land management, five habitat-types can be identified: highlands (dense woodland patches with scarce pasture areas), slopes (abundant trees, scrub and pasture patches), flat zones in mid-slope (open habitat with some scrub and large pasture patches), dry lowlands (flat open habitat with productive pastures punctuated by trees and scrub) and wet lowlands (highly productive open grasslands, close to a temporal stream bed).

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 point was surveyed for rabbit abundance and several habitat features in spring (April-June), summer (July-September) and winter (January-March). Being the hunting season, autumn data were not considered in this study.

Rabbit abundance was assessed by pellet counts in permanent clearance plots. Pellet counting has been widely used to estimate the abundance of lagomorphs (Palomares 2001). Feeding is the predominant activity when rabbits are above ground (Myers 1955) and pellet distribution will reflect mainly their feeding distribution. Two dung plots of 0.5 x 0.5 m were laid out, avoiding woody vegetation cover 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 persistence can differ between habitats and seasons (Taylor and Williams 1956). Thus, we estimated "pellet decay rates" in the three seasons and in lowland (wetter) and upland (drier) zones in order to ensure that the period between pellet clearance and count was adequate.

Rabbit faecal pellet diameter is positively correlated with the size and age of the animals producing them (Simonetti and Fuentes 1982). Pellets were separated into smaller and larger than 6 mm in diameter using a sieve. This technique was used by Bhadresa (1982), in order to compare juvenile and adult rabbit diet. Pellets larger than 6 mm were considered deposited by adults, whereas those pellets smaller than 6 mm were considered deposited by juveniles and kittens. Rabbits are considered as adults at 6-9 months of age (Pongrácz and Altbäcker 2000).

To quantify food abundance, percentage visual green cover was measured in two, randomly placed, permanent 0.5 x 0.5 m quadrats. Green cover was chosen to quantify food availability, because grazing species will actively select green parts of plants from a relatively dry sward during the dry season (summer in our study) (Jarman and Sinclair 1979). In winter and spring most of the vegetation remained green. The cover of grasses, legumes and composites was estimated in the three seasons in order to assess rabbit preferences in terms of community composition.

In arid and semi-arid zones, water is key to biological activity. Thus, we measured water availability as the shortest distance to surface water from every point. Scrub cover was assessed as percentage cover in a 10 m radius circular plot around each point of: holm oak, *Lavandula* and *Retama* bushes, and rushes in wetter areas. Warrens and warren entrance density were recorded in a 50 m radius circular plot around each point since feeding range is restricted to about 100 m from warrens for adult rabbits (Chapuis 1990) and 63 m for juveniles (Künkele and von Holst 1996). Also, mean herbaceous vegetation volume was determined at each point. This variable was defined as the mean plant height multiplied by total percentage plant cover, and is related to differences associated with overhead and lateral visibility. Animals might benefit from overhead cover to hide from aerial predators (Duncan and Jenkins 1988), but in contrast, lateral cover can make terrestrial predators more difficult to detect (Murray *et al*. 1995). Vegetation volume provides a measure of the openness of an area and the likelihood of detecting stalking predators.

Number of rabbit pellets, herbaceous vegetation parameters and water availability were measured in each season. Woody vegetation cover and density of burrows were measured only once, since they remain relatively unchanged throughout the seasons.

Data analyses

One-way ANOVAs were used to assess differences in adult and juvenile pellet counts, separately, between the three seasons and between the five habitat-types (highland, slope, flat area in mid-slope, dry lowland and wet lowland). Rabbit pellet deposition rate can vary between seasons (Lockley 1962) and probably between adult and juvenile individuals. For this reason, adult and juvenile pellet abundances were not compared directly. Stepwise multiple regression analyses were used to determine the factors that influence habitat preferences of different-aged rabbits. The dependent variable was the number of rabbit (adult or juvenile) pellets per m^2. This variable was root transformed to attain normality and homocedasticity. Independent variables were: percent cover of green herbaceous vegetation (green food), percent cover of composites and legumes, mean volume of herbaceous vegetation, percent cover of holm-oak, *Lavandula*, *Retama*, and rushes, shortest distance to a water source, and density of warren entrances. To avoid colinearity in the analysis, we did not use cover of grasses and density of warrens because they were highly correlated with green herbaceous cover and density of warren entrances, respectively.

3. Results

Adult and juvenile rabbit pellet abundances in each season

Adult and juvenile rabbit pellet numbers changed significantly between spring, summer and winter (adults: F = 71.76, p = 0.000; juveniles: F = 4.85, p = 0.006) (**Fig. 4.1**). Adult pellets were most abundant in summer and less abundant in winter. Juvenile pellets were most abundant in spring and least abundant in summer.

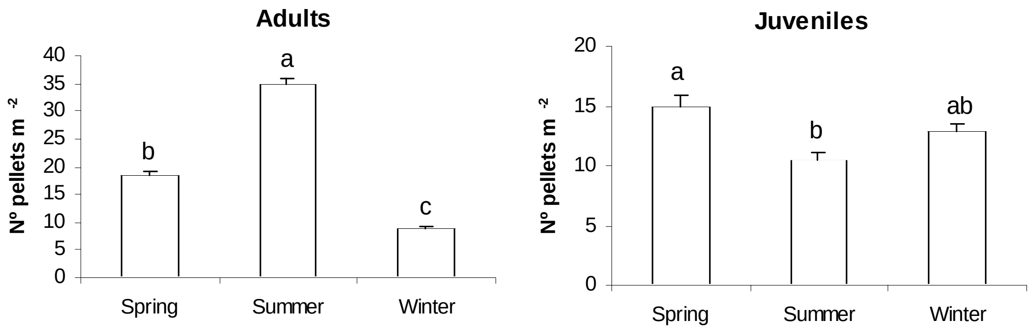

Figure 4.1: Mean adult and juvenile rabbit faecal pellet density per season. Different letters indicate statistical differences in pellet numbers between the three seasons (Tukey-test, P < 0.05). Error bars represent S.E of the mean.

Adult and juvenile rabbit pellet abundances in each habitat-type

In spring and winter, adult rabbits were similarly abundant in the five land-types (spring: F = 1.03, p = 0.39; winter: F = 1.63, p = 0.167) (**Fig. 4.2**). In summer, there was a barely significant trend (F = 2.31, p = 0.058), being the number of adult rabbit pellets deposited in wet-lowlands higher than in the slopes. For juveniles, there were significant differences in the use of the five land-types in each season (spring: F = 6.16, p = 0.001; summer: F = 3.68, p = 0.0063; winter: F = 12.65, p < 0.0001) (**Fig. 4.2**). Juveniles were, in general, more abundant in flat areas in mid-slope and were always less abundant in wet lowlands.

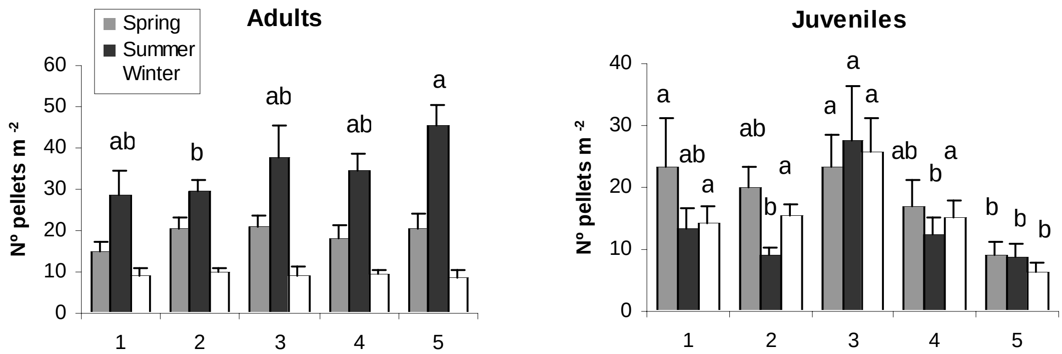

Figure 4.2: Mean adult and juvenile rabbit faecal pellet density per season in the five habitat types. 1 = Highland; 2 = Slope; 3 = Flat area in mid-slope; 4 = Lowland; 5 = Wet lowland. Different letters indicate statistical differences in pellet numbers between land-types within each season. No letters indicate no statistical differences found (Tukey-test, P < 0.05). Error bars represent S.E of the mean.

Table 4.1: Regression coefficients of each variable and their contribution to total R^2 for juvenile and adult rabbits in spring, summer and winter. Water (shortest distance to a water point) did not influence juvenile and adult rabbit abundances in neither season.

	Adults						**Juveniles**					
	Spring		*Summer*		*Winter*		*Spring*		*Summer*		*Winter*	
Factor	Regres coeffic	Contr to R^2	Regres coeffic	Contr to R^2	Regres coeffic	Contr to R^2	Regres coeffic	Contr to R^2	Regres coeffic	Contr to R^2	Regres coeffic	Contr to R^2
Green cover	----	----	0.87	0.11	----	----	- 1.70	0.29	----	----	- 1.50	0.20
Composites	0.15	0.03	----	----	0.13	0.02	0.26	0.05	----	----	0.41	0.05
Legumes	- 0.13	0.03	----	----	0.10	0.02	----	----	----	----	0.59	0.08
Holm oak	----	----	0.11	0.01	----	----	----	----	0.37	0.05	----	----
Lavandula	- 0.09	0.02	- 0.15	0.02	----	----	----	----	----	----	----	----
Retama	----	----	0.11	0.01	----	----	----	----	0.10	0.01	----	----
Rushes	----	----	0.35	0.05	----	----	----	----	----	----	----	----
Warren entrances	0.12	0.03	----	----	0.22	0.04	0.46	0.08	0.59	0.08	0.41	0.05
Vegetation volume	- 0.69	0.15	----	----	- 0.49	0.08	----	----	- 0.44	0.06	----	----

Factors influencing habitat selection by adult rabbits

Multiple regression analysis indicated that adult rabbit abundance in spring was significantly related to vegetation volume, cover of legumes, composites, and *Lavandula*, and density of warren entrances ($R^2 = 0.33$, $p = 0.000$) (**Table 4.1**). In summer, adult abundance was significantly related to green cover and to the cover of rushes, *Lavandula*, holm oak, and *Retama* ($R^2 = 0.22$, $p = 0.000$). In winter, it was significantly related to vegetation volume, density of warren entrances, and cover of composites and legumes ($R^2 = 0.22$, $p = 0.000$).

Factors influencing habitat selection by juvenile rabbits

Multiple regression analysis showed that juvenile rabbit abundance in spring was significantly related to green cover, density of warren entrances, and cover of composites ($R^2 = 0.44$, $p = 0.000$) (**Table 4.1**). In summer, juvenile abundance was significantly related to density of warren entrances, vegetation volume, cover of holm oak and *Retama* ($R^2 = 0.21$, $p = 0.000$). In winter, juveniles were significantly related to green cover, cover of legumes and composites, and density of warren entrances ($R^2 = 0.36$, $p = 0.000$).

4. Discussion

Seasonal adult and juvenile rabbit abundances

Total rabbit abundance showed seasonal fluctuations with a peak in summer and lowest levels in winter. Similar population dynamics have also been observed in other areas of Spain (Beltran 1991) and Portugal (Martins *et al*. 2003). Relatively low rabbit abundances in winter may be due to cumulative factors, such as an increase in the incidence of diseases (Orueta *et al*. 1995), autumn hunting (500-600 rabbits hunted per year in our study area) or the difficulty to survive the drastic depletion of resources during summer. Higher adult rabbit abundances in summer are due to an increase in the population after reproduction. Several studies highlight the strong effects of climate and weather on body condition, reproduction and population dynamics of rabbits (Soriguer and Rogers 1981, Wheeler and King 1985). In fact, rabbit gonadal development is strongly correlated with plant water content and vegetation biomass, which reaches its maximum value in spring, when reproductive activity is highest (Gonçalves *et al*. 2002). In Mediterranean type climates, the rabbit breeding season starts when autumn rains cause germination of the vegetation and ceases when the higher temperatures of early summer dry off the pastures (Gonçalves *et al*. 2002). The year we carried out this study, rains started early in autumn, and in winter the number of juvenile pellets was high, indicating that rabbits were able to start breeding in the autumn.

Adult and juvenile habitat selection

Juveniles were linked to warrens in all the seasons. Young rabbits are born in one of the burrows of a warren (Chapman and Schneider 1984) or in breeding stops dug by pregnant females (Lockley 1961). The period of rabbit maternal dependence lasts just 20-30 days (Villafuerte 2002). Juvenile dispersers leave their original territory between the first and fifth month of life (Andersson and Meurling 1977) and it has been seen that from the first week of life on the surface, young rabbits do not show a close association with their original burrow and they use different ones (Vitale 1989). Juveniles were mainly concentrated in habitats with a high density of warrens (highlands, slopes and lowlands) or in nearby areas (flat areas in mid-slope). Flat areas in mid-slope accumulate water and nutrient runoff and thus have higher fertility (unpublished data) and more abundant vegetation (but the density of warrens is low). These areas are surrounded by slopes, which contained more and larger warrens (8.88 warrens/ha and 83.43 warren entrances/ha in slopes contrasting with 2.60 warrens/ha and 11.71 warren entrances/ha in wet lowlands).

Large warrens provide better refuge and more successful breeding (Cowan 1987). Juveniles can feed in flat-areas in mid-slope, but still have large "slope-warrens" nearby for protection. Feeding near areas with a high density of warren entrances would allow young rabbits to spend more time feeding than vigilant, as the escape distance once a predator is sighted is reduced. Juveniles were always less abundant in the ample wet lowlands. In these areas, they do not have convenient `slope-warrens´ within a practical distance, and scrub cover is almost non-existent. Wet lowland areas can be flooded during the rainy period, and rabbit warren building is usually limited to places with low flooding risk (Palomares 2003). Additionally, living in a wet lowland in winter would force juveniles to invest extra energy on thermoregulation. Poor quality refuge cover in these areas increases the vulnerability of juveniles to both predation and adverse weather conditions.

Adult rabbits used the five habitat-types equally. The main shift occurred in summer, when adult abundances increased in wet lowlands. During winter and spring, the growing periods of annuals, these plants can satisfy rabbit nutritional needs (Cooke 1981). In summer, there is a depletion of succulent green food and an increase in intra-specific competition as a consequence of spring reproduction. This forces adult rabbits to enlarge their home ranges and forage in areas with less protection, but where the vegetation remains green for longer. Adult rabbits were linked to warrens in spring and winter, but this relationship disappeared in summer. Wild adult rabbits are known to be strongly territorial, especially during the reproductive season (Mykytowycz 1964), maintaining strong ties with a particular burrow when raising a litter. In summer, the non-breeding season, rabbits from different warrens interchange and establish new territories (Mykytowycz and Gambale 1965). In this season, adults were influenced by rush cover, only present in lowlands and wet lowlands, and often used by rabbits as refuge (pers. obs.).

Adults in spring and winter and juveniles in summer avoided areas with high values of herbaceous vegetation volume. This may be explained by the perception of predation risk by rabbits foraging in such high-volume swards. The height and cover of vegetation varied seasonally, and the ability of rabbits to detect potential predators could decrease when herbaceous vegetation was taller. Tall swards can alter predation risk for an animal, either by providing cover and protection in the event of an attack, or conversely by obstructing its view of approaching predators (Lazarus and Symonds 1992, Arenz and Leger 1997). Several studies confirm that herbivores are more vigilant in dense vegetation because of the potential presence of stalking predators (Loughry 1993). Iason *et al*. (2002) found that wild rabbits strongly selected those areas with a shorter sward (but lowest intake rate), probably as a way to avoid predation. This seems to be confirmed by both our data and those of Carvalho and Gomes (2004), who found that rabbits were less abundant in places where herbaceous cover reached extreme values. Other factors may also contribute to rabbits avoidance of areas with dense and tall swards. In structurally complex environments, rabbits are hindered by the difficulty to penetrate dense vegetation or the lower foraging efficiency of feeding on tall plants (Van de Koopel *et al*. 1996). Traditional mowing of wet lowland areas at the beginning of summer may allow rabbit use of these areas either by reducing predation risk perception or by facilitating foraging efficiency.

Plant community composition and distance to drinking water affected both adult and juvenile rabbit abundances equally, and this effect depended on seasonal changes. In winter, adults and juveniles were more abundant in areas of high legume cover, suggesting a need for a highly nutritious diet either because of breeding (adults) or growth (juveniles). In spring, rabbits were more abundant in areas with high composite cover. Composites are an important part of rabbit diet (Soriguer 1988). In this season, juveniles showed a negative association with green food, probably because its abundance is highest in the flooded wet lowlands. All rabbits show a strong positive relationship with holm oak and *Retama* shrub cover in summer. Rabbits eat the bark, leaves and acorns of holm-oak (Martins *et al*. 2002) during periods of drought when herbaceous productivity is abnormally low. Rabbits are also known to intensively browse *Retama* shrubs (Gómez-Sal *et al*. 1999) and feed on their fruits, thereby dispersing the seeds (Cerván and Pardo 1997, Dellafiore *et al*. 2006).

Water intake is important for herbivore distribution and survival. For rabbits, water plays an important role in thermoregulation, being necessary for the dissipation of metabolic heat (Hayward 1961). Juvenile and adult water requirements are different since juveniles need more water given their higher metabolic rates and energy expenditure required for active growth (Richards 1979). Unexpectedly, drinking water did not influence adult and juvenile abundances in either season. In the absence of water rabbits require green food for their survival (Cooke 1982). In summer, pastures remain green for longer in wet lowlands, areas highly selected by adults in this season. Therefore, our results suggest that juvenile dependence on refuge provided by warrens constrained their access to water during the summer drought.

Summarising, vigilance/foraging trade-off differed between juveniles and adults. Juvenile rabbits are much more vulnerable to predation than adults (Angulo 2004) and this vulnerability favoured segregated habitat selection. Juveniles preferred to forage near areas that contained a high density of burrows in order to minimise escape distance and allow for longer foraging time. Adults selected short standing swards, ensuring a wide sensory range for the detection of approaching predators. Vigilance time is reduced in such areas because predators can be spotted long before they approach within striking distance. In general, juvenile and adult rabbits preferred foraging in habitats that offer abundant protection, at the expense of food quality, adjusting their foraging selectivity to plant community seasonal changes. With the arrival of summer and its associated food depletion, adult rabbits were forced to shift towards more productive areas where green vegetation persists and represents a source of both water and forage. In these open areas rabbits are more vulnerable. Such higher risk may be overcome by adults (but not juveniles) through experience and higher sprint speed.

5. Conclusions

By using a broad scale approach, we have shown that adult and juvenile rabbits have different habitat preferences throughout the year. Importantly, rabbits showed seasonal shifts in habitat use depending on predation risk and energy needs. Adult and juvenile rabbits require different habitat structures at different times of year, and heterogeneity at the local, within-habitat scale is particularly important. Traditional dehesa management involves low levels of human disturbance such as tree management, ploughing and extensive livestock grazing. This creates a mosaic of pastures, low-intensity cultivation, scrub and woodland, which can be considered a mixture of different habitat-types (Díaz *et al*. 1997). In these areas rabbits can have access to high-quality resources in terms of food and cover throughout the year. Consequently, adult and juvenile rabbits have a greater chance to achieve high reproductive and survival rates, which will lead to an increase in population numbers. Since the 1950s dehesas are becoming increasingly homogenous landscapes through overgrazing, reduced tree management, land-irrigation and rural abandonment (Pulido *et al*. 2001). Habitat loss and the introduction of diseases have caused a strong decline in European rabbit populations in their native habitat (Moreno *et al*. 1996) that has had devastating consequences on Mediterranean food webs since rabbits are the main prey for almost 29 raptors and mammalian carnivores (Delibes and Hiraldo 1981), including several endangered species. Thus, to support and increase rabbit populations, dehesas should be managed with habitat diversity in mind, encouraging the maintenance of traditional land management practices.

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