Seasonal habitat use by the European rabbit (*Oryctolagus cuniculus*) in a coastal dune system in SW Spain

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Abstract

*Seasonal habitat use by the European rabbit (*Oryctolagus cuniculus*) in a coastal dune system in SW Spain.—* We studied habitat use by the wild European rabbit (*Oryctolagus cuniculus*) in a coastal sand dune system in the south–western Iberian peninsula. Our goals were to define the use of this habitat by rabbits in relation to food and shelter availability between seasons. Rabbit density, food availability and refuge abundance were analysed using multiple regression analyses. We found that, independently of season, habitat selection was principally related to cover by the woody shrub *Retama monosperma* which rabbits use both as a food resource and as protection against predators. Although it is an invasive native plant, the benefits that *R. monosperma* provides to the wild rabbit population should be taken into account when deciding wild rabbit management strategies.

Key words: *Retama monosperma*, Iberian peninsula, Rabbit predation risk, Feeding site, Seed dispersal

Resumen

*Uso estacional del hábitat por parte del conejo de monte (*Oryctolagus cuniculus*) en un sistema de dunas costeras en el suroeste de España.—* Estudiamos el uso del hábitat por parte del conejo de monte silvestre (*Oryctolagus cuniculus*) en un sistema de dunas costeras del suroeste de la península ibérica. Nuestros objetivos fueron definir la utilización que los conejos hacen de este hábitat en relación con la disponibilidad de alimentos y cobijo entre estaciones. Se analizaron la densidad de conejos, la disponibilidad de alimentos y la abundancia de refugios mediante análisis de regresión múltiple. Observamos que, independientemente de la estación, la selección del hábitat estaba principalmente relacionada con la cubierta del arbusto leñoso *Retama monosperma*, que los conejos utilizan como fuente de alimento y como protección contra los predadores. A pesar de que se trata de una planta nativa invasora, los beneficios que *R. monosperma* aporta a la población de conejos silvestres deberían tenerse en cuenta a la hora de decidir cuáles deben ser las estrategias de gestión para esta especie.

Palabras clave: *Retama monosperma*, Península ibérica, Riesgo de predación, Área de alimento, Dispersión de semillas

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Introduction

Habitat selection is a vital decision for animals as it affects food, shelter and reproduction (Hargis & McCullough, 1984; Pulliainen & Tunkkari, 1987; Morrison et al., 1998; Bond et al., 2002). This decision can be influenced by species' life history traits, individual characteristics such as age and sex, and environmental factors such as competition, predation pressure and seasonal food supply (*e.g.* Bos & Carthew, 2003; Lombardi et al., 2007; Hernandez–Aguilar et al., 2013; Lisón et al., 2014).

Over the last decade, wildlife researchers have made great efforts to better understand the pressures acting on prey species to select certain habitat types and the implications of avoiding predators. Several studies have shown the ecological flexibility of the European rabbit (*Oryctolagus cuniculus*) in Mediterranean ecosystems, and its wide plasticity to adapt its behaviour to predator pressure and food availability (Jaksic & Soriguer, 1981; Lombardi et al., 2003, 2007; Stott, 2003; Sarmento et al., 2012).

The European rabbit is a key prey species in Southern Europe (Delibes–Mateos et al., 2008a) with great capacity to colonize different habitat types (Thompson & King, 1994). On the Iberian Peninsula, the rabbit has a wide distribution and it has been observed in diverse ecosystems, from Mediterranean scrublands to dehesa agroecosystems, mountainous areas, and coastal sand dunes (*e.g.* Rueda et al., 2008a, 2008b; Barrio et al., 2009; Dellafiore et al., 2009; Tapia et al., 2010, 2014). The coastal sand dune ecosystem represents 40% of the 7,880 km of the Iberian coast (Ley et al., 2011) and rabbit populations have been observed in almost all such sand dune areas (Villafuerte, 2002), but they have been poorly studied to date. The lack of interest could be because these coastal sand dunes hold no hunting interest and house no endangered predators.

In this study we focused our research on the dune system of 'La Flecha de El Rompido' in the southwest of the Iberian Peninsula. Most dune systems in this area are currently expanding and La Flecha dune system is growing by more than 30 m per year at its eastern edge (Gallego–Fernández et al., 2006). It is inhabited by a large population of rabbits (Dellafiore, 2007). Hares (*Lepus granatensis*) are also present in this ecosystem, but at a lower density, and red fox (*Vulpes vulpes*) is the main predator (Dellafiore, 2007).

Previous studies have established that rabbit habitat selection is based on two main drivers: food provision and predator avoidance (*e.g.* a preference for sheltered habitats) (Lombardi et al., 2007; Satilli & Bagliacca, 2010). Therefore, to define habitat selection by rabbits in a coastal sand dune system in the southwestern Iberian peninsula we were particularly interested in assessing the effect of food and shelter availability on habitat use and also habitat use in different seasons. Our study of habitat use in sand dune areas was designed to contribute to understanding the rabbit's huge capacity for adaptation to a wide range of environments and the flexibility of its spatial behaviour. Such information could be of value when determining management strategies for the species.

Materials and methods

Study area and environmental units

This study was conducted on El Rompido spit, on the seaward side of the Piedras River estuary (Huelva Province, SW Spain, 37º 12' N, 7º 10' W). The spit extends eastwards for 12 km, running parallel to the coast, with a width ranging between 300 and 700 m. The area consists of 527 ha of natural sandy soil, of which 293 ha is composed of inner stabilized dunes (fig. 1). The climate has a Mediterranean pattern of wet winters and dry summers, with a mean annual temperature of 18.2ºC and mean annual rainfall of 620 mm.

The study area has various vegetation communities related to local geomorphology, including the beach and active dune system, salt marshes, inner stabilized dunes, wet depressions, and tidal swales. The active dune zone is mainly covered by *Ammophila arenaria* (marram grass) and *Elymus farctus* (sand couch–grass). Due to adverse conditions, vegetation is sparse and low. There is a vegetation gradient inland according to local environmental conditions. The inner stabilized dune zone is the main spit surface area (56%) and is largely covered by the woody shrub *Retama monosperma* (bridal veil broom). *Retama monosperma* can grow up to 3.5 m in height with variable cover. The plant occurs with chamaephytic species such as *Thymus carnosus, Artemisia crithmifolia,* and *Helychrysum picardii*, which show diverse distribution patterns along the spit. The *R. monosperma* canopy contributes to the high number of herbaceous plants, largely consisting of winter annuals. Wet depressions are covered by hygrophytic vegetation (usually not exceeding 1.5 m in height), dominated by the perennial *Scirpus holoschoenus* and/or *Juncus acutus* and, occasionally, *Scirpus maritimus* (depending on water availability). These wet depressions are also colonized by several annual herbaceous species, especially winter annuals. Tidal swales are depressions between dune ridges connected with the river channel and dominated by halophytic vegetation (for details see Gallego Fernández et al., 2006; Annex).

We used geomorphologic features and vegetation composition to classify the study area into 10 environmental units: (1) dune scrubland, (2) *R. monosperma* with *Thymus carnosus*, (3) *R. monosperma* with *Artemisia crithmifolia,* (4) *R. monosperma* with *Helichrysum picardii*, (5) inland dunes with *R. monosperma,* (6) wet depressions, (7) active dune area, (8) tidal swales, (9) salt marshes, and (10) sandy shore (table 1, also see Gallego Fernández et al., 2006, Dellafiore et al., 2008).

Sampling design and data collection

Using a stratified random sampling model, 146 points were selected throughout the study area on the basis of the environmental units present. The number of points in each environmental unit was estimated according to the area of each unit and taking a minimum of 10 points in the smallest unit (distance between points ranged from 10–55 m). Points in each unit were selected based on a randomly generated table of geographic coordinates.

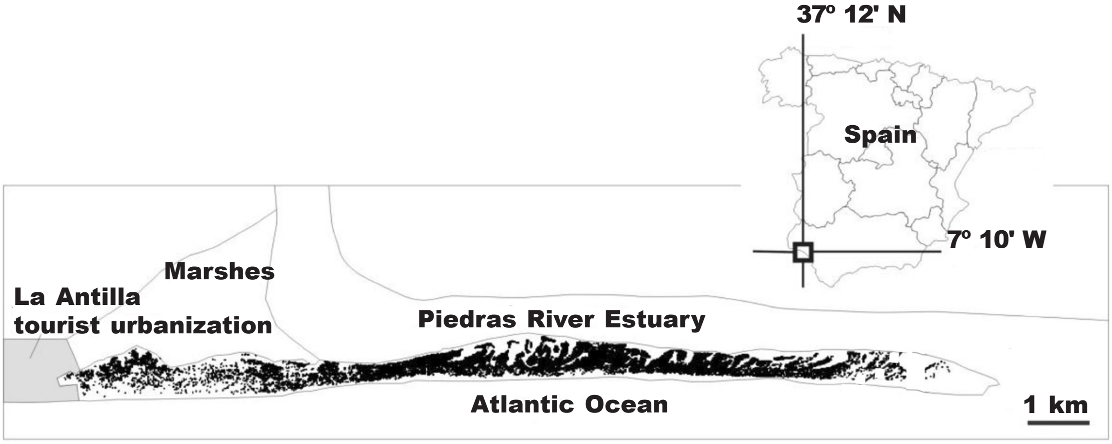

Fig. 1. Geographical location of the study area and *Retama monosperma* distribution (in black).

Fig. 1. Localización geográfica de la zona de estudio y distribución de Retama monosperma *(en negro).*

Each point was surveyed in winter (January–March) and spring (April–June) of 2004, and during the summer (July–September) and autumn (October–February) of 2005. We measured rabbit relative abundance and food and refuge availability at each sampling point per season.

Rabbit relative abundance

Pellet counts are considered an effective method for estimating rabbit relative abundance and for evaluating habitat use by lagomorph species (Myers, 1955; Jaksic et al., 1982). In consequence, rabbit relative abundance was assessed by pellet counts in dung clearance plots (Palomares, 2001; Fernández de Simon et al., 2011a). One permanent dung plot of 0.5 × 0.5 m was placed at each of the 146 sampling points. Efforts were made to avoid latrines and sites under shrubs because they can be used as refuge or resting sites. Each plot was cleaned 25–35 days before pellet collection and counts. To standardise all pellet counts, a defecation rate per day was calculated for each count which was obtained by dividing the number of pellets at each counting station by the number of days since the last count at the same station (Rouco et al., 2011). Pellet persistence can differ between habitats and seasons (Taylor & Williams, 1959; Iborra & Lumaret, 1997; Palomares, 2001; Fernández de Simon et al., 2011b) therefore a 'pellet decay rate' was estimated to ensure an adequate period between pellet clearance and counting, following the method of Fernández de Simon et al. (2011b).

Food availability

To quantify food abundance, a second permanent plot (1 × 1 m) was placed at each of the 146 sampling points. Total green vegetation cover and cover per plant species were estimated seasonally following the method proposed by Braun–Blanquet (1979). Green cover was chosen to quantify food availability because grazing species will actively select green parts of plants from a relatively dry sward during dry seasons (Jarman & Sinclair, 1979). A high number of herbaceous species were identified during sampling, so to reduce the number of variables, we grouped species by family. Thus, a total of 32 families were considered in the analysis (Gallego Fernández et al., 2006).

Refuge availability

Warren density was assessed only in spring, in a 3–ha circular plot placed around each sampling point ($N = 146$). Due to the length of our study, we assumed that rabbit density did not change. A circular plot of 3 ha was selected because it is similar to the largest home range observed in European rabbit populations in a nearby area (Fernández, 2005). Each warren within a circular plot was geo–referenced and the distance between sampling point and the nearest warren was measured using ArcGIS 9.3.

Scrub cover (mainly *R. monosperma*) was estimated as a percentage of cover in the 3–ha circular plot placed around each sampling point. Percentage cover was assessed by using ArcGIS 9.3 to digitalize each *R. monosperma* bush from aerial photographs (scale 1:5,000) taken in 2001.

Data analysis

We used pairwise correlations to test for co–linearity between the explanatory variables (*i.e.* percentage total green cover and percentage herb cover by each family, warren density, distance to nearest warren, and percentage *R. monosperma* cover). As no case of co–linearity was observed, all variables were considered in the model. In order to define

Table 1. Environmental units on the 'La Flecha de El Rompido' study area, SW Spain.

Tabla 1. Unidades ambientales en la zona de estudio de la Flecha del Rompido, SO España.

Environmental units	Area (ha)	%	Sample points
Dune scrubland	26.6	5.06	10
R. monosperma with *Thymus carnosus*	72.8	13.84	18
R. monosperma with *Artemisia crithmifolia*	112.3	21.44	26
R. monosperma with *Helichrysum picardii*	46.9	8.92	13
Inland dunes with *R. monosperma*	11.4	2.17	10
Active dune area	61.9	11.77	16
Tidal swales	93.4	17.76	20
Salt marshes	32.7	6.22	10
Sandy shore	46.0	8.74	13
Wet depression	21.4	4.07	10
Study area total	522.4	100	146

habitat preference by rabbits at our study site, a multiple regressions analysis per season was used to generate models that included all our explanatory variables as predictors, and rabbit relative abundance as our dependent variable. Using a model selection approach based on information theory (Burnham & Anderson, 2002) we identified the set of models best supported by the data. The Akaike information criterion (AIC) was used to rank and weigh competing models, using the difference between AICs of each model and the minimum AIC found (ΔAIC) (Burnham & Anderson, 2002). These ΔAIC values were also used to calculate Akaike's weighting of each model w_i (Burnham & Anderson, 2002). The values of w_i were standardized across the candidate set of models. Weightings also provide a way to define the relative importance of each predictor. This measure can be calculated as the sum of w_i values over all the models that include the predictor of interest. However, it is virtually impossible to discern the relative influence of different predictors when they all appear in the best set of models, so we used the standardized regression coefficients to rank the importance of the predictors in the best model.

All statistical analyses were performed using Statistica (StatSoft, Inc., 2003) and Spatial Analyses in Macroecology (SAM) (Rangel et al., 2005).

Results

Rabbit relative abundance

Mean faecal pellet persistence was 0.99 and no differences were observed between seasons. Average pellet defecation rate per day per site was similar throughout the year 0.71 (+ 0.015), 0.64 (+ 0.010), 0.98 (+0.021), 0.55 (+0.014) in winter, spring, summer and autumn, respectively; however, significant differences were observed between summer and autumn ($Z = –1.6$; $P = 0.052$).

A new species of *Laemostenus* Bonelli, 1810 (Coleoptera, Carabidae) from Els Ports Natural Park (Catalonia, northeastern Iberian peninsula)

Summer models

For summer we obtained 11 models with $\Delta AIC < 2$ and each explaining a similar amount of variance (approx. 20%) (table 2). Warren density variables were present in all models. However, the Akaike weights suggested that the best model includes warren density and *R. monosperma* cover ($w_i = 0.087$). The higher standardized coefficients of both variables provided strong evidence that these are the main factors driving habitat use by rabbits in summer at El Rompido spit.

Autumn models

For autumn, four equivalent models were obtained with $\Delta AIC < 2$ and each explained a similar amount of variance (approx. 92%) (table 3). *R. monosperma* cover and warren density were common predictors for all models. However, the Akaike weightings suggested that the best model included warren density, *R. monosperma* cover and cover of herbs of the Geraniaceae family (negative) ($w_i = 0.272$). The higher standardized coefficients of warren density and *R. monosperma* cover provided strong evidence that these two variables were the main factors driving habitat use by rabbits in autumn.

Table 2. Multiple regression models for European rabbits in summer. Models are ranked by AIC from best– to worst–fitting, and only models with ∆AIC < 2 are presented. AICs have been corrected for the presence of spatial autocorrelation in the model residuals. For each variable entering the model we included its standardized coefficient to evaluate its relative importance: Wd. Warren density; *Rm. Retama monosperma;* Chen. Chenopodiaceae; Plum. Plumbaginaceae.

Tabla 2. Modelos de regresión múltiple para el conejo de monte en verano. Los modelos están ordenados del mejor al peor valor de AIC. Solo presentamos modelos cuyo ∆AIC < 2. Los valores de AIC de los modelos restantes se corrigieron para tener en cuenta la existencia de autocorrelación espacial. Para cada variable del modelo incluimos un coeficiente estandarizado para evaluar su importancia relativa: Wd. Densidad de madrigueras; Rm. Retama monosperma*; Chen. Chenopodiaceae; Plum. Plumbaginaceae.*

Wd	Rm cover (%)	Chen cover (%)	Cover of herbs (%)	Plum cover	AIC	∆AIC	r^2	w_i
0.394	0.151				1237.6	0	0.208	0.087
0.395	0.154	−0.105			1237.7	0.1	0.220	0.082
0.386	0.160		−0.092		1238.1	0.5	0.218	0.068
	0.140				1238.1	0.5	0.193	0.066
0.441		−0.102			1238.5	0.9	0.203	0.055
0.405	0.134			−0.09	1238.6	1	0.215	0.053
0.438				−0.10	1238.6	1	0.203	0.053
0.388	0.163	−0.09	−0.074		1238.8	1.2	0.226	0.047
0.436			−0.084		1238.1	1.5	0.200	0.042
0.398	0.148	−0.08	−0.077		1239.4	1.8	0.222	0.035
0.402	0.145		−0.083	−0.059	1239.5	1.9	0.222	0.033

Winter models

For winter, four equivalent models were obtained with ∆AIC < 2, each explaining a similar amount of variance (approx. 37%) (table 4). Four variables were common to all models: warren density, *R. monosperma* cover, cover of herbs of the Urticaceae family and total herb cover (negative). The Akaike weightings suggested that the best model included the four variables mentioned above (w_i = 0.314). The higher standardized coefficients of warren density, *R. monosperma* cover and cover of Urticaceae herbs provided strong evidence that these three variables were the main factors driving habitat use by rabbits in winter.

Spring models

For spring, 10 models were obtained with ∆AIC < 2 each explaining a similar amount of variance (approx. 40%) (table 5). Cover of herbs of the Boraginaceae family, warren density and *R. monosperma* cover were present in all models. The Akaike weightings suggested that the best model included the three variables mentioned above plus total herb cover (negative), cover of Chenopodiaceae herbs (negative) and cover of Geraniaceae herbs (negative) (w_i = 0.140). The higher standardized coefficients of cover of herbs of the Boraginaceae family, warren density, and *R. monosperma* cover provide strong evidence that these three variables are the main factors driving habitat use by rabbits in spring.

Discussion

Coastal dune systems with wet depressions have been considered a favourable habitat for wild rabbits because wet areas would provide sufficient food resources (Palomares, 2003; Gálvez–Bravo, 2011) and allow the animals to build large warrens (Palomares, 2003). Other authors have also found this environmental unit was that most commonly used by rabbits to build warrens (Dellafiore et al., 2008). The explanation for this finding could be the very high cover of *R. monosperma* (90–100%) in this ecosystem (Vallés et al., 2011), intertwined with tall old shrubs and providing excellent protection (for rabbits and warrens) against predators (Delibes–Mateos et al., 2008a). *R. monosperma* also appears to be an important source of food for rabbits (Gómez Sal et al., 1999; Dellafiore et al., 2006). It is not therefore surprising that *R. monosperma* has been found to be selected by wild rabbits independently of season in most well–supported models.

Table 3. Multiple regression models for European rabbits in autumn. Models are ranked by AIC from best– to worst–fitting, and only models with ΔAIC < 2 are presented. AICs have been corrected for the presence of spatial autocorrelation in the model residuals. For each variable entering the model, we included its standardized coefficient to evaluate its relative importance: Rm. *Retama monosperma;* Wd. Warren density; Ger. Geraniaceae; Amar. Amaryllidaceae.

Tabla 3. Modelos de regresión múltiple para el conejo de monte en otoño. Los modelos están ordenados del mejor al peor valor de AIC. Solo presentamos modelos cuyo ΔAIC < 2. Los valores de AIC de los modelos restantes se corrigieron para tener en cuenta la existencia de autocorrelación espacial. Para cada variable del modelo incluimos un coeficiente estandarizado para evaluar su importancia relativa: Rm. Retama monosperma*; Wd. Densidad de madrigueras; Ger. Geraniaceae; Amar. Amaryllidaceae.*

Rm cover (%)	Wd	Ger cover (%)	Amar cover (%)	AIC	ΔAIC	r^2	w_i
0.678	0.476	−0.119		721.9	0	0.926	0.272
0.628	0.482			722.2	0.3	0.924	0.237
0.704	0.445		−0.096	722.9	0.9	0.925	0.172
0.757	0.452	−0.107	−0.073	723.4	1.5	0.926	0.132

Although we observed some seasonal differences between the variables that predicted habitat use by rabbits (tables 2–5), our results showed that warren density and *R. monosperma* cover were the main predictors throughout the whole year. The differences observed between seasons could be due to changes in vegetation availability. For example, Boraginaceae cover appeared as a likely predictor of rabbit habitat use in spring because the species of this family are annuals that flower and fruit in spring; and grow exclusively on inland dunes with *R. monosperma.* The same applied to the Urticaceae family in winter. The species of this family are annuals, that flower and fruit from February to June, and are present only in environmental units with *R. monosperma* and dune scrubland. Both families could be associated with rabbit habitat selection because both are palatable to rabbits (Dellafiore, 2007; Dellafiore et al., 2009) and have a higher occurrence on inland dunes with *R. monosperma*, which is the habitat selected by rabbits for warren building (Dellafiore et al., 2008).

On the other hand, total herb cover and Chenopodiaceae and/or Geraniaceae cover were negatively associated with rabbit presence during autumn, winter

Table 4. Multiple regression models for European rabbits in winter. Models are ranked by AIC from best– to worst–fitting, and only models with ΔAIC < 2 are presented. AICs have been corrected for the presence of spatial autocorrelation in the model residuals. For each variable entering the model we included its standardized coefficient to evaluate its relative importance: Wd. Warren density; Rm. *Retama monosperma;* Urtic. Urticaceae; Prim. Primulaceae; Plum. Plumbaginaceae.

Table 4. Modelos de regresión múltiple para el conejo de monte en invierno. Los modelos están ordenados del mejor al peor valor de AIC. Solo presentamos los modelos cuyo ΔAIC < 2. Los valores de AIC de los modelos restantes se corrigieron para tener en cuenta la existencia de autocorrelación espacial. Para cada variable del modelo incluimos un coeficiente estandarizado para evaluar su importancia relativa: Wd. Densidad de madrigueras; Rm. Retama monosperma*; Urtic. Urticaceae; Prim. Primulaceae; Plum. Plumbaginaceae.*

Wd	Rm cover (%)	Urtic cover (%)	Herb. cover (%)	Prim cover (%)	Plum cover (%)	AIC	ΔAIC	r^2	w_i
0.293	0.258	0.213	−0.172			1185.6	0	0.373	0.314
0.291	0.259	0.217	−0.174	0.079		1186.4	0.8	0.379	0.213
0.299	0.255	0.206	−0.172		–0.073	1186.6	1	0.378	0.187
0.303	0.254	0.209	−0.176	0.079	–0.069	1187.6	2	0.384	0.118

Table 5. Multiple regression models for European rabbits in spring. Models are ranked by AIC from best– to worst–fitting, and only models with ∆AIC < 2 are presented. AICs have been corrected for the presence of spatial autocorrelation in the model residuals. For each variable entering the model we included its standardized coefficient to evaluate its relative importance: Bor. Boraginaceae; Wd: Warren density; Rm. *Retama monosperma;* Chen. Chenopodiaceae; Ger. Geraniaceae; Prim. Primulaceae.

Tabla 5. Modelos de regresión múltiple para el conejo de monte en primavera. Los modelos están ordenados del mejor al peor valor de AIC. Solo presentamos los modelos cuyo ∆AIC < 2. Los valores de AIC de los modelos restantes se corrigieron para tener en cuenta la existencia de autocorrelación espacial. Para cada variable del modelo incluimos un coeficiente estandarizado para evaluar su importancia relativa: Bor. Boraginaceae; Wd. Densidad de madrigueras; Rm. Retama monosperma*; Chen. Chenopodiaceae; Ger. Geraniaceae; Prim. Primulaceae.*

Bor	Wd	Rm cover (%)	Chen cover (%)	Herb cover (%)	Ger cover (%)	Prim	AIC	∆AIC	r^2	w_i
0.346	0.304	0.276	−0.129	−0.115	−0.115		1030.2	0	0.419	0.140
0.339	0.314	0.267	−0.136		−0.119		1030.4	0. 8	0.409	0.127
0.343	0.316	0.285	−0.132	−0.117	−0.120	0.071	1031	0.8	0.425	0.094
0.348	0.292	0.267	−0.12	−0.114			1031.4	1.2	0.406	0.092
0.343	0.305	0.105	−0.125				1031.6	1.4	0.394	0.070
0.338	0.327	0.272	−0.139		−0.119	0.06	1031.8	1.6	0.412	0.062
0.356	0.290	0.274	−0.111	−0.129		0.083	1032	1.8	0.412	0.062
0.352	0.289	0.264		−0.119			1032.	1.8	0.393	0.056
0.347	0.302	0.277		−0.114	−0.100		1032.	1.8	0.401	0.054

and spring (tables 2–5). Species of Chenopodiaceae are abundant in tidal swales, salt marshes and on sandy shores whereas species of Geraniaceae are abundant on active dunes and in dune scrubland. The lack of shelter for predators in these environmental units could explain why rabbits did not select these units.

Other authors found seasonal differences in habitat use by rabbits in grassland environments (Rueda García, 2006; Rueda et al., 2008a, 2008b). In our study area, although we did not test for differences in habitat use between seasons, we found no change in habitat use in each season. This may indicate that food availability in the vicinity of warrens remains relatively constant over time; hence rabbits do not need to move long distances for feeding. Grassland and herbaceous vegetation biomass in our study area decrease during summer due to the high temperatures and low rainfall. However, feeding sites selected by rabbits remained constant and were always correlated with warren density and *R. monosperma* cover. Thus, rabbits may feed almost entirely on such fruits until late autumn; in winter, when those fruits become scarce, rabbits feed on herbaceous vegetation, which is highly available due to rainfall in that season. Accordingly, when herbaceous vegetation is scarce, fruit availability is high and rabbits can feed in areas protected from predators.

Although the density of individuals might be a poor indicator of habitat quality in some conditions (Van Horne, 1983; Lyra–Jorge et al., 2010), mostly it is a good proxy for the suitability (*i.e.* quality) of a particular area. For European rabbit populations, the key limiting factors are the inability to dig warrens and the lack of available refuges and food (Rogers & Myers, 1979; Palomares & Delibes, 1997; Fa et al., 1999; Lombardi et al., 2003; Virgos et al., 2003; Cabrera Rodríguez, 2006). In coastal dune systems, where the terrain is firm sand, warren construction is not a limiting factor (Moseby et al., 2005). Food availability should not be a limiting factor either considering the high presence of *R. monosperma* fruits, which are highly consumed by rabbits in our study site (Dellafiore et al., 2006). Refuge availability, for protection against predators, however, may be the key factor for this particular population. A previous study showed that European rabbits at our study site required high cover of *R. monosperma* (90–100%) for warren building (Dellafiore et al., 2008). This would occur more likely in sand dune areas where there is no structural support (*i.e.* no shrub roots), making them unsuitable for warren building (*e.g.* Martins et al., 2002; Palomares, 2003). *R. monosperma* also provides dense overhead cover and facilitates the establishment and growth of other plant species, mainly herbaceous annuals, under the shrub canopies. This vegetation would also provide food for rabbits (Muñoz–Vallés et al., 2014), characteristics that are correlated with rabbit occurrence and relative abundance in scrubland habitats (Martins et al., 2002; Beja et al., 2007). Unfortunately, predator presence was not monitored at our study site, but predators such as the red fox (*Vulpes vulpes*) are quite common in the area and they may affect the viability of the rabbit populations, since they could act as facultative predator of rabbits (Delibes–Mateos et al., 2008b).

In conclusion, our results show that in a coastal sand dunes ecosystem in the south–western Iberian Peninsula, scrub cover, and in particular *R. monosperma* cover, is highly preferred by European rabbits, independently of season. Although *R. monosperma* has recently been categorized as a native–invasive plant in coastal dune systems (Muñoz–Vallés et al., 2014), the species seems to benefit wild rabbit populations in such ecosystems. It provides a comprehensive habitat for rabbits: on the one hand, its canopy provides protection against predators (*e.g.* against aerial predators) and its root system provides structure to the soil to enable warren building, while on the other hand, it provides food by mean of its fruits and by favouring herbaceous growth underneath. Therefore, the benefits of *R. monosperma* should be taken into account when deciding on future management strategies for wild rabbits. For example, rabbits in coastal dunes could be used as a potential population source to increase rabbit numbers for conservation purposes in adjacent habitats.

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Annex. Presence of families of herbaceous species in each environmental unit in the study area.

Anexo. Presencia de las familias de especies herbáceas en cada unidad ambiental de la zona de estudio.

Family name
Amaryllidaceae
Apiaceae
Asteraceae
Boraginaceae
Brasicaceae
Caryophyllaceae
Chenopodiaceae
Cistaceae
Convolvulaceae
Cucurbitaceae
Cyperaceae
Euphorbiaceae
Fabaceae
Frankeniaceae
Geraniaceae
Juncaceae
Lamiaceae
Liliaceae
Orobanchaceae
Oxalidaceae
Papaveraceae
Poaceae
Polygonaceae
Plantaginaceae
Plumbaginaceae
Primulaceae
Ranunculaceae
Rubiaceae
Scrophulariaceae
Solanaceae
Valerianaceae
Urticaceae