



Grain sowing aimed at wild rabbit *Oryctolagus cuniculus* L. enhancement in Mediterranean environments

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ABSTRACT

Although habitat management practices focussed on the enhancement of hunting and protection of threatened species are common, the scientific validation of such practices is scarce. The wild European rabbit *Oryctolagus cuniculus* L., a hunted and threatened species in its native range, is at the same time a key species for the preservation of threatened Mediterranean predators. Cereal sowing is one of the most common practices to augment the food supply of rabbits, and it is used not only by hunters but also by conservationists. At present, limited scientific information is available regarding the effectiveness of cereal sowing. To evaluate its effectiveness, we analysed data on sowing trials conducted in 125 plots, located in 14 private estates throughout central Spain, most of them with low density populations. Brush was cleared from 44 of these plots prior to sowing. Our results indicated that rabbits preferentially selected sown areas over control (unsown) areas. This selection increased in plots that represented suitable habitats for rabbits, such as pasturelands, as well as when thicket islands and natural or artificial shelters were available within the sown plots. Local enhancement of rabbit populations was also observed. These positive results were also obtained regardless of the initial habitat conditions, not only in the treatment plots but also in the surrounding area. Our recommendations can be broadly applied for managing rabbit-dependent threatened species.

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Introduction

The wild rabbit (*Oryctolagus cuniculus* L.) is a Near Threatened mammal (Smith & Boyer 2008). In its native range it is considered as Vulnerable in Spain (Villafuerte & Delibes-Mateos 2007) and as Near Threatened in Portugal (Cabral et al., 2006). And it is also the main small game species in Spain (MAGRAMA, 2014). But it is also one key species in Mediterranean ecosystems (Delibes-Mateos et al., 2007), and several endangered species depend on it. Among these species are Bonelli's eagle (*Aquila fasciata* Vieillot; Moleón et al., 2009), the Spanish imperial eagle (*Aquila adalberti* Brehm), and the Iberian lynx (*Lynx pardinus* Temminck; Ferrer & Negro, 2004). For the preservation of threatened species that depend on wild rabbits, and considering only projects financed by

the EU LIFE programme, current funding has reached 100 M€ for rabbit-dependent species (Life Programme 2011).

The severe decline in wild rabbit populations observed in Spain during the last half of the 20th century is due primarily to the outbreak of two viral diseases, myxomatosis and rabbit haemorrhagic disease (Cooke 2002; Virgos et al., 2007), although the decline cannot be attributed only to diseases. It may also have been caused by changes in rural environmental management, such as intensification in pasturelands and agricultural areas or cessation of production in mountain and forest areas (Delibes-Mateos et al., 2010), both linked to a high loss of structural environmental diversity (Pineda 2001). Changes in hunting management practices during recent decades have also had an influence, including an increase in game hunting, especially red deer and wild boar (Cabezas-Díaz et al., 2010; Herruzo and Martínez-Jáuregui, 2013), an intensification in game management (Beja et al., 2009), and, in many areas, absence of predator control (Banks 2000; Delibes-Mateos et al., 2008; Fernández de Simón, 2013).

Food quality and abundance controls wild rabbits' reproduction (De Blas, 1989; Gonçalves et al., 2002). Breeding season starts

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when rabbits consume more than a certain value of protein in their diet (De Blas, 1989). This high value of protein is found on certain food, such as green grasses or legumes (San Miguel, 2006). Therefore increasing availability of quality food may enhance rabbit reproduction index, thus aiding in population recovery (San Miguel, 2006).

To solve problems associated with reduced rabbit populations, many measures have been taken, in the framework of different conservation projects and strategies (Moreno et al., 2004; García 2005; San Miguel 2006) and hunting management strategies (Delibes-Mateos et al., 2008). One of the basic results obtained from programmes implemented to date is that, in order to enhance rabbit populations, environmental management is a crucial tool (San Miguel 2006; Delibes-Mateos et al., 2008; Godinho et al., 2013). Populations are favoured by different practices applied to their habitat (Ferreira et al., 2013), including firebreaks with sowing (Ferreira & Alves, 2009), burning of scrubland in order to promote pastures (Moreno & Villafuerte, 1995), provision of shelter with enclosures (Catalán et al., 2008), or shelter construction (Fernández-Olalla et al., 2010). One of the most frequently used measures to enhance populations of small game is sowing of food crops (Delibes-Mateos et al., 2008; Casas & Viñuela, 2010), which has seldom been considered as a management tool for the threatened predators (but see Guerrero-Casado et al., 2013). Previous studies have assessed how habitat selection by rabbits is affected by different types of crops in small experimental areas (Muñoz 2005). However, information on the use of dryland farming is still lacking.

The objective of this study was to evaluate the efficacy of cereal sowing for increasing density of wild rabbit populations. Our initial hypothesis was that this measure could be considered effective if rabbits preferred the sown areas. Thus, we first assessed whether rabbits select sown over control (unsown) areas. We then aimed to determine the characteristics of sowing that influenced a positive selection by rabbits. After the treatments were implemented, we evaluated whether differences in the evolution of the relative abundance of rabbits between treatment and control plots were evident.

Material and methods

Study area

The study was carried out in 14 private estates that are part of the Natura 2000 network in central Spain (Albacete, Cáceres, Ciudad Real, Jaén, and Toledo Provinces; Fig. 1). More precisely, the study plots were located in the following Sites of Scientific Interest (SCIs): *Rumblar, Guadalén y Guadalmena* basins (four estates), *Sierra Morena* (three estates), *Sierra del Relumbrar y las Estribaciones de Alcaraz* (five estates), *Montes de Toledo* (one estate), and *Sierra de San Pedro* (one estate). Some of these areas are also considered Special Protection Areas (SPAs).

From a biogeographical point of view, all sites are located in the western Iberian Mediterranean Province (Rivas-Martínez et al., 2004) and are characterized by acid lithology and nutrient-poor soils. The area has a meso-Mediterranean climate, with ombroclimate from dry to sub-moist, continental, with important year-to-year fluctuations, high summer droughts, and year to year rainfall variations (MMA 2002). As a result, most of the study area is covered by a mosaic of forest (mainly oak thickets in initial successional states, with rockrose *Cistus ladanifer* L. and *Cistus monspeliensis* L. dominated brush, therophytic herbaceous grasses, rocky areas, and thick bushes, viz. the so-called Mediterranean mancha).

The estates' main use is big game rearing, although most of them also secondarily raise livestock (González & San Miguel, 2005). In

most of the study area, rabbits have low or very low population numbers (Guzmán et al., 2004), similar to other protected areas (Delibes-Mateos et al., 2009).

Essay: Cereal sowing

In total, we sowed 125 plots, hereafter referred to as 'treatment plots'. In 44 plots, prior brush clearing was achieved by several cross-passes with a deep plough. Here, cereal sowing acts to reduce recolonization by thickets (Muslera & Ratera, 1993) and increases the availability of high-quality food (fodder during winter and spring, and grain in summer) for rabbits, big game, and livestock.

Cereals (barley and oat seed) were sown (150 kg ha^{-1}), no fertilizer was used, and only one estate was permanently closed to grazing. For sowing, we used a spinning compost machine and covering. Per estate, the number of treatment plots varied between 3 and 19 (mean $\pm \text{SD} = 8.93 \pm 6.04$), and plot surface area varied from 0.04 to 43.07 ha (mean $\pm \text{SD} = 2.55 \pm 5.54 \text{ ha}$). As a rule, plots were smaller than those generally used for livestock or big game (San Miguel 2006). When plot size exceeded 0.5 ha (67 plots), small thickets inside the sown plot tended to be left as rabbit shelters (at least 10 m^2 and representing at least 5% of the plot surface; these were provided in 53% of total plots and in the 60% of plots $>0.5 \text{ ha}$). For sowing, we avoided slopes exceeding 10%, and the shapes of the sown plots were adapted to the local topography. We preferred elongated forms in order to obtain a high perimeter/surface relationship. Sown plots were established in eight estates ($n=46$ plots) during summer 2004, six estates ($n=34$) in 2005, and six estates ($n=45$) in 2006.

Field data: Rabbit and treatment survey

To determine positive selection of treatment plots over control areas, we established transects to detect signs in both treated and control areas with similar ecological characteristics. Signs included the presence of latrines (Myktytowycz, 1968), defined as an accumulation of at least 20 excrements (Virgós et al., 2003), which are widely used in studies of habitat use (Palma et al., 1999; Virgós et al., 2003; Guzmán et al., 2004; Guerrero-Casado et al., 2013; but see Fernández de Simón et al., 2011). All latrines observed during transect surveys were counted. The distance covered along each transect was recorded to standardize effort. To maximize the probability of finding latrines, transects were established along the border of treatment areas (Moreno & Villafuerte, 1995). Transect length was adapted to the treatment area perimeter (mean $\pm \text{SD} = 0.39 \pm 0.35 \text{ km}$). Therefore, transect length increased with increasing treatment area perimeter, and we attempted to cover entire perimeters. Transects were also established in the control areas and covered a similar distance. Control transects were designed mainly through paths, as rabbits tend to mark on them (Monclús & De Miguel, 2003), and surveyed the most similar ecological conditions as its equivalent treatment transect. Treatment and control transects were designed to be spatially close, but with a separation between treatment and control with at least 200 m. We chose this distance because it is considered the longest distance traversed by rabbits on one day (Lombardi et al., 2003). Monitoring was done during late spring, when rabbit abundance and use of sowing are generally highest (Beltrán, 1991; Cacho et al., 2002).

In parallel with the treatment survey, wild rabbit abundance was surveyed at each estate, as this may influence the use of habitat and feed (Lombardi et al., 2003; Muñoz, 2005). For monitoring, we basically followed the method proposed by Palomares (2001). In each estate a net comprising several linear transects was established. The number of transects was not homogeneous between estates (2–15). The season chosen for the survey was late spring

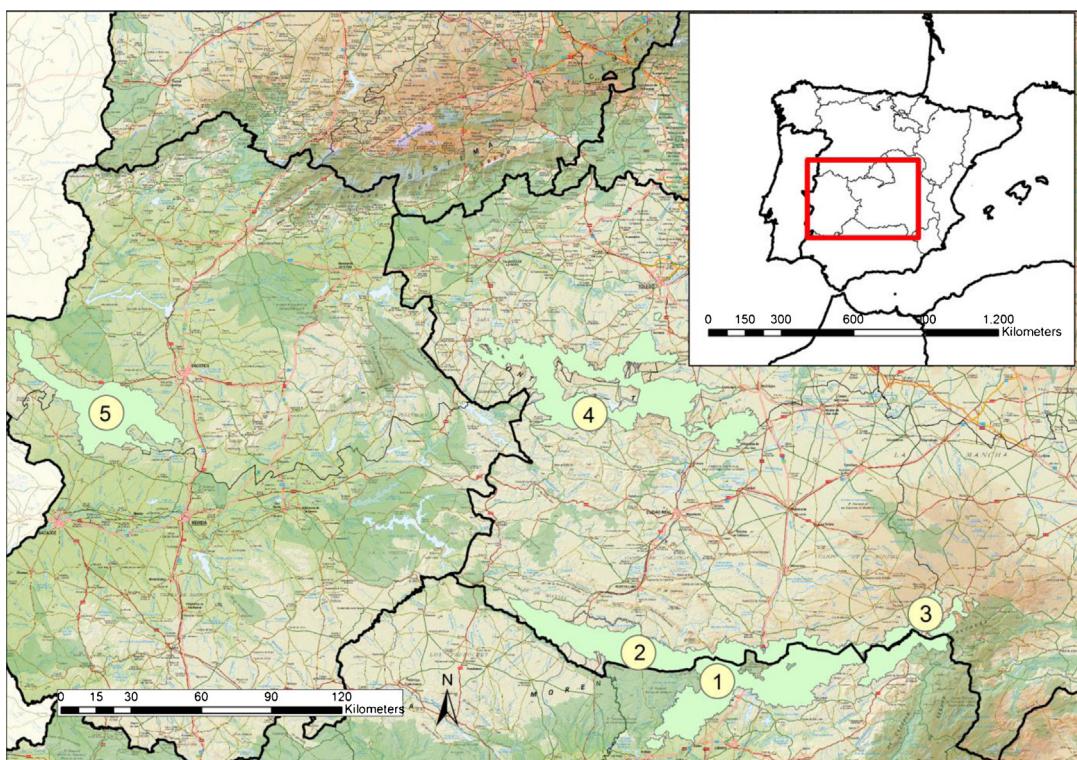


Fig. 1. Sites of scientific interest (SCIs) included in the study area. Number 1 corresponds to SCI *Cuenca del Rumbrar, Guadalén y Guadalmena*, no. 2 SCI and Special Protection Area (SPA) *Sierra Morena*, no. 3 SCI *Sierra del Relumbrar y las Esteraciones de Alcaraz*, no. 4 SCI and SPA *Montes de Toledo*, and no. 5 SCI and SPA *Sierra de San Pedro*.

and early summer, as this is considered the season of highest rabbit abundance (Beltrán, 1991). Transects were walked at dawn or dusk. Transect distance generally ranged between 1.5 and 2 km, and included all different habitats existing in the estate. Rabbits were counted along fixed 10-m strips. Sampling was repeated at least three times per season, and the sampling with the most rabbits observed was chosen for the analysis. Thus, we obtained a kilometric abundance index for each transect, i.e. the maximum number of rabbits per kilometre detected along the paths. For analytical purposes, we only considered the relative abundance of rabbits along the closest transect to the treatment plot. The remaining transects at each estate were used as controls. To select the transects, we used a space analysis with ArcGIS 9.2.

Statistical analysis

All statistical analyses were conducted in Statistica 7.0 and R.2.15.2 (R Development Core Team 2012) environments, with the standard probability ($p < 0.05$), and considering treatment plots as sample units. We used the Wilcoxon sign-rank test to analyse differences in the use of treated and control areas, based on the number of latrines found per kilometre (Quinn & Keough, 2002). All the results are presented as mean \pm SD.

To analyse sowing characteristics that enhanced the use of certain plots by rabbits, a general linear mixed-effect model was used for the dependent variable 'Selection of treatment plots'. This variable was implemented using the number of latrines per kilometre in control (C_{cont}) and treatment (C_{tre}) areas, and was defined as $C_{\text{tre}}/(C_{\text{tre}} + C_{\text{cont}})$ (Manly et al., 2002). As random independent variables, we included 'Year' (2004, 2005, and 2006) and location variables, which included the 'SCI' where treatments were implemented and 'Estate' as an expression of the total territory management unit. Thus Estate was a nested variable within SCI. The other fixed independent variables included in the model were

- **Treatment type:** categorical variable explaining the treatment type: only sowing or sowing with clearing.
- **Habitat:** categorical variable describing the habitat around the sown area. As a result of the influence of rabbit abundance, habitat was established at four different levels: grassy, cleared brush, dense thicket, and forest (Lombardi et al., 2003).
- **Shelter presence:** two levels were chosen, viz. '1' if natural bushes or artificial shelters were available inside a sown plot, and '0' if there were none.
- **Rabbit abundance:** covariate explaining rabbit abundance in the closest transect to the sown area, derived from the kilometric abundance index and expressed in rabbit km^{-1} .
- **Perimeter/surface relationship:** covariate defined by $r_{p-s} = p/(2\pi \times \sqrt{S/\pi})$ where p is the treatment perimeter, and S is its surface area. This relationship was used as an estimator of rabbit accessibility to the treatment area (Moreno & Villafuerte, 1995).

For this analysis, we excluded 23 values derived from plots with no latrines found neither in the treatment areas nor in control areas. We considered first-order interactions and simplified the models using parsimony principles (following Crawley 2007) until the best fitting model was reached. Akaike's Information Criterion was used to compare between models. We used the statistical 'nlme' package (Pinheiro et al., 2012), and 'lsmeans' package (Lenth, 2014) for post hoc Tukey tests (Crawley 2007). Spatial autocorrelation was discarded using Moran's I function in 'ape' package (Paradis et al., 2004).

To determine whether sowing had any influence on rabbit abundance, we used $r_{abun} = (Ab_{+1} - Ab_0)/Ab_0$ to characterize the variations in relative rabbit abundance, where Ab_0 is the relative rabbit abundance during spring, and Ab_{+1} is the relative rabbit abundance in the following year. We calculated this index in the closest transect to each sowing treatment and in control transects, viz. all the remaining transects in the estate where no treatment

Table 1

Main estimators of answer variable per estate, including number of treatment plot, evaluation year, and values of answer variable (including average latrine value per Km and SD) observed in treatment (treat) and control plots (cont).

Natura 2000 area	Estate	No. of plots	Evaluation year	$\bar{x} \pm SD$ treat (latrines/km)	$\bar{x} \pm SD$ cont (latrines/km)
Cuencas del Rumbler,	1	3	2004	9.7 ± 10.74	1.4 ± 2.43
Guadalén y	2	3	2004	20.28 ± 17.2	28.77 ± 38.76
Guadalmena	3	6	2006	78.3 ± 65.21	2 ± 0.56
	4	18	2004 and 2006	29.88 ± 35.39	1.64 ± 3.33
Sierra Morena	5	8	2004 and 2005	6.24 ± 7.08	2.03 ± 2.45
	6	19	2004 and 2005	117.4 ± 81.29	47.49 ± 40.25
	7	2	2005	5.33 ± 0.00	2.13 ± 0.77
Sierra del Relumbrar y	8	19	2004 and 2005	121.93 ± 108.18	53.95 ± 51.19
Estribaciones de	9	12	2006	25.38 ± 25.19	14.86 ± 19.87
Alcaraz	10	9	2006	3.57 ± 10.70	2.66 ± 5.30
	11	5	2006	38.53 ± 39.20	7 ± 14.19
	12	11	2004 and 2005	17.18 ± 22.50	7.74 ± 11.03
Montes de Toledo	13	6	2006	8.25 ± 7.99	0.7 ± 1.72
Sierra de San Pedro	14	4	2004 and 2005	3.07 ± 2.76	2.44 ± 2.38

was implemented. Plots with no rabbits detected during all years were not included in the present study. We analysed differences in r_{abun} between the closest transects to the treatment plots and control transects, i.e. the remaining transects in each estate. Differences were analysed using the Wilcoxon sign-rank test.

Results

Selective use of treatment areas by rabbits

When comparing latrines per kilometre in treatment versus control areas, we detected a higher use of treatment plots by rabbits ($n=46$; $Z=-7.135$; $p < 0.0001$). Treatment plots were used more than control plots in 85 plots as compared to 17 with lower use and 23 with the same level of use (in all of these latter cases, no latrines were found in treatments or in control plots). The average latrines per kilometre in treatment areas are 51.79 ± 73.64 , while in control areas is 19.32 ± 34.07 . More detailed information per estate is provided in Table 1. In all but one estate, the index of average latrines per kilometre was higher in treatment than in control areas.

Selected variables

The model selection procedure involved nine steps (see Table 2). Variables shown in Table 3 were selected for the final model. According to Tukey post hoc tests, there were differences for most of the habitats. There are differences between grassy and cleared brush ($p=0.0248$), dense thicket ($p=0.0001$), and forest ($p=0.001$) and between cleared brush and dense thicket ($p=0.0166$), but not between cleared brush and forest ($p=0.0634$) and between dense thicket and forest ($p=0.953$).

The highest values for the variable 'Selection of treatment plots' were recorded in plots surrounded by grassland (mean \pm SD = 0.832 ± 0.226), followed by plots surrounded

by cleared brush (0.757 ± 0.210), plots surrounded by forest (0.733 ± 0.210) and plots surrounded by dense thicket (0.616 ± 0.396).

Rabbit presence in sown surroundings

The mean (\pm SD) relative rabbit abundance was 1.33 ± 1.56 rabbits km^{-1} (max 9.3), in transects closest to treatment plots during the late spring–early summer, when these plots were surveyed. In control areas, the mean (\pm SD) relative abundance was 3.29 ± 4.23 . In the following year, mean (\pm SD) relative abundance was 1.99 ± 2.92 (max 13.3) and 2.99 ± 3.16 rabbits km^{-1} , respectively. After treatment, differences in r_{abun} between sowing and control transects were observed ($n=94$; $Z=3.527$; $p=0.00042$). A relative increase in the rabbit population was observed in the closest transect in 64 out of 94 plots, and a decrease in 30 plots.

Discussion

Several factors control rabbit population dynamics, including weather conditions (Bell & Webb, 1991), predators (Banks 2000), viral diseases (Calvete et al., 2002) and habitat (Lombardi et al., 2003), as well as interactions among these elements (Calvete 2006). Evaluating the effectiveness of treatments aimed at habitat enhancement thus becomes difficult. Studies validating the efficacy of rabbit management are scarce (San Miguel, 2006; Delibes-Mateos et al., 2008; Ferreira et al., 2013). Our results offer the first support for the use of cereal sowing to obtain a positively selected environment for wild rabbits, as has previously only been suggested (Martins et al., 2002; García 2005; San Miguel 2006; Ferreira et al., 2013). Our study evidences the positive influence of shelters and types of habitat on the level of selection. Our results suggest a statistically significant difference in rabbit abundance evolution in the surroundings of treated plots as compared to the rest of the estate.

Table 2

Model selection procedure. The best fit was determined according to the lowest Akaike's information criterion (AIC). ΔAIC , the difference in AIC from that of the best-fitting model; d.f., degrees of freedom; LL, log-likelihood ratio.

Step	Model steps	AIC	ΔAIC	d.f.	LL
0	Initial model, including all first order interactions	6.637	10.407	30	–
1	Deleting treatment type and shelter presence interaction	4.704	8.474	29	0.067
2	Deleting rabbit abundance and perimeter/surface relationship interaction	2.774	6.544	28	0.07
3	Deleting rabbit abundance and treatment type interaction	1.529	5.299	27	0.755
4	Deleting shelter presence and perimeter/surface relationship interaction	0.098	3.868	26	0.569
5	Deleting rabbit abundance and treatment type interaction	0.098	3.868	26	1
6	Deleting rabbit abundance and habitat interaction	-1.77	2.000	23	4.132
7	Deleting rabbit abundance and perimeter/surface relationship as covariates	-1.77	2.000	23	1
8	Deleting treatment type and habitat as fixed factors	-1.77	2.000	23	1
9	Deleting SCI as random factor	-3.77	0	22	0.0005

Table 3

Variables included in the final model with interactions, including type, degrees of freedom and statistical values; *for variables with more than one d.f. parameter estimates are provided as average \pm S.D.

Variable	Type	d.f.	p-Value	Parameter estimate*
Intercept	–	1	<0.001	0.453
Year	Random factor	–	–	–
Estate	Random factor	–	–	–
Shelter presence	Fixed factor	1	<0.001	0.146
Rabbit abundance \times shelter presence	Interaction	2	0.0004	0.01 \pm 0.04
Shelter presence \times habitat	Interaction	6	0.0578	0.04 \pm 0.62
Habitat \times treatment type	Interaction	4	0.1196	0.41 \pm 0.25
Habitat \times perimeter/surface relationship	Interaction	4	0.1151	0.13 \pm 0.32
Treatment type \times perimeter/surface relationship	Interaction	1	0.0015	–0.39

The ability of rabbits to select both feeding areas and types of food inside these areas has already been established (Soriguer 1987; Cacho et al., 2002; Muñoz 2005). Some studies have shown changes in rabbit diets in areas with access to sowing (Martins et al., 2002; Ferreira & Alves, 2009). Although according to this management evidence, rabbits select sown areas (Barrio et al., 2010), until now, the selection of sown areas has not been quantified and factors influencing this selection have not been described (but see Muñoz 2005). However, this study (Muñoz 2005) had several limitations, as it considered only limited sowing characteristics (i.e. sown species and densities) and was only developed within one estate.

(1) First, with regard to elements that influence habitat selection, it is important to highlight that our results may be both influenced by the characteristics of the implemented treatments and the survey design. Characteristics and implementation of the treatments were relatively homogeneous. We attempted to improve their effectiveness for rabbits, considering the a priori hypothesis that smaller treatment areas are better than larger areas, and that their efficacy in promoting rabbit populations increases with increased perimeter/surface relationship (Moreno & Villafuerte, 1995; Villafuerte et al., 2001; San Miguel 2006). Artificial shelters were built, both inside the sown plots and in the surrounding areas, for all sowing treatments regardless of their size. This may be the reason underlying the fact that the influence of morphological characteristics (perimeter/surface relationship) of treated plots was less important than expected (appeared only in interactions, in treatment \times perimeter/surface relationship and in habitat \times perimeter/surface relationship). Moreover, no direct differences were detected between treatment types (i.e. with or without clearing), probably because the treatments were very alike (Delibes-Mateos et al., 2008). Treatment type is included in the final model within the interaction factor treatment \times perimeter/surface relationship. We can consider there might be more adequate sizes for the different treatments, but this should be confirmed in further studies.

The survey design may have also influenced the results. Latrine surveys have been extensively used, but there might be several factors affecting latrines' distribution. There are social (Ruiz-Aizpurua et al., 2013), environmental and ecological factors affecting its distribution (Dominguez-Cebrian & De Miguel, 2013). Border latrine counts may not even be suitable for counting the highest pellet proportion (Moreno & Villafuerte, 1995). But border latrine counts in sown plots have several advantages: they can be done with independence of the sowing state of development, they can be easily repeated and are less time consuming than other techniques, such as pellet counts.

(2) Our first hypothesis was that sown areas with shelter, either thicket islands or artificial shelters, would be the most used, as these areas are considered the safest, combining thickets and sparsely covered sites (Moreno et al., 1996) as occur under natural conditions (Palomares et al., 2001). Our results support this hypothesis. For other taxa, e.g. birds, the existence of natural vegetation

elements is essential, mainly in agricultural areas (Vepsäläinen et al., 2005; Herzon & O'Hara, 2008).

(3) On the other hand, when the treatments were planned, we searched for areas with high-quality natural rabbit shelters in areas with scarce thickets (Beja et al., 2007), grasslands, or areas with granitic stones (Carvalho & Gomes, 2004). Despite our efforts, these requirements were not always fulfilled and some sowings were located in less favourable habitats. Our results highlight grasslands as the most favourable habitat for locating sowings for enhancing rabbits populations. This might be because of the presence of refuge, mainly scarce trees, shrubs and rocks (Gea-Izquierdo et al., 2006). The following habitats are clear brush and forest. The similar selection values between forest and cleared-brush plots may be due to the fact that in most of our cases, the existing forests were old abandoned pastures and brushwood now covered by sparse thickets (Plieninger 2006). Clear shrubs have been considered as one of the most favourable habitat for rabbits (Lombardi et al., 2003). According to our results, dense thickets are the less favourable areas for locating sown plots. This habitat has already been described as inappropriate for rabbits (Lombardi et al., 2003; Fernández 2005). Dense thicket might be selected as refuge for ungulates that are in competition with rabbits (Soriguer, 1987) or for rabbit predators (Cabezas-Díaz et al., 2010). Other habitats simultaneously provide shelter and extra feed to treatment areas (Moreno & Villafuerte, 1995; Lombardi et al., 2003; Cabezas & Moreno, 2007).

The differences between previous results and ours might be due to two factors: simplification and use. Simplification, because we have characterized each plot only with one habitat and most of the habitat selection studies have been developed through radio tracking (i.e. Lombardi et al., 2003), with a difference in resolution (Orrock et al., 2000). And use, because our results point out the most favourable area for locating sowings, not the most favourable area for rabbits. Therefore, when selecting areas for sowing, it is important to consider surrounding habitat (Fernández-Olalla et al., 2010) to cover all rabbit requirements.

Habitat has appeared in the final model within three interactions, the aforementioned habitat \times perimeter/surface relationship, in habitat \times treatment type and in shelter presence \times habitat. According to this results, we might conclude that habitat plays a major role. We have considered this aspect as a necessity of different treatments in each habitat to reach an ideal rabbit habitat (Lombardi et al., 2003; Fernández, 2005; Ferreira et al., 2013). So there might be more adequate treatments for the different habitats (i.e. sowings might be more usable in areas with lower food levels, such as forests, or vice versa). As for other interactions, further and wider studies might confirm this.

(4) Rabbit abundance did not have a strong influence on selection. Rabbit abundance has appeared in the final model within an interaction (rabbit abundance \times shelter presence). So, according to our results, in general, in areas with a low abundance of rabbits, the positive selection of treated areas by rabbits was relatively independent of their abundance. Even considering areas with very low rabbit abundance (<1 rabbit km^{-1}), rabbits chose treated areas. The

fact that rabbits respond to sowing is relatively independent of their abundance (in the range considered in this study) is a management opportunity (Catalán et al., 2008). In contrast, a high rabbit abundance may have a negative effect on the development of cereal sowing (due to the consumption of the first leaves, even the seed leaves; Muñoz 2005) and on other crops (such as vineyards; Barrio et al., 2010), with important social conflicts as a consequence.

(5) We found a significant difference in rabbit abundance evolution in the treated plots compared to the remaining plots in the estates, which is in contrast with other results. Delibes-Mateos et al. (2008) demonstrated in a large-scale and long-lasting study that no enhancement in rabbit populations occurred in sites where sowing was done as a means to enhance rabbit populations. However, we believe that the main reason for these opposing results is the difference in the scales used. Our results suggest positive population effects in areas surrounding sowing sites, but not in the rest of the estate. Three complementary hypotheses are considered as possible explanations for our results: (1) Rabbit abundance is directly determined by food (Villafuerte et al., 1997), i.e. when quality and quantity of food increase, rabbit populations increase (Cabezas & Moreno, 2007). (2) Cereal sowing allows reproductive improvement, thus surpassing predation effects (Trout & Tittensor, 1989; Banks 2000). (3) Establishment of an area with mixed shelter and feeding areas allows for higher rabbit abundance (Lombardi et al., 2003).

Conclusions

Threatened species depending on rabbit preservation, such as the Spanish imperial eagle or Iberian lynx, can be supported by habitat management measures such as cereal sowing, with or without prior clearing. However, according to our results, a posteriori rabbit abundances (average 1.3 rabbits km⁻¹ in the summer of the year when the sowing is implemented and 1.99 in the following year) are insufficient to sustain a reproductive female Iberian lynx in that area (minimum requirement is 4 rabbits ha⁻¹ during summer and 1 rabbit ha⁻¹ during autumn, Palomares et al., 2001). Palomares (2001), stated that 1 rabbit km⁻¹ is equivalent to 0.57 rabbit ha⁻¹. So, 1.99 rabbits km⁻¹ should be close to the requirements of the Spanish imperial eagle (1 rabbit ha⁻¹; Margalida et al., 2007). Considering that rabbit abundance apparently has no direct influence on the positive selection of sown areas, we can assume that activities such as cereal sowing can favour rabbits, even in cases of low abundance, similar to other practices (Catalán et al., 2008; Sarmento et al., 2011). As measures that can easily be included in agri-environment programmes, we suggest a high perimeter/surface relationship and the presence of natural thicket islands and shelters or construction of artificial shelters. Such treatments, accompanied by other practices such as feed supplementation can help in the recovery of rabbit populations in Mediterranean areas (Catalán et al., 2008; Delibes-Mateos et al., 2008; Fernández-Olalla et al., 2010).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.jnc.2014.08.011>.

References

- Banks, P. B. (2000). Can foxes regulate rabbit populations? *Journal of Wildlife Management*, 64, 639–648.
- Barrio, I. C., Bueno, C. G., & Tortosa, F. S. (2010). Alternative food and rabbit damage in vineyards of southern Spain. *Agriculture, Ecosystems and Environment*, 138(1–2), 51–54.
- Beja, P., Pais, M., & Palma, L. (2007). Rabbit *Oryctolagus cuniculus* habitats in Mediterranean scrubland: The role of scrub structure and composition. *Wildlife Biology*, 13, 28–37.
- Beja, P., Gordinho, L., Reino, L., Loureiro, F., Santos-Reis, M., & Borralho, R. (2009). Predator abundance in relation to small game management in southern Portugal: Conservation implications. *European Journal of Wildlife Research*, 55, 227–238.
- Bell, D. J., & Webb, N. J. (1991). Effects of climate on reproduction in the European wild rabbit (*Oryctolagus cuniculus*). *Journal of Zoology*, 224(4), 639–648.
- Beltrán, J. F. (1991). Temporal abundance pattern of the wild rabbit in Doñana, SW Spain. *Mammalia*, 55, 591–599.
- Cabezas, S., & Moreno, S. (2007). An experimental study of translocation success and habitat improvement in wild rabbits. *Animal Conservation*, 10, 340–348.
- Cabezas-Díaz, S., Virgos, E., Mangas, J. G., & Lozano, J. (2010). The presence of a competitor pit effect compromises wild rabbit (*Oryctolagus cuniculus*) conservation. *Animal Biology*, 61(3), 319–334.
- Cabral, M. J., Almeida, J., Almeida, P. R., Dellinger, T., Ferrand, N., & Oliveira, M. E., et al. (Eds.). (2006). *Livro Vermelho dos Vertebrados de Portugal*. Lisboa: Instituto da Conservação da Natureza.
- Cacho, C., Muñoz, J., Guil, F., & San Miguel, A. (2002). Selección y utilización de pastos sembrados por una población de conejos de los Montes de Toledo. In A. B. Robles (Ed.), *Pastos, desarrollo y conservación* (pp. 525–530). Granada: SEEP-Junta de Andalucía.
- Calvete, C. (2006). Modelling the effect of population dynamics on the impact of rabbit hemorrhagic disease. *Conservation Biology*, 20(4), 1232–1241.
- Calvete, C., Estrada, R., Villafuerte, R., Osacar, J. J., & Lucientes, J. (2002). Epidemiology of viral haemorrhagic disease and myxomatosis in a free-living population of wild rabbits. *Veterinary Record*, 150, 776–782.
- Carvalho, J. C., & Gomes, P. (2004). Influence of herbaceous cover, shelter and land cover structure on wild rabbit abundance in NW Portugal. *Acta Theriologica*, 49(1), 63–74.
- Casas, F., & Viñuela, J. (2010). Agricultural practices or game management: Which is the key to improve red-legged partridge nesting success in agricultural landscapes? *Environmental Conservation*, 37(2), 177–186.
- Catalán, I., Rodríguez-Hidalgo, P., & Tortosa, F. S. (2008). Is habitat management an effective tool for wild rabbit (*Oryctolagus cuniculus*) population reinforcement? *European Journal of Wildlife Research*, 54(3), 449–453.
- Cooke, B. D. (2002). Rabbit haemorrhagic disease: Field epidemiology and the management of wild rabbit populations. *Revue Scientifique et Technique—Office International des Epizooties*, 21(2), 347–358.
- Crawley, M. J. (2007). *The R book*. Chichester: Wiley and Sons.
- De Blas, C. (1989). *Alimentación del conejo*. Madrid: Ediciones Mundi-Prensa.
- Delibes-Mateos, M., Redpath, S. M., Angulo, E., Ferreras, P., & Villafuerte, R. (2007). Rabbits as a keystone species in southern Europe. *Biological Conservation*, 131(1), 146–159.
- Delibes-Mateos, M., Ferreras, P., & Villafuerte, R. (2008). Rabbit populations and game management: The situation after 15 years of rabbit hemorrhagic disease in central-western Spain. *Biodiversity and Conservation*, 17, 559–574.
- Delibes-Mateos, M., Ferreras, P., & Villafuerte, R. (2009). Rabbit (*Oryctolagus cuniculus*) abundance and protected areas in central-southern Spain: Why they do not match? *European Journal of Wildlife Research*, 55(1), 65–69.
- Delibes-Mateos, M., Farfán, M. A., Olivero, J., & Vargas, J. M. (2010). Land-use changes as a critical factor for long-term wild rabbit conservation in the Iberian Peninsula. *Environmental Conservation*, 37(2), 169–176.
- Dominguez-Cebrian, I., & De Miguel, F. J. (2013). Selected factors influencing the spatial relationship between latrines and burrows in rabbits *Oryctolagus cuniculus* (L.) in a suburban area of Madrid (Spain). *Polish Journal of Ecology*, 61(4), 819–823.

- Fernández, N. (2005). Spatial patterns in European rabbit abundance after a population collapse. *Landscape Ecology*, 20(8), 897–910.
- Fernández de Simón, J., Díaz-Ruiz, F., Cirilli, F., Sánchez-Tortosa, F., Villafuerte, R., Delibes-Mateos, M., et al. (2011). Towards a standardized index of European rabbit abundance in Iberian Mediterranean habitats. *European Journal of Wildlife Research*, 57(5), 1091–1100.
- Fernández de Simón, J. (2013). Predation and the recovery of European rabbit populations in central-southern Iberian Peninsula. In *An assessment of the predator pit hypothesis*. Universidad de Castilla-La Mancha (Ph.D. thesis).
- Fernández-Olalla, M., Martínez-Jauregui, M., Guil, F., & San Miguel, A. (2010). Provision of artificial warrens as a means to enhance native wild rabbit populations: What type of warrens and where should they be sited? *European Journal of Wildlife Research*, 56(6), 829–837.
- Ferreira, C., & Alves, P. C. (2009). Influence of habitat management on the abundance and diet of wild rabbit (*Oryctolagus cuniculus algirus*) populations in Mediterranean ecosystems. *European Journal of Wildlife Research*, 55(5), 487–496.
- Ferreira, C., Touza, J., Rouco, C., Díaz-Ruiz, F., Fernández-de-Simón, J., Ríos-Saldaña, C. A., et al. (2013). Habitat management as a generalized tool to boost European rabbit (*Oryctolagus cuniculus*) populations in the Iberian Peninsula: A cost-effectiveness analysis. *Mammal Review*, 44(1), 30–43.
- Ferrer, M., & Negro, J. J. (2004). The near extinction of two large European predators: Super specialists pay a price. *Conservation Biology*, 18(2), 344–349.
- García, J. F. (2005). *Manual técnico para el fomento de las poblaciones de conejo. Informe interno*. Madrid: Dirección General para la Biodiversidad. Ministerio de Medio Ambiente.
- Gea-Izquierdo, G., Muñoz-Igualada, J., & San Miguel-Ayanz, A. (2006). Rabbit Warren distribution in relation to pasture communities in Mediterranean habitats: Consequences for management of rabbit populations. *Wildlife Research*, 32(8), 723–731.
- Godinho, S., Mestre, F., Ferreira, J. P., Machado, R., & Santos, P. (2013). Effectiveness of habitat management in the recovery of low-density populations of wild rabbit. *European Journal of Wildlife Research*, 59, 847–858.
- Gonçalves, H., Alves, P. C., & Rocha, A. (2002). Seasonal variation in the reproductive activity of the wild rabbit (*Oryctolagus cuniculus algirus*) in a Mediterranean ecosystem. *Wildlife Research*, 29(2), 165–173.
- González, L. M., & San Miguel, A. (2005). *Manual de buenas prácticas de gestión en fincas de monte mediterráneo de la Red Natura 2000*. Madrid: Organismo Autónomo Parques Nacionales.
- Guerrero-Casado, J., Carpio, A. J., Ruiz-Aizpurua, L., & Tortosa, F. S. (2013). Restocking a keystone species in a biodiversity hotspot: Recovering the European rabbit on a landscape scale. *Journal for Nature Conservation*, 21(6), 444–448.
- Guzmán, J. N., García, J. F., Garrote, G., Pérez de Ayala, R., & Iglesias, C. (2004). *El lince ibérico (Lynx pardinus) en España y Portugal: Censo-diagnóstico de sus poblaciones*. Madrid: Organismo Autónomo Parques Nacionales.
- Herzon, I., & O'Hara, R. B. (2008). Effects of landscape complexity on farmland birds in the Baltic States. *Agriculture, Ecosystems and Environment*, 118(1–4), 296–307.
- Herrero, A. C., & Martínez-Jauregui, M. (2013). Trends in hunters, hunting grounds and big game harvest in Spain. *Forest Systems*, 22(1), 114–122.
- Lenth, R. V. (2014). *lsmeans: Least-squares means. R package version 2.05*. Available at <http://cran.r-project.org/package=lsmeans>. Accessed 2014 June 6.
- Life Programme. (2011). *Project database*. Life Programme. Available at <http://ec.europa.eu/environment/life/project/Projects/index.cfm>.
- Lombardi, L., Fernandez, N., Moreno, S., & Villafuerte, R. (2003). Habitat-related differences in rabbit (*Oryctolagus cuniculus*) abundance, distribution, and activity. *Journal of Mammalogy*, 84(1), 26–36.
- MAGRAMA. (2014). *2012 Spanish national annual forestry and game statistics*. MAGRAMA. Available at http://www.magrama.gob.es/es/biodiversidad/estadisticas/forestal_anuarios.todos.aspx (Last accessed on 08-08-2014).
- Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., & Erickson, W. E. (2002). *Resource selection by animals: Statistical design and analysis for field studies* (2nd ed.). London: Chapman and Hall.
- Margalida, A., González, L. M., Sanchez, R., Oriá, J., Prada, L., Caldera, J., et al. (2007). A long-term large-scale study of the breeding biology of the Spanish imperial eagle (*Aquila adalberti*). *Journal of Ornithology*, 148, 309–322.
- Martins, H., Milne, J. A., & Rego, F. (2002). Seasonal and spatial variation in the diet of the wild rabbit (*Oryctolagus cuniculus* L.) in Portugal. *Journal of Zoology*, 258(3), 395–404.
- MMA. (2002). *Valores normales y estadísticos de observatorios meteorológicos principales (1971–2000)* (vol. 5) Madrid: Ministerio de Medio Ambiente (Andalucía y Melilla).
- Moleón, M., Sánchez-Zapata, J. A., Real, J., García-Charton, J. A., Gil-Sánchez, J. M., Palma, L., et al. (2009). Large-scale spatio-temporal shifts in the diet of a predator mediated by an emerging infectious disease of its main prey. *Journal of Biogeography*, 36(8), 1502–1515.
- Monclús, R., & De Miguel, F. J. (2003). Distribución espacial de las letrinas de conejo (*Oryctolagus cuniculus*) en el monte Valdelatas (Madrid). *Galemys*, 15, 157–165.
- Moreno, S., & Villafuerte, R. (1995). Traditional management of scrubland for the conservation of rabbits *Oryctolagus cuniculus* and their predators in Doñana National Park, Spain. *Biological Conservation*, 73(1), 81–85.
- Moreno, S., Delibes, M., & Villafuerte, R. (1996). Cover is safe during the day but dangerous at night: The use of vegetation by European wild rabbits. *Canadian Journal of Zoology*, 74(9), 1656–1660.
- Moreno, S., Villafuerte, R., Cabezas, S., & Lombardi, L. (2004). Wild rabbit restocking for predator conservation in Spain. *Biological Conservation*, 118, 183–193.
- Muñoz, J. (2005). *Fomento del conejo de monte (*Oryctolagus cuniculus* L.) en ecosistemas mediterráneos de suelos ácidos: Ecología de madrigueras, selección y utilización de pastos y repoblaciones con conejos*. Madrid: Universidad Politécnica de Madrid (Ph.D. thesis).
- Muslera, E., & Ratera, C. (1993). *Praderas y forrajes*. Madrid: Ediciones Mundi-Prensa.
- Mykytowycz, R. (1968). Territorial marking by rabbits. *Scientific American*, 218(5), 116–126.
- Orrock, J. L., Pagels, J. F., McShea, W. J., & Harper, E. K. (2000). Predicting presence and abundance of a small mammal species: The effect of scale and resolution. *Ecological Applications*, 10(5), 1356–1366.
- Palma, L., Beja, P., & Rodrigues, M. (1999). The use of sightseeing data to analyse Iberian lynx habitat and distribution. *Journal of Applied Ecology*, 36(5), 812–824.
- Palomares, F. (2001). Comparison of 3 methods to estimate rabbit abundance in a Mediterranean environment. *Wildlife Society Bulletin*, 29(2), 578–585.
- Palomares, F., Delibes, M., Revilla, E., Calzada, J., & Fedriani, J. M. (2001). Spatial ecology of Iberian lynx and abundance of European rabbits in Southwestern Spain. *Wildlife Monographs*, 148, 1–34.
- Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20(2), 289–290.
- Pineda, F. D. (2001). Intensification, rural abandonment and nature conservation in Spain. In R. G. H. Bunce, M. Pérez-Soba, B. S. Elbersen, M. J. Prados, E. Andersen, & M. Bell, et al. (Eds.), *Examples of European agri-environment schemes and livestock systems and their influence on Spanish cultural landscapes*, Alterra-rapport No. 309 (pp. 23–46). Alterra: Wageningen.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Development Core Team. (2012). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-117. Available at <http://CRAN.R-project.org/package=nlme>. Accessed 2014 June 6.
- Plieninger, T. (2006). Habitat loss, fragmentation, and alteration—Quantifying the impact of land-use changes on a Spanish dehesa landscape by use of aerial photography and GIS. *Landscape Ecology*, 21, 91–105.
- Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. New York, NY: Cambridge University Press.
- R Development Core Team. (2012). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Rivas-Martínez, S., Penas, A., & Díaz, T. E. (2004). *Bioclimátic map of Europe*. Available at <http://www.globalbioclimatics.org>.
- Ruiz-Aizpurua, L., Planillo, A., Carpio, A. J., Guerrero-Casado, J., & Tortosa, F. S. (2013). The use of faecal markers for the delimitation of the European rabbit's social territories (*Oryctolagus cuniculus* L.). *Acta Ethologica*, 16(3), 157–162.
- San Miguel, A. (2006). *Manual de gestión del hábitat del lince ibérico (Lynx pardinus Temminck) y de su presa principal, el conejo de monte (Oryctolagus cuniculus L.)*. Madrid: Fundación CBD-BHabitat.
- Sarmiento, P., Cruz, J., Paula, A., Eira, C., Capinha, M., Ambrosio, I., et al. (2011). Occupancy, colonization and extinction patterns of rabbit populations: Implications for Iberian lynx conservation. *European Journal of Wildlife Research*, 58(3), 523–533.
- Smith, A. T., & Boyer, A. F. (2008). *Oryctolagus cuniculus*. IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. Available at <http://www.iucnredlist.org/details/41291/0>.
- Soriguer, R. C. (1987). Alimentación del conejo (*Oryctolagus cuniculus* L. 1758) en Doñana, SO, España. *Doñana Acta Vertebrata*, 15(1), 141–150.
- Trout, R. C., & Tittensor, A. M. (1989). Can predators regulate wild rabbit (*Oryctolagus cuniculus*) population density in England and Wales? *Mammal Review*, 19(4), 153–173.
- Vepsäläinen, V., Pakkala, T., Piha, M., & Tiainen, J. (2005). Population crash of the ortolan bunting *Emberiza hortulana* in agricultural landscapes of southern Finland. *Annales Zoologici Fennici*, 42(2), 91–107.
- Villafuerte, R., Lazo, A., & Moreno, S. (1997). Influence of food abundance and quality on rabbit fluctuations: Conservation and management implications in Doñana National Park (SW Spain). *Revue d'écologie*, 52(4), 345–356.
- Villafuerte, R., Calvete, C., Angulo, E., Moreno, S., de la Puente, A., & Branco, M. S. (2001). Análisis de la efectividad de las repoblaciones de conejo y otras medidas de gestión en el Parque Nacional de Doñana. Inedit report. IREC-CSIC-UCLM-JCCM.
- Villafuerte, R., & Delibes-Mateos, M. (2007). *Oryctolagus cuniculus Linnaeus, 1758. In L. J. Palomo, J. Gisbert, & J. C. Blanco (Eds.), Atlas y Libro Rojo de los Mamíferos Terrestres de España* (pp. 487–491). Madrid: Dirección General para la Biodiversidad-SECEM-SECEMU.
- Virgos, E., Cabezas, S., Malo, A., Lozano, J., & López-Huertas, D. (2003). Factors shaping European rabbit abundance in continuous and fragmented populations of central Spain. *Acta Theriologica*, 48(1), 113–122.
- Virgos, E., Cabezas-Díaz, S., Malo, A., & Lozano, J. (2007). Is the endemic wild rabbit (*Oryctolagus cuniculus*) an endangered species in Spain? Sociological constraints in the conservation of species. *Biodiversity and Conservation*, 16(12), 3489–3504.