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Free housing for declining populations: optimizing the provision of artificial breeding structures.

Short title: **Artificial warren effectiveness for wild rabbits.**

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Abstract:

The improvement of habitat quality and reproductive success through the implementation of artificial breeding structures is one of the most widespread *in situ* conservation strategies applied to the recovery of declining wildlife populations. Several past studies have monitored the use of artificial breeding structures in the wild, but virtually none of them have investigated which demographic and environmental factors actually determine their effectiveness in facilitating reproductive success. Therefore, the aim of the present study was to identify those factors influencing breeding success in artificial structures. With this purpose we surveyed a declining population of a keystone species of Mediterranean ecosystems, namely the European wild rabbit. In Doñana National Park, we sampled during the course of two years the breeding success of wild rabbits from 47 artificial warrens, experimentally provided under different

demographic and environmental conditions. In order to determine the relative importance of such factors, we applied an AIC model selection procedure to alternative biological hypothesis groups, postulating that breeding success in artificial structures would primarily depend on population density, food availability and/or predator limitation. We found that the efficiency of artificial warrens in facilitating rabbit reproductive success can vary, with an increase associated with greater pasture availability. Predator limitation by fencing also positively affected rabbit reproduction, but only in combination with high pasture availability. On their own, fencing treatment and population reinforcements had low and null effectiveness facilitating reproduction, respectively, as well as entailing significant economic and biological costs. The best way to improve breeding success in artificial structures, therefore, was through their strategic placement in potential high-quality habitats, *i.e.* with suitable pasture availability. We suggest that vegetation management can effectively increase carrying capacity and consequently the target species' reproductive success, especially in fast breeding species like the European wild rabbit. The provision of artificial breeding structures for conservation purposes may significantly benefit from the elaboration of concurrent experimental studies similar to the present research, which can help establish useful guidelines for optimizing future conservation efforts.

Keywords

Artificial warrens; reproduction; European wild rabbit *Oryctolagus cuniculus*; habitat management; food availability; predator limitation by fencing; restockings.

Introduction

Anthropogenic changes are negatively affecting all existing ecosystems as well as most animal species, including abundant ones (Vitousek et al., 1997; Gaston and Fuller, 2008). In order to mitigate population declines, researchers and wildlife managers are working on the development and application of different *in-situ* and *ex-situ* conservation actions (Soulé et al., 1986; Balmford et al., 1995). Some of these strategies entail environmental modifications, with the aim of improving or restoring habitat quality for concerned species (*e.g.* vegetation management, supplementary provision of drinking troughs and resting

sites: Smallidge and Leopold, 1997; Epaphras et al., 2008; Polo-Cavia et al., 2010). In this context, one widespread measure has been the installation of artificial structures across natural areas to provide wild species with additional breeding and shelter sites (Bolton et al., 2004; Lindenmayer et al., 2009).

Artificial breeding structures have long been used with several different *taxa*, from the well-known bird nest-boxes to artificial burrows for reptiles or mammals (Stamp et al., 2002; Souter et al., 2004; Catalán et al., 2008). Their primary purpose is to compensate for the loss of natural shelters and the subsequent high offspring mortality suffered by target species (Møller, 1989; Fargallo et al., 2001). In some cases, these structures have successfully increased reproductive success and recruitment (Griffith et al., 2008; Libois et al., 2012); however their efficiency might highly depend on local demographic and environmental characteristics. Indeed, several factors such as population density, stress conditions, food availability and young predation are likely to modulate breeding success (Tapper et al., 1996; Siikamäki, 1998; DeMaso et al., 2013), and consequently the effectiveness of artificial structures for reproduction. Therefore, in order to optimize habitat management and conservation efforts, the identification of suitable locations for the installation of artificial breeding structures is of paramount importance. Nevertheless, no previous research has examined this issue, and for this reason the main purpose of the present study is to investigate the demographic and environmental factors which determine reproductive success in artificial structures. More specifically we focus on the relative roles of site-specific population density, food availability and predation risk.

Given this objective, we used as a study model the provision of artificial warrens for the conservation of the European wild rabbit *Oryctolagus cuniculus* Linnaeus, 1758, in southern Spain. This is a keystone species in Mediterranean ecosystems of south-western Europe, where it is the essential prey for the endangered Iberian lynx *Lynx pardinus* Temminck, 1827 and Iberian imperial eagle *Aquila adalberti* Brehm, 1861 (Delibes-Mateos et al., 2007). The wild rabbit is an ecosystem engineer (Gómez-Sal et al., 1999; Gálvez-Bravo et al., 2009) and one of the most harvested game species within its original distribution range, where hunting has great socio-economic importance (Villafuerte et al., 1998; Letty et al., 2008). Indigenous rabbit populations have severely declined in the last 50 years, mainly due to new epizootics (myxomatosis and rabbit hemorrhagic disease; Virgós et al., 2007); although the modification

of landscape use (Letty et al., 2008) and climate change (Tablado and Revilla, 2012) are also contributing factors. Today, hunters and wildlife managers are working to reverse this decline, usually by trying to increase rabbit abundance, either directly via restockings (Calvete et al., 1997; Moreno et al., 2004) or indirectly through the improvement of survival and reproduction (Moreno and Villafuerte, 1995; Ferreira et al., 2009). The provision of artificial warrens is the oldest and most commonly used practice which attempts to enhance rabbit breeding success and recruitment (Thompson and King, 1994) through the increase of reproduction site availability and the limitation of kitten mortality (Fernández-Olalla et al., 2010; Rouco et al., 2011). Nevertheless, there are still no studies which try to identify the demographic and environmental variables affecting rabbit reproductive success in artificial warrens. Therefore, we applied a model selection procedure to alternative biological hypotheses, in order to verify the relative importance of the factors determining the efficiency of artificial warrens as breeding sites.

The first hypothesis incorporated only the month and year of the surveys (the null model) given that wild rabbit breeding success can present intrinsic temporal variation (Tablado et al., 2009). The second hypothesis suggests that reproductive success in artificial warrens will be positively related to the density of potential breeders, as is the case in natural burrows (Villafuerte et al., 1997; Moreno et al., 2004). Alternatively, a negative density-dependent effect corresponding to extremely high population abundance may also be possible (Myers and Poole, 1962; Rödel et al., 2004). Moreover, wild rabbit restocking (independently or interacting with density) can negatively affect breeding success since the sudden intrusion of foreign potential breeders can disrupt the previously established social structure (Cowan and Garson, 1985; Moreno et al., 2004).

According to the third hypothesis, reproduction success within artificial warrens will be primarily related to food availability, either alone or in combination with density and restocking. Pasture availability improves several rabbit reproductive parameters (Poole, 1960; Tablado et al., 2009) and it can limit kitten malnutrition mortality (Stodart and Myers, 1966; Rödel et al., 2009), and as a result the effectiveness of artificial warrens may strongly depend on their access to green pastures.

116 The fourth hypothesis postulates that wild rabbit breeding success in artificial warrens will mainly depend
 117 on predator pressure, again in combination with density and restocking. Predation is often managed by
 118 exclusion fencing (Calvete and Estrada, 2004; Cabezas et al., 2011), which attempts to limit access to
 119 carnivore species actively feeding on breeders, newborns and juveniles. Furthermore, predator presence
 120 intrinsically increases breeder stress levels (Monclús et al., 2005, 2009), thus reducing their fecundity
 121 (von Holst, 1998). Finally, we also included a group of models which test different combinations of the
 122 above hypotheses, including the full model.

123

124 The identification of the demographic and environmental factors affecting rabbit breeding success in
 125 artificial warrens would provide the information necessary to strategically place these structures in the
 126 wild, in order to optimize their use. Moreover, the present case study could also provide an example
 127 applicable to declining populations of other species, with the aim of improving a frequently implemented
 128 conservation practice: the provision of artificial breeding structures.

129

130 **Materials and methods**

131

132 *Study area*

133

134 This study was carried out within the Doñana Biological Reserve (DBR, south-western Spain: 36°59' N,
 135 6°26' W), an area of approximately 7000 ha localized within the Doñana National Park (DNP; Fig. 1).

136 Climate in the area is Mediterranean sub-humid with Atlantic influence.

137

138 Wild rabbits are present predominately in the Mediterranean scrubland ecosystem, positively related with
 139 pasture availability, which is greater close to wetlands (*i.e.* marshlands and lagoons; Palomares et al.,
 140 2001; Fig. 1). Within our study area there was a wide-scale management project with the aim of
 141 recovering the wild rabbit populations of the DBR (Román et al., 2006; Palomares et al., 2007). This
 142 project was focused on two experimental zones denominated *Vera* and *Lagunas* (each of them 600 ha;
 143 Fig. 1).

144

145 *Warren building and experimental treatments*

146

147 Within the *Vera* and *Lagunas* zones the above mentioned conservation project established 24 and 18 five-
 148 ha experimental sites, respectively (Román et al., 2006; Palomares et al., 2007; in the present study we
 149 only surveyed 8 experimental sites per zone, see below in *Data collection*). Every experimental site was
 150 provided with five artificial warrens, each consisting of a two-floor wooden structure (15 m x 3 m x 1 m)
 151 with 30 entrances and covered with a metallic net, ground cloth and sand (Román et al., 2006; Palomares
 152 et al., 2007).

153

154 Just prior to the present study, DBR wild rabbit populations had extremely low densities (0.01-0.03
 155 individual per ha; Palomares, 2004). Therefore, both experimental zones were restocked prior to the wild
 156 rabbit breeding season (*i.e.* mainly during the months of October and November; 2004 for *Vera* and 2005
 157 for *Lagunas*; Appendix 1), with the aim of minimizing social structure disruptions (Moreno et al., 2004).

158

159 The wild rabbit sex ratio in natural populations tends to be balanced (*i.e.* 1:1; Villafuerte, 1994; von Holst
 160 et al., 2002); nevertheless, this is a polygynous species and with the aim to optimize the probabilities of
 161 reproduction we released 2-3 females for each introduced male. The applied restocking density varied
 162 depending on experimental site location (for more details see Fig. 1 and Appendix 2). Within all the
 163 experimental sites, scrubland management was carried out to increase pasture availability (Moreno and
 164 Villafuerte, 1995; López-Albacete et al., 2003).

165

166 Half of the experimental sites in both *Vera* and *Lagunas* zones were fenced (Fig. 1) in order to limit the
 167 access of wild rabbit terrestrial generalist predators (*e.g.* red fox *Vulpes vulpes*, large grey mongoose
 168 *Herpestes ichneumon* and European badger *Meles meles*). Fences comprised a 2 m tall metallic net, which
 169 extended 0.5 m underground (more details in Román et al., 2006). Other studies conducted in these
 170 experimental sites have demonstrated the effectiveness of this fencing treatment in reducing the access of
 171 terrestrial generalist carnivores (Martínez-Fontúrbel, 2008; Monclús et al., 2009).

172

173 *Data collection*

174

175 During the spring (2005 and 2006 for *Vera*, and 2006 for *Lagunas*; Appendix 1) we surveyed rabbit
 176 reproductive success through spotting-scope observations of kittens in focal artificial warrens. We
 177 sampled in the spring because it is the main rabbit breeding season in our study area (Delibes and
 178 Calderón, 1979; Villafuerte, 1994). We surveyed 16 experimental sites, eight within both the *Vera* (27
 179 focal warrens) and *Lagunas* (20 focal warrens) zones. Experimental sites and also artificial warrens with
 180 different environmental features (pasture availability) and treatments (fencing and release densities) were
 181 equally sampled (Fig. 1).

182

183 We surveyed one experimental site per day, without overlapping between observation rounds. We define
 184 an observation round as the survey of all the experimental sites. The survey was carried out during the last
 185 60 minutes of daylight, since the probability of detecting rabbit activity is greatest at dusk (Villafuerte et
 186 al., 1993). In each spotting session we observed all visible artificial warrens (ranging from two to five),
 187 scanning each one of them consecutively every two minutes. We conducted the same number of
 188 observations for every surveyed warren. For each observation, we recorded the maximum number of
 189 kittens detected simultaneously within two meters of the artificial breeding structure, given that their
 190 movements are usually limited to the vicinity of the warren (Parer and Wood, 1986; Kolb, 1991).

191

192 In order to obtain the density of potential breeders of every experimental site, we firstly estimated the
 193 site-specific autumnal rabbit density. To this end, prior to the wild rabbit breeding season (*i.e.* mainly
 194 during the months of September and October; 2004 and 2005 for *Vera*, and 2005 for *Lagunas*; Appendix
 195 1) we conducted a pellet count (a modification of the method described by Palomares, 2001; Appendix 2)
 196 in 25 one-meter-diameter circular sampling plots distributed according to a regular grid within each
 197 experimental site. The autumnal rabbit density of every experimental site should be added to the site-
 198 specific release density (respectively 10 and 0 rabbits per hectare for *Vera* in 2004 and 2005; and 19, 13,
 199 5 or 0 for *Lagunas* in 2005), with the aim to obtain the site-specific rabbit density at the time of release.
 200 Nevertheless, wild rabbit restockings are characterized by high short-term mortality (Calvete et al., 1997;
 201 Moreno et al., 2004). For this reason, the site-specific rabbit density at the time of release must be
 202 corrected for the short-term mortality. We therefore deducted the zone average short-term mortality rates

(Appendix 2 and 3) from the site-specific release densities, and the resulting values have been then added to the site-specific autumnal density, yielding the density of potential breeders of every experimental site (Table 1). The short-term mortality rate was obtained by daily radio-tracking of 101 translocated rabbits equally distributed along the environmental gradients and applied treatments of both *Vera* and *Lagunas* zones (Appendix 3).

To estimate pasture availability (which usually improves rabbit breeding success: Poole, 1960; Rödel et al., 2009; Tablado et al., 2009), we surveyed the same grid used for pellet counts. In the same set of one-meter-diameter circular sampling plots of the above described survey, we also estimated the mean percentage of green grass (*Graminae*). Utilizing these values we then calculated the mean percentage of green grass for every experimental site (Table 1).

Statistical analysis

With the aim of determining the best conditions to improve artificial warren effectiveness in facilitating rabbit breeding success, we carried out an Akaike information criterion (AIC) model selection (Burnham and Anderson, 2002) based on the comparison of generalized linear mixed models (GLMMs hereafter).

For each GLMM, the response variable was the *number of detected kittens per sampled artificial warren and observation*. We applied a Poisson error distribution and log-link function for every fitted GLMM. Two explanatory variables (*year* and *month* of the survey) were present in all models, including the null model. The rest of explanatory variables characterizing the experimental sites were: *density of potential breeders*, *absence/presence of wild rabbit release* (in the year of observation), *mean percentage of green grass* and *absence/presence of fencing treatment* (Table 1). These variables were included in the respective GLMMs according to the different hypotheses (Table 2). We used the identity code of every surveyed *artificial warren*, *experimental site* and *experimental zone* as nested random variables. We excluded from the statistical analyses the dataset concerning observation rounds in which we did not detect any offspring, *i.e.* before the beginning and after the end of the detected breeding season.

In order to better interpret the AIC model selection, we previously established the five hypothesis groups described above, each of them containing one or more GLMMs (Table 2): the null model group, the density hypothesis group (four GLMMs regarding the relevance of density and restocking in facilitating rabbit reproductive success in artificial warrens), the food availability hypothesis group (two GLMMs), the predation hypothesis group (two GLMMs), and a final group with two models incorporating a combination of previously explained hypotheses (including the full model, which contained all the above described explanatory variables).

We selected the most parsimonious hypotheses from all fitted GLMMs using AICc (Burnham and Anderson, 2002). We also applied Akaike weights (w_{AICc} ; Burnham and Anderson, 2002) to calculate the relative support for every given model (ranging from 0 to 1, with larger numbers indicating greater support). In order to be conservative in our inferences, we selected as plausible GLMMs only those models with $\Delta AICc < 2$ (Burnham et al., 2011).

Results

During the spring of 2005 and 2006 we carried out 343 artificial warren observations, distributed throughout six observation rounds (February/March, March/April, April/May, May/June, June/July and July/August). In both experimental zones (*Vera* and *Lagunas*) we made opening and closing observation rounds in which we did not detect any kittens (the observation rounds of February/March and July/August, which were then excluded from statistical analyses). From late March to early July we conducted 222 warren observations, detecting the presence of young rabbits in 25% of them (121 individuals, 0.54 kittens per observation). Nevertheless, the fitted GLMMs showed dispersion values ranging from 0.77 to 0.79.

The number of kittens per observation was higher in the spring of 2005 (0.80 in the *Vera*) than during the spring of 2006 (0.38 in the *Vera* and *Lagunas* together). This value also varied monthly: 0.66 kittens in March/April, 0.53 in April/May, 0.41 in May/June and 0.04 in June/July (parameter estimates in Table 3).

Regarding model selection, there were two plausible GLMMs according to the $\Delta AICc < 2$ provision. The first was the food base model, and the second a GLMM containing time, grass and fencing variables (model numbers six and ten, respectively; Table 2). Both of best supported models included the *mean percentage of green grass* explanatory variable (Table 2), which positively affected wild rabbit breeding success within artificial warrens (parameter estimates in Table 3; Fig. 2). In addition, *fencing treatment* positively affected rabbit breeding success in artificial warrens when combined with the effect of pasture availability (parameter estimates in Table 3; Fig. 2); with the second ranked model including these two factors (Table 2). Finally, both *density* and *release* variables were absent from the best supported models with $\Delta AICc < 2$ (Table 2). Given these results, we can infer that pasture availability is the variable primarily affecting rabbit breeding success in artificial warrens, with fencing treatment a minor contributing factor.

Discussion

The observed results support our third hypothesis, which suggests that the efficiency of artificial breeding structures in facilitating wild rabbit reproductive success is mainly determined by food availability. This variable, along with the presence of fencing treatment, increased wild rabbit breeding success in artificial warrens (Fig. 2). This result is in agreement with previous studies which demonstrated that carrying capacity was the main factor determining both rabbit abundance and restocking success (Rogers and Myers, 1979; Moreno et al., 1996, 2004). Grass availability simultaneously affects individual and population levels, in the former by enhancing body condition indispensable for reproduction (Gibb et al., 1985; Tablado et al., 2009), and in the latter by increasing the carrying capacity of a given area (Moreno et al., 1996, 2004). Therefore, the results of the present study strongly suggest that artificial warrens for wild rabbit reproduction should be provided preferably within areas that have suitable pasture availability, which for this species represents potential high-quality habitat. The presence of green pastures can be increased through appropriate habitat management (Moreno and Villafuerte, 1995; López-Albacete et al., 2003; Ferreira et al., 2013), thus providing the possibility of locally improving the rabbit breeding success in artificial warrens even within sub-optimal habitats. Food availability is one of the main drivers of reproductive success for animal populations, including several declining ones in which the provision of

artificial breeding structures is usually applied. This is the case for other mammal species including some arboreal rodents (Bright and Morris, 1995) and chiropterans (Sedgeley and O'Donnell, 2004), as well as several bird species (Mínguez et al., 2003; Katzner et al., 2005), particularly endangered passerines (Komdeur, 1996; Castro et al., 2003). In all these cases artificial breeding structures should be provided predominately in areas with an appropriate abundance of feeding resources as we have suggested.

Once pasture availability was suitable, the limitation of predator pressure through fencing management was also found to increase the effectiveness of artificial warrens for wild rabbit reproduction (Fig. 2). Predation can reduce rabbit reproductive success, directly by young mortality (Wood, 1980) or indirectly by chronic stress negatively affecting the fertility of breeders (von Holst, 1998; Monclús et al., 2005, 2009). Previous studies conducted in our experimental sites showed that the utilized fences limited terrestrial predator access to artificial warrens (Martínez-Fontúrbel, 2008), thereby reducing the perceived risk and individual stress of breeders (Monclús et al., 2009), and also predation rates. Nevertheless, we have to consider that the observed positive effect of fencing treatment on wild rabbit reproductive success could also be due to concurrent causes, such as the limitation of potential breeder dispersal and ungulate competition (Soriguer, 1983; Calvete and Estrada, 2004). However, in our results the fencing treatment was always less important than pasture availability in facilitating breeding success, and therefore we suggest that predator limitation through enclosures should be only applied in optimal habitats or conveniently managed areas. Fencing treatment also entails higher economic costs and human effort in comparison with vegetation management, which should be always prioritized. This strategy should be implemented in the case of the European wild rabbit, as well as more generally wherever artificial breeding structures are protected by fencing (Ivan and Murphy, 2005; Parker and Laurence, 2008; Wilson, 2008) or by even less expensive treatments, such as nest-box predator guards (Kight and Swaddle, 2007; Ransom and Frentress, 2007).

The density of potential breeders and the presence of rabbit release did not show any substantial positive or density-dependent effects on the breeding success in artificial warrens. This may be because the European wild rabbit is a hierarchical and territorial species (Mykytowycz and Gambale, 1965; Villafuerte and Moreno, 1997) in which the use of spatially distributed resources may be overexploited by

dominant individuals (Putman and Staines, 2004; Rouco et al., 2011). Consequently, an increase in the density of potential breeders might not result in higher breeding success, because some of them (especially the females) might be excluded from the reproductive use of the warren (Mykytowycz and Gambale, 1965; Bell, 1986). A possible solution may be to provide a greater number of smaller artificial warrens, at least within areas exhibiting a relative high rabbit density (Rouco et al., 2011), with the aim to increase the breeding possibilities of subordinate females. On the other hand, the applied methodology represents one of the possible approximations to estimate the density of released wild rabbits, and further research would be useful about this issue. Regarding wild rabbit restocking, its first consequences are usually agonistic interactions between resident and released individuals, as they compete for territories and warrens (Cowan and Garson, 1985; Künkele, 1992). The resulting social structure disruption has already been suggested as a factor limiting breeding success (Moreno et al., 2004). Since wild rabbit restocking is a practice involving extremely high biological and economic costs (Calvete et al., 1997; Cotilla and Villafuerte, 2007; Letty et al., 2008), its inefficiency in increasing breeding success should be considered in future conservation strategies. Wildlife population reinforcements should be limited to specific critical situations, as recently reaffirmed by the International Union for Conservation of Nature (IUCN/SSC, 2013). In these cases, reinforcements must always be combined with appropriate efforts to minimize their intrinsic biological costs.

The present study shows that the enhancement of breeder body condition through the provision of suitable pasture availability is a better strategy to improve wild rabbit reproductive success compared with both the reduction of the predation on young individuals and the increase of breeder abundance through restocking. This is probably due to the fact that the European wild rabbit is a fast breeding mammal with a naturally high young mortality (Heppell et al., 2000; Dobson and Oli, 2008). In this study we do not have data about the actual recruitment and the subsequent population size into the next generation, but we expect that these demographic parameters will benefit from the observed increase in breeding success. We therefore suggest that the recovery of declining wild rabbit populations should focus primarily on the facilitation of its reproduction, which has been already described as a key factor for wild rabbit population dynamic (Villafuerte et al., 1997; Tablado et al., 2009). The provision of artificial warrens is a conservation practice which can be utilized in this context, if applied within optimal or conveniently

managed habitats. Furthermore, habitat improvement is certainly easier and more economical to implement than either predator limitation by fencing or disease prevention; and the natural density increase subsequent to the reproduction improvement can help wild rabbit populations counteract naturally both predation and epizootics (Newsome et al., 1989; Fenner and Ross, 1994). The same paradigm may be applied to other declining populations of fast breeding species (for example other lagomorphs, as well as rodents, several lemurs and marsupials, and small passerines), prioritizing the improvement of reproductive success instead of the reduction of mortality.

Conclusions

The present study shows that the reproductive success of a fast breeding species facilitated by artificial structures primarily depends on food availability, which for a broad range of species can be one of the main factors determining habitat quality. We therefore present our case study as an example of the optimization of conservation expenditures, suggesting how to reduce the biological and economic costs often associated with *in-situ* interventions. As a conclusion, we encourage the careful planning of expensive management actions such as wide-scale provisioning of artificial breeding structures, ensuring optimum food availability and habitat quality before the implementation of other measures. We also recommend the development of concurrent experimental studies verifying the effectiveness of these actions.

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693 **Tables and Figures**

694

695 **Table 1. Description of explanatory variables of the fitted GLMMs.** The arithmetic mean and standard
 696 deviation, as well as the range (minimum and maximum recorded values) are provided for every
 697 continuous variable.

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Explanatory variables	Categories	Average	Range
Year of the survey	2005 2006	-	-
Month of the survey	March/April April/May May/June June/July	-	-
Density of potential breeders (individuals/ha)	-	3.020 ± 2.273	0.01 - 8.86
Wild rabbit release	Present (with translocated rabbits in the year of survey) Absent (only resident rabbits in the year of survey)	-	-
Mean percentage of green grass	-	32.940 ± 21.329	5.20 - 65.2
Fencing treatment	Present Absent	-	-

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Table 2. Factors affecting the number of detected kittens per sampled artificial warren and observation; model ranks by AIC weights (wAICc). The five hypothesis groups are subdivided by lines. In the Models column, the abbreviations y and m refer to the variables designated as year and month, respectively. $\Delta AICc$ is the relative difference of a given AICc value compared to the smallest AICc value. The best supported models ($\Delta AICc < 2$) are highlighted in grey. AIC weights indicate the relative support for every model (the weights of all the models in the candidate set have the sum of 1). Evidence ratio (ER) is the ratio of wAICc, comparing the best supported model with every competing one. The response variable was the number of detected kittens per sampled artificial warren and observation; see Table 1 for a description of explanatory variables.

Hypothesis Group	Models	AICc	$\Delta AICc$	wAICc	Rank	ER
Null	1: year + month	381.8	4.4	0.055	3	8.8
Density	2: y + m + density	383.9	6.5	0.019	8	25.3
	3: y + m + density + (density*density)	384.9	7.5	0.011	10	42.1
	4: y + m + release	382.3	4.9	0.041	5	15.5
	5: y + m + density + release + (density*release)	384.4	7.0	0.015	9	32.6
Food	6: y + m + grass	377.4	0.0	0.483	1	1.0
	7: y + m + grass + density + release + (density*release)	381.8	4.4	0.055	3	8.8
Predation	8: y + m + fence	383.9	6.4	0.019	7	25.1
	9: y + m + fence + density + release + (density*release)	386.6	9.7	0.005	11	97.5
Combination	10: y + m + grass + fence	378.3	0.9	0.307	2	1.6
	11: y + m + grass + fence + density + release + (density*release)	382.9	5.5	0.031	6	15.5

Table 3. Factors affecting the number of detected kittens per sampled artificial warren and observation; parameter estimates from the best supported models. In the Parameter estimates column, values in parentheses represent standard errors (SE). The response variable was the *number of detected kittens per sampled artificial warren and observation*.

Models	Explanatory variables	Variable categories	Parameter estimates ($\pm$ SE)
GLMM number 6 (First ranked)	Intercept		-3.59 ($\pm$ 0.828)
	Year	2005	0.48 ($\pm$ 0.199)
		2006	0
	Month	March/April	0.43 ($\pm$ 0.221)
		April/May	0
		May/June	-0.03 ($\pm$ 0.243)
		June/July	-0.88 ($\pm$ 0.645)
	Pasture availability		0.05 ($\pm$ 0.018)
GLMM number 10 (Second ranked)	Intercept		-3.34 ($\pm$ 0.828)
	Year	2005	-0.46 ($\pm$ 0.198)
		2006	0
	Month	March/April	0.42 ($\pm$ 0.221)
		April/May	0
		May/June	-0.26 ($\pm$ 0.243)
		June/July	-0.83 ($\pm$ 0.649)
	Pasture availability		0.05 ($\pm$ 0.019)
	Fencing treatment	Present	0
		Absent	-0.91 ($\pm$ 0.784)

Figure 1. Study area and design of experimental sites. Squares with continuous and dashed lines are fenced and unfenced surveyed experimental sites, respectively. *Vera* release density was uniformly 10 individual/ha in the autumn of 2004 (there was no release in the autumn of 2005). *Lagunas* release density varied according to shade intensity of the squares, from lighter to darker grey: 5, 13 and 19 individual/ha (white squares were fenced and unfenced sites without wild rabbit restocking). Grey arrows within the largest inset indicate *a priori* gradient of grass availability (more grass close to wetland and lagoons). The acronyms DNP and DBR correspond to Doñana National and Natural Parks and Doñana Biological Reserve, respectively.

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772 **Figure 2. Factors affecting wild rabbit breeding success per artificial warren.** On the left (a): the
 773 relationship between wild rabbit breeding success in artificial warrens and pasture availability. Dotted
 774 lines are upper and lower standard errors. The graph data were fitted from the sixth GLMM, the best
 775 supported model. On the right (b): the relationship between wild rabbit breeding success in artificial
 776 warrens and enclosure treatment: fenced versus unfenced experimental sites. The graph data were fitted
 777 from the tenth GLMM, the second ranked model and the best one including the fencing variable.