Title: Effect of artificial warren size on a restocked European wild rabbit population

Short title: Artificial warren size and wild rabbit response

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Abstract

In the time since the decline of the wild rabbit in southern Europe, various techniques and methods have been explored with a view to restoring wild rabbit populations or increasing rabbit resilience, for both conservation and game purposes. Rabbit restocking and habitat management are among the measures most often applied. Some efforts have been made to increase refuges for wild rabbits, mainly through the construction of artificial warrens. The present study evaluates the response of a wild rabbit population introduced to artificial warrens of varying sizes. This involves comparisons of the density of rabbits in the warrens, rabbit density change between seasons of low and high rabbit population density, and the productivity index for large and small warrens in rabbit populations living under semi-natural conditions. Our results show that large warrens had higher rabbit abundance than had small warrens, but significantly lower rabbit density. No differences in density increase or productivity index were found with respect to warren size. The results suggest that it is preferable to build many small warrens for conservation of wild rabbit populations, but, in the event that only a few warrens are built, it is advisable that they be large.

Keywords

Oryctolagus cuniculus, productivity, rabbit conservation, recovery program, warren size

Introduction

The European wild rabbit (*Oryctolagus cuniculus*) is considered a pest in many countries, and numerous studies aimed at reducing or controlling rabbit numbers have been carried out (Thompson & King, 1994). In the Iberian Peninsula the problem is very different, as the rabbit is native to this area but has undergone a progressive decline in abundance in many regions during the last 50 years (Delibes-Mateos, Ferreras & Villafuerte, 2009). In Iberian Mediterranean ecosystems the rabbit is a keystone species (Delibes-Mateos *et al.,* 2007), and, in the Iberian Peninsula, rabbits are the staple prey of at least 30 predators (Delibes-Mateos, Ferreras & Villafuerte, 2008), including threatened species such as the black vulture (*Aegypius monachus*), Bonelli´s eagle (*Hieraaetus fasciatus*), the imperial eagle (*Aquila adalberti*), and the Iberian lynx (*Lynx pardinus*). Imperial eagles and Iberian lynxes are especially dependent on rabbits (Aldama, Beltrán & Delibes, 1991; Ferrer & Negro, 2004), so the decline in rabbit numbers within the range of these species is of major concern with respect to their survival and conservation. In addition to its ecological importance, the rabbit is one of the most important game species in the region (Angulo & Villafuerte, 2003).

Myxomatosis and rabbit hemorrhagic disease (RHD) have been the most important causes of rabbit population declines (Ratcliffe *et al.,* 1952; Villafuerte *et al.,* 1995), although other factors including habitat change, overhunting, and climate change also appear to have contributed to the decline in the Iberian Peninsula (Moreno & Villafuerte, 1995; Fa, Sharples & Bell, 1999).

As a consequence of this situation, management techniques have been applied to the restoration of wild rabbit populations and to efforts to increase their resilience. Restocking and habitat management have been the strategies most frequently employed (Moreno & Villafuerte, 1995; Cabezas & Moreno, 2007; Rouco *et al.,* 2008).

Because rabbits largely depend on warrens for protection against predators (Parer & Libke, 1985, Richardson & Wood, 1982), for refuge against climatic extremes (Wallage-Drees & Michielsen, 1989; Villafuerte *et al.,* 1993), for establishing social ties (Mykytowycz, 1968; Roberts, 1987), and for breeding (Parer & Libke, 1985; Villafuerte, 1994), some efforts have been made to increase warren size or number in order to favour wild rabbit population, mainly through the construction of artificial warrens. In addition, warrens could also have other important role respect to the impact of RHD. On the one hand, warren size is closely related with rabbit abundance (Parer and Wood, 1986), and it seems that disease impact could be lower in high-density populations in habitats with high carrying capacity (Calvete, 2006). Thus, artificial warrens could be a useful management tool to increase carrying capacity in an area with poor habitat.

Many different warren designs have been used in southwestern Europe, and various materials including bricks, plastic, rocks, trunks, and branches have been employed (Letty *et al.,* 2000; García, 2005; Cabezas & Moreno, 2007; Rouco *et al.,* 2008; 2010). Despite the proliferation of artificial warrens and the economic investment devoted to wild rabbit recovery programs, little research has explored the effects of artificial warren size.

In this study we evaluated the response of a wild rabbit population to two artificial warren sizes. We first analyzed the capacity of two sizes of warren (small and large) to house rabbits. We compared the number and density of rabbits in each type of warren during seasons of naturally high and low annual rabbit population densities, and developed an index of productivity for each warren size. This allowed us to evaluate how warren size might affect the dynamics of rabbit populations, and to establish criteria for the warren size that would optimize rabbit population recovery.

Materials and Methods

Study area

The study was carried out from November 2004 to May 2005 in Los Melonares area, located in the south of Sierra Norte of Seville Natural Park (southwest Spain). It has two main biotopes: grassland and scrubland. The scrubland (mainly *Cistus ladaniferus*) occupies the slopes of the hillocks, while the grassland, with dispersed Holm oaks (*Quercus ilex*), occupies most of the remainder of the area (70%).

Rabbit abundance was low in Los Melonares before rabbit restocking was carried out in the area. During autumn 2002, 180 rabbits were released into purpose-built restocking plots (for details see Rouco *et al.,* 2008). Threatened raptor species, including the Spanish Imperial eagle, the black vulture and the Bonelli's eagle, also nest in the area or its immediate vicinity.

Two plots (4 ha each) separated by 2 km (Fig. 1) were fenced (1.0 m below ground, 2.5 m above ground, with an electrified wire on top) to completely exclude terrestrial carnivore predators. Each plot had 18 artificial warrens (described below) that comprised the main rabbit refuges. Near each warren, water and commercial rabbit food were provided in suppliers throughout the study period. Additional refuges (heaped wooden branches, 2 m diameter, n = 44 per plot) and feeding areas (cropland) were placed in identical locations within each restocking plot (Fig. 1).

Artificial warrens of two sizes were included in each plot; 12 small and 6 large. Warrens consisted on a skeleton of wooden pallets covered by earth and branches. Each large warren ($48m^2$) was the size of 4 small warrens ($12m^2$). The cost of constructing each of the large warrens was almost three times that of the small warrens. During rabbit restocking in autumn 2002 (following IUCN guidelines for animal reintroduction, IUCN, 1996), 5 rabbits were released into each small warren, and 20 rabbits were released into each large warren. Thus, we would expect that the rabbit abundance will be four times higher in the large warrens that in the small ones.

Each warren had an effective capture device consisting of a wire net fence with metal traps (3 traps in small and 5 in large warrens) attached to holes in the fence. Capture involved activation of the capture devices at midday, when the rabbits were less active and most were underground (Villafuerte *et al.,* 1993). The following morning the rabbits trapped inside the cages were counted and handled. This trapping system permitted capture inside the warren of 50–60% of the rabbits on any one night (data not shown).

Experimental procedure

To test the effect of artificial warren size, differences in the density of rabbits inside the warrens, the density increase and the productivity index were compared between large and small warrens for the two plots used in the study. Thus, three captures were carried out during the study: the first in November 2004, just before the breeding season, when the rabbit population was at its lowest density (Beltrán, 1991); the second in February 2005, during the breeding season; and the third in May 2005, when the rabbit population was close to the greatest density annually for southern Iberian Mediterranean ecosystems (Beltrán, 1991).

We considered as rabbit density in small warrens, the number of animals captured in such warren for each capture event. Because surface of large warrens was 4 times that of small ones, we standardized the rabbit density in large warrens by dividing the number of animals captured in each by 4. Thus, we compared the density of rabbits inhabiting each warren size between low and high population density seasons. We compared rabbit density increase between the lowest and highest population density periods as a function of warren size. For each warren a density increase variable was calculated by dividing the maximum density of rabbits in the warren by the minimum density recorded for that warren between both captures. Finally we calculated and compared a productivity index for rabbits inhabiting each warren, as the number of captured juveniles divided between the number of adult females. The number of juveniles was taken as those captured in one warren in February 2005, and the number of adult females was taken as the number of adult females captured in that warren in November 2004, that we considered as potentially breeding females. Juveniles were categorized as those animals weighing less than 810 g for males and 750 g for females (Villafuerte, 1994) at the time of capture.

Data analysis

Evaluation of the effect of warren size on rabbit density was carried out using generalized linear mixed models within SAS 8.2 (Littell *et al.,* 1996). The following models were performed:

Model 1 evaluated the variation in rabbit density during the entire study as a function of different warren size. The dependent variable was density of rabbits per warren during each capture event, which was fitted to a lognormal distribution with an identity link function. We included the following independent variables: size (two levels; small and large), captures (three levels; November, February and May) and the interaction between size and captures. The plots (two levels) and warren nested inside plot (36 levels) were included as random variables in the model.

Models 2 and 3 evaluated the density increase and productivity index, respectively, as a function of warren size. We fitted 'density increase' and 'productivity index' to a lognormal distribution with an identity link function; the independent variable for both models was size (two levels). Plot (two levels) was included as a random variable in both models.

Tukey’s HSD (honestly significant difference) test was applied to each of the three models to evaluate differences in animals captured for the two warren sizes included in the final fitted model. The degrees of freedom in the denominator were estimated using

Satterthwaite's formula (Littell *et al.,* 1996). In these tests, selection of the best model was carried out by starting from the fully saturated models, and sequentially removing the effects farthest from statistical significance, starting from the highest order interactions. We also compared our results with that recorded by Cowan (1983) in a field study of European wild rabbits in United Kingdom. Finally, the Spearman rank order correlation was used to compare frequency distributions.

Results

A total of 1,318 animals were handled during the study. The maximum number of captures occurred during February in plot 1 and May in plot 2 (Fig. 2). The total number of captured animals per warren was always greater in large warrens than in small ones (Fig. 2). In plot 1 there were 2.14-fold more animals in large than in small warrens during the November capture. This reduced to 1.81-fold during the capture in February, and 1.53-fold for the capture in May (Fig. 2). The mean rabbit population increase per warren from November to February was 2.23±0.98-fold (mean±standard error) for small warrens and 1.82±0.66-fold for large warrens. In plot 2 there were 2.52-fold more animals in large than in small warrens during the November capture. This reduced to 1.65-fold during the capture in February, and increased to 1.80-fold for the capture in May (Fig. 2). The mean rabbit population increase per warren from November to February was 4.05±0.82-fold (mean±standard error) for small warrens and 2.78±0.61-fold for large warrens.

Model 1 showed significant differences in rabbit density during different capture seasons, and with respect to warren size (Table 1). The mean density of rabbits was greater in small than in large warrens (Tukey test; $P<0.001$). Model 2 showed no difference, with respect to warren size, in the rabbit density increase between the seasons of minimum and maximum population density (Table 1). Small warrens showed a somewhat greater density increase than did large warrens, but the difference was not significant (Tukey test; *P*=0.338). Model 3 showed no difference in productivity index between small and large warrens (Table 1). The index was slightly higher for small than for large warrens, but these differences were not significant (Tukey test; *P*=0.77).

However, we found a negative relationship between the productivity index and the number of females inhabiting a given warren at the beginning of the breeding season (*R*=–0.44, n=33, *P*=0.010) (Fig, 3).

Moreover, we found no significant correlation in the proportions of warrens with different numbers of females at the beginning of the breeding season between small and large warrens (*R*=–0.29, n=10, *P*=0.409). Correlation of number of breeding females between large warrens and natural warrens (Cowan, 1983) was neither significant(*R*=–0.04, n=10, *P*=0.906). However, we did find a significant correlation in female group size proportion between small warrens and natural warrens (Cowan, 1983), with any given group size of breeding females (*R*=0.64, n=10, *P*=0.046) (Fig. 4).

Discussion

Four factors mainly control rabbit population dynamics: food, predation, disease and migration (Myers & Pole, 1962; Villafuerte, 1994). In our study food was available *ad libitum* during the entire period; predation by terrestrial predators was prevented by the plot fence; aerial predators did not differ between the two plots (unpublished data); no myxomatosis or rabbit hemorrhagic disease outbreaks were detected during the study; and migration was prevented by the fence surrounding each plot. Therefore, the differences of the rabbit numbers inside the warrens could be explained mainly by differences in warren size.

Our results indicate that the maximum rabbit density was reached at different times in each plot (Fig. 2), since both populations are independent to each other. However, the effect of warren size was similar in each plot. We found that large warrens had greater rabbit abundance than had small warrens, but lower animal density, a reduced density increase, and a lower productivity index. The occurrence of higher numbers of rabbits in larger warrens has been reported in other studies (Parer and Wood 1986), but no reports have discussed the effect of the size of artificial warrens on rabbit density and productivity. Therefore, other factors, probably related to intraspecific relationships, must be responsible for the lower population increase and productivity in larger warrens (Vickery *et al.,* 1991). For example, competition for space (Cowan & Garson, 1985), limitation in the number of sites available for breeding (Mykytowycz, 1958), or other social relationships inside warrens are factors that could determine the number of rabbits in the warrens. Although life in large groups could provide several advantages, including shared vigilance against predators (Roberts, 1988), excessive numbers in any rabbit population could have negative effects including an increase in aggressive behavior (Lockley, 1961) and reduced fecundity (Myers & Pole, 1963).

For example, Cowan (1983; 1987) observed that rabbit social groups that established hierarchical relations according to gender contained few animals (typically four of five individuals), and showed that the number of females inhabiting warrens at the beginning of the breeding season rarely exceeded six (mean value = 2.7 females per warren for the 51 groups studied; Cowan, 1983), even though the burrows were larger than those used in our study. The number of females in each social group is related to warren size, although this relationship is not linear (Cowan, 1983). In high-density areas, the feeding ranges of different social groups can overlap, as can their refuges (Cowan, 1987; Villafuerte, 1994). In contrast, access to warrens by 'foreign' rabbits is not tolerated, especially prior to and during the breeding season (Cowan, 1983; 1987), suggesting that sizable groups of females may not readily coexist in large artificial warrens. In fact, we did not find any large warren with more than 10 adult females prior to the breeding season (Fig. 3). Moreover, in high-density populations, confrontations among females occur mainly between members of the same social group, primarily related to maintenance of domination in the warren and defense of offspring (Myers & Pole, 1959). In such situations, rabbit fecundity could be significantly reduced (Lockley, 1961; Myers & Pole, 1962), and this may explain why productivity in the large warrens of our study was lower than in small warrens, thus explaining the reduced density increase.

However, the relationship between rabbit group size and warren size is not linear because one social group may utilize several small warrens (Parer & Wood, 1986), and a single large warren may be used by several social groups (Parer, Fullagar & Malafant, 1987).

On the other hand, when we compared the proportion of adult females group of our study recorded on November with that recorded by Cowan (1983), we found that the size of the female groups in small warrens was similar to that observed in the cited study (Fig. 4). As well, we found correlation between the proportion of small and natural warrens with any given number of females at the beginning of the breeding season (adults females group) (Fig. 4). Thus, independent of burrow size, in most natural burrows the female groups consisted of 3–5 females. Although both studies were performed in different places, and although it is recognized the results must be interpreted with caution, it seems that social conditions in the small warrens of our study were similar to those found by Cowan (1983).

Implications for conservation

Although further research in other habitats is necessary, small warrens appear to be more appropriate for rabbit recovery purposes. It is true that lower abundance was recorded in small warrens, but animal density was higher than in large warrens; there was no difference in productivity; and the number of adult females was similar to that found in the wild. On the other hand, a higher density of animals inside the warren, as occur in the small warrens, could favor a lower impact of the RHD, as predicted by theoretical models (Calvete, 2006). Although large warrens offer refuge to a greater number of rabbits, the increased proportion of adults results in lower productivity in larger warrens. Furthermore, large warrens are more expensive to build and construction is more complicated. So, for rabbit conservation purposes, it is preferable to build many small warrens and not a lower number of large warrens, although if only a few warrens are able to be built, they should be large.

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Table 1. *F* value statistics for mixed models controlled for plot and warren nested inside plot in model 1 (density of rabbits inside the warren during the study period), and controlled for plot in model 2 (population increase) and model 3 (productivity index).

	Predictors	DF	F	p
	Size	1, 70	26.88	<0.001
Model 1	Season	2, 70	10.19	<0.001
	Size*Season	2, 68	0.63	0.538
Model 2	Size	1, 33	0.94	0.338
Model 3	Size	1, 33	0.09	0.77

Figure captions

Figure 1. (A) Location of the Los Melonares area (●) on the Iberian Peninsula. (B) Scheme of the main biotypes present in Los Melonares, and the location of the experimental translocation plots (■). (C) Structure of a translocation plot comprising artificial warrens (large warrens: white; small warrens: black), refuges, and water and food suppliers. (D) Detail of an artificial warren surrounded by a warren pen, with the location of the water and food suppliers.

Figure 2. Mean number (±standard error) of rabbits captured per warren in the three captures performed during the study (November 2004, February 2005 and May 2005), as a function of warren size in the two plots.

Figure 3. The relationship between the productivity index (number of juveniles per female) and the number of breeding females per group prior to the breeding season.

Figure 4. Percentage of natural warrens (Cowan 1983) and artificial warrens (small and large, this study) in relation to the number of breeding females per group prior to the breeding season (November 2004 capture).