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

2 **Short title:** Artificial warren size and wild rabbit response

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26 **Abstract**

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

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46 **Keywords**

47 *Oryctolagus cuniculus*, productivity, rabbit conservation, recovery program, warren
48 size

49

50 **Introduction**

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

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

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

75 Because rabbits largely depend on warrens for protection against predators (Parer &
76 Libke, 1985, Richardson & Wood, 1982), for refuge against climatic extremes (Wallage-
77 Drees & Michielsen, 1989; Villafuerte *et al.*, 1993), for establishing social ties (Mykytowycz,
78 1968; Roberts, 1987), and for breeding (Parer & Libke, 1985; Villafuerte, 1994), some
79 efforts have been made to increase warren size or number in order to favour wild rabbit
80 population, mainly through the construction of artificial warrens. In addition, warrens could
81 also have other important role respect to the impact of RHD. On the one hand, warren size
82 is closely related with rabbit abundance (Parer and Wood, 1986), and it seems that disease
83 impact could be lower in high-density populations in habitats with high carrying capacity
84 (Calvete, 2006). Thus, artificial warrens could be a useful management tool to increase
85 carrying capacity in an area with poor habitat.

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

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

98

99 **Materials and Methods**

100

101 **Study area**

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

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

112 Two plots (4 ha each) separated by 2 km (Fig. 1) were fenced (1.0 m below ground,
113 2.5 m above ground, with an electrified wire on top) to completely exclude terrestrial
114 carnivore predators. Each plot had 18 artificial warrens (described below) that comprised
115 the main rabbit refuges. Near each warren, water and commercial rabbit food were
116 provided in suppliers throughout the study period. Additional refuges (heaped wooden
117 branches, 2 m diameter, n = 44 per plot) and feeding areas (cropland) were placed in
118 identical locations within each restocking plot (Fig. 1).

119 Artificial warrens of two sizes were included in each plot; 12 small and 6 large.
120 Warrens consisted on a skeleton of wooden pallets covered by earth and branches. Each
121 large warren (48m²) was the size of 4 small warrens (12m²). The cost of constructing each
122 of the large warrens was almost three times that of the small warrens. During rabbit
123 restocking in autumn 2002 (following IUCN guidelines for animal reintroduction, IUCN,
124 1996), 5 rabbits were released into each small warren, and 20 rabbits were released into

125 each large warren. Thus, we would expect that the rabbit abundance will be four times
126 higher in the large warrens than in the small ones.

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

133 ***Experimental procedure***

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

142 We considered as rabbit density in small warrens, the number of animals captured in
143 such warren for each capture event. Because surface of large warrens was 4 times that of
144 small ones, we standardized the rabbit density in large warrens by dividing the number of
145 animals captured in each by 4. Thus, we compared the density of rabbits inhabiting each
146 warren size between low and high population density seasons. We compared rabbit
147 density increase between the lowest and highest population density periods as a function
148 of warren size. For each warren a density increase variable was calculated by dividing the
149 maximum density of rabbits in the warren by the minimum density recorded for that warren

150 between both captures. Finally we calculated and compared a productivity index for rabbits
151 inhabiting each warren, as the number of captured juveniles divided between the number
152 of adult females. The number of juveniles was taken as those captured in one warren in
153 February 2005, and the number of adult females was taken as the number of adult females
154 captured in that warren in November 2004, that we considered as potentially breeding
155 females. Juveniles were categorized as those animals weighing less than 810 g for males
156 and 750 g for females (Villafuerte, 1994) at the time of capture.

157 ***Data analysis***

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

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

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

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

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

181

182 **Results**

183 A total of 1,318 animals were handled during the study. The maximum number of
184 captures occurred during February in plot 1 and May in plot 2 (Fig. 2). The total number of
185 captured animals per warren was always greater in large warrens than in small ones (Fig.
186 2). In plot 1 there were 2.14-fold more animals in large than in small warrens during the
187 November capture. This reduced to 1.81-fold during the capture in February, and 1.53-fold
188 for the capture in May (Fig. 2). The mean rabbit population increase per warren from
189 November to February was 2.23 ± 0.98 -fold (mean $\pm$ standard error) for small warrens and
190 1.82 ± 0.66 -fold for large warrens. In plot 2 there were 2.52-fold more animals in large than
191 in small warrens during the November capture. This reduced to 1.65-fold during the
192 capture in February, and increased to 1.80-fold for the capture in May (Fig. 2). The mean
193 rabbit population increase per warren from November to February was 4.05 ± 0.82 -fold
194 (mean $\pm$ standard error) for small warrens and 2.78 ± 0.61 -fold for large warrens.

195 Model 1 showed significant differences in rabbit density during different capture
196 seasons, and with respect to warren size (Table 1). The mean density of rabbits was
197 greater in small than in large warrens (Tukey test; $P < 0.001$). Model 2 showed no
198 difference, with respect to warren size, in the rabbit density increase between the seasons
199 of minimum and maximum population density (Table 1). Small warrens showed a

200 somewhat greater density increase than did large warrens, but the difference was not
201 significant (Tukey test; $P=0.338$). Model 3 showed no difference in productivity index
202 between small and large warrens (Table 1). The index was slightly higher for small than for
203 large warrens, but these differences were not significant (Tukey test; $P=0.77$).

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

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

214

215 **Discussion**

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

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

240 For example, Cowan (1983; 1987) observed that rabbit social groups that established
241 hierarchical relations according to gender contained few animals (typically four of five
242 individuals), and showed that the number of females inhabiting warrens at the beginning of
243 the breeding season rarely exceeded six (mean value = 2.7 females per warren for the 51
244 groups studied; Cowan, 1983), even though the burrows were larger than those used in our
245 study. The number of females in each social group is related to warren size, although this
246 relationship is not linear (Cowan, 1983). In high-density areas, the feeding ranges of
247 different social groups can overlap, as can their refuges (Cowan, 1987; Villafuerte, 1994).
248 In contrast, access to warrens by 'foreign' rabbits is not tolerated, especially prior to and

249 during the breeding season (Cowan, 1983; 1987), suggesting that sizable groups of
250 females may not readily coexist in large artificial warrens. In fact, we did not find any large
251 warren with more than 10 adult females prior to the breeding season (Fig. 3). Moreover, in
252 high-density populations, confrontations among females occur mainly between members of
253 the same social group, primarily related to maintenance of domination in the warren and
254 defense of offspring (Myers & Pole, 1959). In such situations, rabbit fecundity could be
255 significantly reduced (Lockley, 1961; Myers & Pole, 1962), and this may explain why
256 productivity in the large warrens of our study was lower than in small warrens, thus
257 explaining the reduced density increase.

258 However, the relationship between rabbit group size and warren size is not linear
259 because one social group may utilize several small warrens (Parer & Wood, 1986), and a
260 single large warren may be used by several social groups (Parer, Fullagar & Malafant,
261 1987).

262 On the other hand, when we compared the proportion of adult females group of our
263 study recorded on November with that recorded by Cowan (1983), we found that the size
264 of the female groups in small warrens was similar to that observed in the cited study (Fig.
265 4). As well, we found correlation between the proportion of small and natural warrens with
266 any given number of females at the beginning of the breeding season (adults females
267 group) (Fig. 4). Thus, independent of burrow size, in most natural burrows the female
268 groups consisted of 3–5 females. Although both studies were performed in different places,
269 and although it is recognized the results must be interpreted with caution, it seems that
270 social conditions in the small warrens of our study were similar to those found by Cowan
271 (1983).

272 **Implications for conservation**

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

285

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392

393 **Table 1.** *F* value statistics for mixed models controlled for plot and warren nested inside
394 plot in model 1 (density of rabbits inside the warren during the study period), and controlled
395 for plot in model 2 (population increase) and model 3 (productivity index).
396

Predictors		DF	F	p
Model 1	Size	1, 70	26.88	<0.001
	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

397

398

399 **Figure captions**

400

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

407

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

411

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

414

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