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HIGH RABBIT ABUNDANCE PROVES DETRIMENTAL TO THE POPULATION GROWTH RATE IN EUROPEAN RABBIT (*ORYCTOLAGUS CUNICULUS* L.) EXTENSIVE BREEDING ENCLOSURES

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Abstract: The European rabbit (*Oryctolagus cuniculus* L.) is a key prey species in Mediterranean ecosystems that has declined in its natural ranges as a result of diseases and loss of habitat. This situation has led to the production of wild rabbits in enclosures in which they can acclimate and breed. The efficiency of these enclosures as extensive breeding systems is defined by their population growth rate (PGR). The aim of this study is to analyse the effect of rabbit abundance on the PGR. This has been done by creating general linear models to explain autumn and spring PGR with the use of rabbit abundance estimates, enclosure size, aerial predation and previous PGR as possible explanatory variables. Rabbit abundance and enclosure size negatively affected the autumn PGR, while only rabbit abundance affected the spring PGR in the best-fit models. It is suggested that maintaining rabbit densities at fewer than 30 rabbits per hectare might help to optimise the efficiency inside enclosures.

Key Words: density-dependent breeding, extensive breeding system, social behaviour.

INTRODUCTION

The European rabbit (*Oryctolagus cuniculus* L.) is a key native species in the Iberian Peninsula (López-Martínez, 2008), the populations of which have declined unevenly across the native range (Ward, 2005) and are still decreasing (Smith and Boyer, 2008) as a result of viral diseases (Moreno *et al.*, 2007; Williams *et al.*, 2007) and a loss of suitable habitat (Calvete *et al.*, 2004). This situation has led to the production of wild rabbits in captive breeding programmes for hunting and predator conservation (Sánchez-García *et al.*, 2012).

The captive breeding of wild rabbits has been carried out in intensive systems, but this process is difficult and not very productive: physical injuries (González-Redondo, 2009) and failures in maternal behaviour (González-Redondo and Zamora-Lozano, 2008; González-Redondo, 2010) have been reported, mostly as a result of unsuitable living conditions and high stress levels. Semi-extensive breeding systems have attained higher productivity (Arenas *et al.*, 2006), but the rabbits' lack of acclimation may result in high mortality when they are released into the wild (Rouco *et al.*, 2010).

The alternatives are extensive systems. Various projects, such as the Iberian Lynx LIFE project (Life-Lince project, 2006-2011), have been responsible for building more than 260 fenced rabbit plots since 2002 (Gil-Sánchez, 2011). These fenced plots may have 2 aims: to establish supplementary feeding stations for predators whose diet includes rabbits (López-Bao *et al.*, 2008), or the creation of centres for the dispersion of rabbits. In the latter case, the enclosures are breeding systems which are protected against terrestrial predators and their aim is to increase rabbit abundance, thus enabling the rabbits to then spread and colonise the surrounding areas (Guerrero-Casado *et al.*, 2013a). When enclosures are managed with this aim, a high and sustained production of rabbits is desirable. The maximum efficiency therefore corresponds to the populations in the exponential growth phase (Hutchinson, 1948), i.e. maximum population growth rate (PGR).

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However, the rabbit population growth rate may be limited within restocking enclosures owing to various factors: an elevated rabbit abundance inside the enclosures, in which rabbits are highly vulnerable, in conjunction with a low rabbit density in the area in general, may attract birds of prey (Rouco, 2008; Guerrero-Casado *et al.*, 2013c). Intrinsic mechanisms such as physiological stress and social interactions (Letty *et al.*, 2008) may also limit population growth, since individuals compete for social rank and territory (Ruiz-Aizpurua *et al.*, 2013). These behavioural traits are density-dependent (Wynne-Edwards, 1959). In rabbit populations, fecundity and population growth decrease as density increases (Myers and Poole, 1962; 1963). More recently, Rödel *et al.* (2004a; 2004b) have shown that there are lower reproduction rates and a higher mortality in high rabbit densities.

The aim of this work is to analyse the effect of rabbit abundance on the rabbit population growth rate within the restocking enclosures in order to improve the efficiency of extensive breeding systems.

MATERIALS AND METHODS

Study area

The fieldwork was carried out in central Sierra Morena, Córdoba, Southern Spain (38° 5' N, 5° 16' W, Figure 1A). This area is very important for the conservation of endangered predators, and the current scarcity of rabbits in Sierra Morena is a major conservation concern, since the Iberian Lynx (*Lynx pardinus*) and the Spanish Imperial Eagle (*Aquila adalberti*) for which rabbits are prey still coexist in this area (Delibes-Mateos *et al.*, 2008). The area is characterised by a Mediterranean climate with an average annual rainfall of 745 mm and average monthly temperatures between 11°C and 29°C. Soils are granitic and hard to dig, and altitudes range between 400 and 800 m.a.s.l. The study area includes 3 species such as holm oak (*Quercus ilex*) and cork oak (*Quercus suber*), pine plantations (*Pinus pinea* and *Pinus pinaster*), Mediterranean scrubland dominated by *Cystus* spp., *Erica* spp., *Pistacia* spp., *Phyllirea* spp., and *Rosmarinus* spp., and pasture areas occupied by oak savannah (*dehesa*) (Junta de Andalucía, 2003). The area currently contains low-density rabbit populations, although rabbits were abundant in the past (Delibes-Mateos *et al.*, 2010). The sport-hunting of red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) is frequent on the hunting estates in the area (Mulero-Mendigorri, 2013).

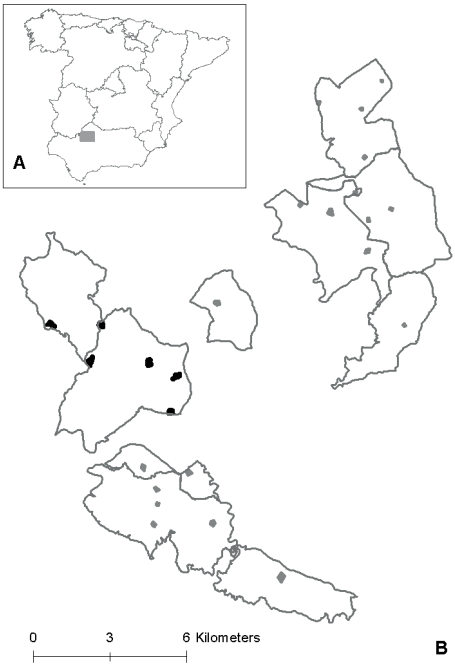

Figure 1: Map of the study area. A: Location of the study area in the south of Spain (38° 5' N, 5° 16' W). B: Location of the enclosures: set 1 (•), set 2 (●). Solid lines delimit the hunting estates.

Rabbit enclosures

This study was framed within a project to improve the black vulture's (*Aegypius monachus*) habitat in Córdoba province, which was managed by the Andalusia Autonomous Government's Environmental Agency. As part of this project, more than 50 rabbit breeding enclosures were built between 2008 and 2012. The data on rabbit abundance included in this study originated from 2 sets of enclosures for restocked rabbits: 25 enclosures in total (Figure 1B), in which there were no rabbits before the restocking, and the rabbit abundance in which it was possible to monitor on a monthly basis after the restocking. The first group included 19 fenced enclosures of 1.21±0.14 standard error (SE) ha, into which rabbits were released in September 2008. Rabbit abundance was recorded on a monthly basis from

October 2008 until July 2009, when the yearly maximum abundance was reached. The second data set originated from another 6 fenced enclosures of 4.44±0.93 ha into which rabbits were released in November 2010 and data were recorded from November 2010 to July 2011. All the enclosures were built to exclude terrestrial predators, pallet warrens (Fernández-Olalla *et al.*, 2010) were built in each plot (3.5±0.4), water and food (grain mixture: oat, wheat and barley in equal proportions) were supplied *ad libitum* during the entire study period, and pasture was not depleted in any of the enclosures during the study. The restocked rabbits had been previously captured in an agricultural area in the south of Córdoba province (37° 34' N, 4° 37' W), and randomly released into the enclosures on the same day as their capture within the natural distribution area of the subspecies *Oryctolagus cuniculus algirus* (Branco *et al.*, 2000) and in the same sex-ratio as in capture (2 males:3 females). The number of rabbits released ranged from 75 to 90 rabbits/ha, and the animals were released inside the artificial warrens. The rabbits did not undergo any kind of sanitary treatment prior to their release, no genetic analyses were carried out, and they were not subsequently submitted to any kind of artificial selection. All capture, transport and release processes were carried out by the same staff from the Andalusia Autonomous Government's Environmental Service.

Aerial predation

In the absence of observable remains of predated rabbits, predation by raptors within the enclosures was estimated by a census of birds of prey at 3 fixed points during winter and springtime, with a total number of 21 h of observation per zone and season (Redpath and Thirgood, 1997). An aerial predation risk index (APRI) was then created by dividing the total amount of flight time of the birds between the observation hours.

Rabbit abundance

Rabbit abundance was estimated by using monthly pellet counts at fixed points (Fernández-de-Simón *et al.*, 2011). A pellet abundance index (PAI) was created by observing the average abundance of pellets/d m^2 for every month and enclosure. All the statistical analyses were performed using the abundance estimates based on pellet counts. Considering the utility of a direct relationship between pellet-counting estimates and the actual number of rabbits in the enclosures, a general linear model (Model 1) was developed using concurrently collected data concerning the number of rabbits released in nine empty enclosures located in the same area as the enclosures used for this study; the size of the enclosures; the number of days the rabbits spent inside the enclosures prior to the first pellet-counts, and the number of pellets counted in them. In these 9 enclosures, the rabbits were released in autumn and provided with the same kind of food *ad libitum*. The number of rabbits released was corrected by a short-term mortality rate of 66% estimated in adjacent predator exclusion fences (Guerrero-Casado *et al.*, 2013b), similar to those estimated in other translocation exclusion fences (Cabezas *et al.*, 2011). The number of rabbits/ha could be calculated as (adjusted R^2=0.73; $F(1,8)$=25.4; P<0.001): No. rabbits/ha=[1323.9 (±262.7)×(No. pellets/m^2 d)+141.75]/(days since the last pellet-count). These data were analysed using R 3.0, and normality and homocedasticity were confirmed according to the model residuals.

Statistical analyses

Three general linear models were developed, with normal distribution of the residuals. To account for the autumn PGR, the relative increase (%) in rabbit abundance was estimated from November to January ($[PAI_{Jan}–PAI_{Nov}]/PAI_{Nov}\times100$). This model included data from 11 of the enclosures in set 1, since in the rest of set 1 rabbits had been released in November 2009, and the autumn PGR might therefore have been affected by the acclimation period after release. A general linear model (Model 2) was developed, in which the autumn PGR was the dependent variable, and the logarithm of November pellet abundance (ln PAI_{Nov}), the logarithm of enclosure size (lnSize) and the aerial predation risk index (APRI) were the independent continuous variables. Both the ln-transformation of the variable Size and PAI improved normality and homocedasticity according to the analysis of model residuals (P-plot and predicted-residuals plot). The spring PGR was estimated in each enclosure as the relative increase in rabbit abundance (%) from March to July ($[PAI_{July}–PAI_{March}]/PAI_{March}\times100$). This model included the data from 16 of the enclosures in set 1 (it was necessary to exclude 2 enclosures owing to management problems and another because the analysis of residuals suggested it to be an outlier) and the 6 enclosures in set 2. A general linear model (Model 3) was developed, in which the spring PGR was introduced as a dependent variable, the logarithm of March pellet abundance ($lnPAI_{March}$), the enclosure size and the aerial predation risk index (APRI) were the independent continuous variables and the data

Table 1: Autumn population growth rate (PGR): best-fit (lowest AICC) general linear models. The predictor variables are: logarithm of enclosure size (lnSize), logarithm of pellet abundance index (lnPAI) and aerial predation risk index (APRI).

No.	d.f.	Variables	AICc	ΔAICc	AICc weights	Deviance	*P*-value	Adjusted R^2
11	4	lnSize[1], lnPAI[1]	48	0	0.882	13.364	0.000	0.85
11	5	lnSize[1], APRI, lnPAI[1]	52.4	4.37	0.099	10.211	0.001	0.86
11	3	lnPAI[1]	56.3	8.24	0.014	45.509	0.001	0.53
11	4	APRI, lnPAI[2]	59.9	11.88	0.002	39.361	0.017	0.55

d.f.: degrees of freedom.

AICc: Akaike Information Criteria corrected for small sample size.

All the significant models ($P<0.05$) are shown and the significance of the variables included is indicated as follows: [1]($P<0.001$), [2]($P<0.05$), no signal ($P>0.05$). Adjusted R^2 corresponds to the whole models.

set (set 1 *vs.* set 2) was the independent categorical variable. The analysis of model residuals suggested normality (P-plot) and homocedasticity (predicted-residuals plot). Once non-significant variables had been excluded from the spring model (Model 3), another model (Model 4) was developed to check the possible effect of the autumn PGR on the spring PGR. Only the data regarding 9 enclosures from set 1 were available for this model. The spring PGR was the dependent variable, and the independent variables were the autumn PGR and $lnPAI_{March}$, the only variable included in the previous model (Model 3). The data were analysed by using R 3.0. Akaike Information Criteria corrected for small sample size (AICc) (Akaike, 1974; Burnham *et al.*, 2011) and Likelihood Ratio Tests (LRT) (Burnham and Anderson, 2002) were used to choose the best-fit models.

RESULTS

Model 2 chose the logarithm of November pellet abundance ($lnPAI_{Nov}$) and the logarithm of enclosure size (lnSize) as the most parsimonious model to explain the autumn PGR (Table 1). According to the LRT, there were no significant differences between the first and the second best models ($P>0.05$), so the model with the lowest number of parameters was chosen. The variable $lnPAI_{Nov}$ described 53.3% of the variability of the model and affected the autumn PGR in a negative manner ($\beta=-2.25\pm0.34$). lnSize additionally described 31.3% of the variability of the model, and also affected the autumn PGR in a negative manner ($\beta=-3.78\pm0.86$).

Model 3 only included the logarithm of March pellet abundance ($lnPAI_{March}$) in the most parsimonious model to explain the spring PGR (Table 2), signifying that partial R^2 coincides with R^2 of the model, and this variable affected the spring PGR in a negative manner ($\beta=-4.82\pm1.07$). According to the LRT, there were no significant differences between the first, and most simple, and the following 4 best models ($P>0.05$), so the model with the lowest number of parameters

Table 2: Spring population growth rate (PGR): best-fit (lowest AICC) general linear models. The predictor variables are: enclosure set, enclosure size, logarithm of pellet abundance index (lnPAI) and aerial predation risk index (APRI).

No.	d.f.	Variables	AICc	ΔAICc	AICc weights	Deviance	*P*-value	Adjusted R^2
22	3	lnPAI[1]	119.3	0	0.497	209.39	0.000	0.48
22	4	set, lnPAI[1]	122.1	2.74	0.126	206.72	0.001	0.46
22	4	APRI, lnPAI[1]	122.1	2.75	0.125	206.87	0.001	0.46
22	4	size, lnPAI[1]	122.1	2.81	0.122	207.38	0.001	0.45
22	5	APRI, lnPAI[1], set	123.8	4.42	0.055	191.21	0.002	0.47
22	5	size, APRI, lnPAI[1]	124.4	5.07	0.039	196.95	0.003	0.45
22	5	set, size, lnPAI[1]	125.5	6.12	0.023	206.62	0.004	0.43
22	6	set, size, lnPAI[1], APRI	127.4	8.08	0.009	189.60	0.007	0.44

d.f.: degrees of freedom.

AICc: Akaike Information Criteria corrected for small sample size.

All the significant models ($P<0.05$) are shown and the significance of the variables included is indicated as follows: [1]($P<0.001$), no signal ($P>0.05$). Adjusted R^2 corresponds to the whole models.

Table 3: Spring population growth rate (PGR): best-fit (lowest AICc) general linear models. Two predictor variables were tested: logarithm of pellet abundance index (lnPAI) and autumn PGR.

No.	d.f.	Variables	AICc	ΔAICc	AICc weights	Deviance	*P*-value	Adjusted R^2
9	3	lnPAI[1]	54.1	0	0.675	65.066	0.027	0.46
9	4	autumn PGR, lnPAI[1]	60	5.83	0.037	55.883	0.068	0.46

d.f.: degrees of freedom.

AICc: Akaike Information Criteria corrected for small sample size.

All the significant models ($P<0.05$) are shown and the significance of the variables included is indicated as follows: [1]($P<0.05$), no signal ($P>0.05$). Adjusted R^2 corresponds to the whole models.

was chosen. As the set variable was not included in this model, we assumed that there were no significant differences between the 2 sub-sets.

According to the LRT, there were no significant differences between the model which included the autumn PGR and $lnPAI_{March}$ to explain the spring PGR, and the model which only included the $lnPAI_{March}$. The autumn PGR was consequently excluded from the most parsimonious model (Model 4, Table 3). As the only significant variable was the logarithm of March pellet abundance ($lnPAI_{March}$), partial R^2 coincides with R^2 of the model, and the variable affected the spring PGR in a negative manner ($\beta=-5.33\pm1.92$).

For practical purposes, the negative and logarithmic relationship between the initial rabbit density (estimated according to PAI and Model 1), and both the autumn and spring PGRs, are depicted in Figure 2, which shows that although the population growth is generally higher in springtime than in autumn, in both cases an initial rabbit density of 30 rabbits/ha implied that the PGR was reduced to half of its highest value.

DISCUSSION

Rabbit abundance negatively affected the population growth rate within the enclosures, thus reducing their efficiency as extensive wild rabbit breeding systems. This result suggests that density-dependent factors were affecting the rabbit enclosures at a population level (Turchin, 1999). This density-dependence may have been caused by 2 factors: a decrease in reproductive rates at higher densities, already reported in rabbits (Myers and Poole, 1962; Rödel *et al.*, 2004b), but see (Trout and Smith, 1998), or an increase in mortality at higher densities, as has also been observed in rabbits (Rödel *et al.*, 2004a).

Our results show that, at a density of 30 rabbits/ha, the PGR was reduced to a half of its highest measured value. However, this value is not necessarily the same in different habitats or with different resources. The rabbit density at which the population growth rate diminished probably depended on the most limiting of the enclosures' resources. Food availability probably did not limit the PGR within the enclosures included in this study, since the pastures were not depleted during the study, and all the enclosures were provided with food and water *ad libitum.* The availability of breeding spots could, however, have been a limiting factor (Guerrero-Casado *et al.*, 2013c). The authors noted that the number of pallet warrens, despite the variability in the number of artificial warrens per enclosure, was probably reduced, and that the availability of places that were suitable for digging burrows limited the maximum rabbit abundance within the enclosures.

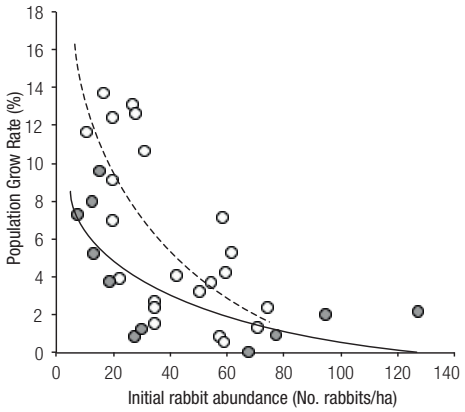

Figure 2: Linear regression for the initial rabbit density (rabbits/ha) and spring ([○], No.=22) and autumn ([●], No.=11) population growth rate (PGR). Logarithmic fit-in for spring data (---). Logarithmic fit-in for autumn data (—).

This study also highlighted the importance of the availability of shelter from predators, although the presence of birds of prey was not included in our best models.

The use of the territory by rabbits should also be taken into account, since the size of the social territories and the home range required by the rabbits could have limited the number of rabbits within the enclosures. Previous studies on similar enclosures measured social territories of between 0.032 and 0.07 ha (Ruiz-Aizpurua *et al.*, 2013). Otherwise, although the average home-range area becomes smaller as rabbit numbers increase (Myers and Poole, 1959), the average home range of wild rabbits can be 2-4 ha (Moseby *et al.*, 2005), so the fact that the size of some of the enclosures in set 1 was below the average area of the home range could have been limiting the population growth inside the enclosures. Enclosure size explained the autumn PGR in a significant manner, although not the spring PGR. The highest PGR corresponded to small enclosures, contrary to evidence which suggests that rabbits undergoing translocations to bigger enclosures will get better acclimated to their new environment (Rouco, 2008). However, the enclosure size was not as relevant during the springtime population growth. This might have been related to the fact that the PGR was generally higher in springtime, or that the range of enclosure sizes was larger than in the autumn PGR model, but more information will be necessary if any hypotheses are to be developed. Further research is therefore advisable.

The variable "set" did not add any relevant information to the spring PGR model, so it was assumed that any differences between set 1 and set 2, associated with the differences between years such as climatic conditions or vegetation growth, were not significant in the best-fit model.

Neither did the aerial predation risk (APRI) add any relevant information to the autumn or spring PGR models. Previous studies on similar enclosures in the area have observed that birds of prey have a great impact on rabbit enclosures, especially during the first weeks after the rabbits' release (Guerrero-Casado *et al.*, 2013b), and that growing rabbit populations might attract birds of prey (Guerrero-Casado *et al.*, 2013c). However, the results of this study suggest that birds of prey do not affect the population growth rate during autumn and spring population peaks, so further research would be interesting to achieve a better understanding of the manner in which birds of prey may affect rabbit restocking actions.

Another finding of this work was the lack of effect of the autumn PGR on the following spring PGR. It has been suggested that in small mammals an increase in fecundity might occur only at the expense of future survivorship or future reproductive output (Speakman, 2008). However, our results did not show any effect of the autumn PGR on the later spring PGR, thus suggesting no limitation as regards PGR due to the physiological cost of previous reproduction

CONCLUSION

Our data suggest that if PGR is to be optimised, rabbit densities within the plots should remain at below 30 rabbits/ha. We suggest that managers should avoid creating small enclosures, although the results of this study show a higher autumn PGR in smaller enclosures. To date, all previous studies indicate that large enclosures are better and more efficient than small ones, and the absence of the size variable in the best-fit spring PGR model suggests that the effect of enclosure size on the population growth rate is not clear in this study. We also suggest that managers should aim to optimise the efficiency of the enclosures, rather than producing rabbits to the full capacity of the enclosures: high rabbit densities will have low population growth rates, will likely attract more predators, and the most limiting resources of the enclosures will probably be depleted. It would be interesting to test different possible methods whereby rabbit populations could be maintained below 30 rabbits/ha.

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