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Original article

Assessing predictors of pellet persistence in European rabbits *Oryctolagus cuniculus*: towards reliable population estimates from pellet counts

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The European rabbit *Oryctolagus cuniculus* is a key species in Mediterranean ecosystems of the Iberian Peninsula, and reliable methods for monitoring its abundance are urgently required. Although clearance plot pellet counts may be useful in monitoring rabbit populations, such counts are potentially affected by variation in the persistence of rabbit pellets. The aim of our study was to assess persistence of rabbit pellets in the Iberian Peninsula for reliable estimates of rabbit abundance from clearance plot counts. We carried out the experiment from July 2006 to November 2007 at seven localities in central southern Spain. Marked fresh pellets were monthly placed at experimental plots, and their persistence was monitored monthly. Persistence was estimated from the proportion of marked pellets remaining between consecutive counts. Independent variables in analysis included slope steepness, vegetation, rabbit and ungulate activity, meteorology and temporal variables. Persistence significantly varied among localities and seasons and with their interaction. The final model showed that pellet persistence was best explained by total rainfall between counts, and also included the time between visits and slope steepness and the interactions rainfall*time between visits and rainfall*slope. Our results suggest that estimating pellet persistence for each locality and season is necessary to make estimates obtained from different localities and months comparable. In the Mediterranean region, early summer at the start of the dry season would be the recommended time for yearly rabbit monitoring based on any pellet-count index, since reduced rainfall favours pellet persistence. Sampling protocols must standardise the number of days between counts, and plots must be established in areas with gentle slope to maximise pellet persistence between counts.

Key words: central southern Spain, European rabbit, Mediterranean, Oryctolagus cuniculus, pellet counts, persistence, rainfall, sampling protocols

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The European rabbit *Oryctolagus cuniculus* is a key species in Iberian Mediterranean ecosystems (Valverde 1967, Delibes-Mateos et al. 2007); more than 40 predator species prey on rabbits (Delibes & Hiraldo 1981), including two endangered species: the Iberian lynx *Lynx pardinus* and the Spanish imperial eagle *Aquila adalberti* (Ferrer & Negro 2004). Rabbits also function as ecosystem engineers (Gálvez et al. 2009) and are an important small game species (Angulo & Villafuerte 2003). Although rabbits are considered a harmful pest species in other parts of the world (Thompson & King 1994), only in some localised areas of Spain does the density of this species become high enough for it to be regarded as an agricultural pest (Barrio et al. 2010, Ríos 2010). The European rabbit numbers on the Iberian peninsula have declined over recent decades, mainly as a consequence of habitat loss (Delibes-Mateos et al. 2010), but also due to the occurrence of two viral diseases: myxomatosis during the 1950s and rabbit hemorrhagic disease (RHD) at the end of the 1980s (Villafuerte et al. 1995). Ongoing declines in rabbit populations in central southern Spain (Moreno et al. 2007, Delibes-Mateos et al. 2008b) produce significant economic and ecological consequences (Delibes-Mateos et al. 2008a). Monitoring of rabbit populations is a major challenge, as is the development of widely applicable and reliable monitoring methods (Delibes-Mateos et al. 2009).

Counting of pellets is one method used to monitor rabbit abundance, and involves enumeration of pellets per unit area (Moreno & Villafuerte 1995, Palomares 2001, Delibes-Mateos et al. 2008b). Sampling units can be placed at permanent plots (Palomares 2001) or on linear transects (Delibes-Mateos et al. 2008b). To obtain absolute density estimates, it is necessary to take into account defecation and pellet persistence rates (Plumptre & Harris 1995). The clearance plot-count method involves counting pellets that accumulate over a known time period, using sampling units from which the pellets are regularly removed and counted. Using this method, it is important to define the period during which the pellet accumulation rate is highest and the disappearance rate lowest (Massei et al. 1998). The method can provide good estimates of rabbit abundance when animal densities are low (Murray et al. 2002), a situation in which the application of other methods is more limited.

Persistence can be expressed either as the proportion of pellets remaining between two consecutive counts (Murray et al. 2005), or as the number of days for which a group of pellets persists (Hemami & Dolman 2005). Persistence has been used frequently in the literature (e.g. Palomares 2001, Sanchez et al. 2009) as well as other related variables such as disappearance (Iborra & Lumaret 1997), decomposition (Cochran & Stains 1961, Flinders & Crawford 1977) or decay (Simonetti 1989, Prugh & Krebs 2004). However, few studies using pellet counts as abundance indices correct for persistence, despite the fact that corrections produce notably different results (Simonetti 1989). To assess pellet persistence rates, three different approaches have been used: 1) exponential decay rate, which allows calculation of a constant persistence rate by the use of which counts can be corrected (McClanahan 1986, Barnes & Jensen 1987); 2) methods that do not assume an exponential decay (Barnes & Barnes 1992); and 3) the variable persistence rate, which requires pilot experiments involving the placement of fresh pellets and subsequent observation to monitor persistence (Plumptre & Harris 1995). In our study, we employed the latter approach with the main aims of 1) studying rabbit pellet persistence in seven localities on the Iberian Peninsula, and 2) analysing the factors affecting persistence in these localities over the different seasons. We discuss our results in terms of the importance of considering pellet persistence in attempts to derive reliable rabbit density estimates from pellet counts at permanent plots.

Material and methods

Our experiments were carried out between July 2006 and November 2007 at seven locations in central southern Spain, each with different rabbit abundances but with similar habitat structure and climate (Fig. 1). Thus, all locations have a Mediterranean climate characterised by wet mild winters and warm dry summers with a marked drought period. The habitats mainly comprised Mediterranean scrubland, pasture, cropland, 'dehesa' (savanna-like formations combining pasture with intermittent cereal cultivation in park-like oak *Quercus* spp. woodlands; Blondel & Aronson 1999) and tree plantations. For each location, we established an experimental site (40 permanent plots) in an ecotone area between Mediterranean scrubland and either pastureland or cropland. We arranged the plots along four parallel lines of 10 plots per line, except in location 6 (see Fig. 1), where we arranged the plots along five parallel lines with eight plots per line, due to terrain constraints. Each plot consisted of a 0.5-m^2 circle with a wooden stake placed vertically in the centre. The distance between plots and lines was 10 m, creating a regular sampling grid at each location. The terrain and habitat covered in the experimental site were homogeneous due to the rather small area of the grid (30×90 m, but 40×70 m in the case of location 6).

We estimated at each plot a rabbit pellet persistence index by means of marking fresh pellets with a small spot of white nail polish (Kufeld 1968), which allows free exposition to environmental factors, though it might affect persistence to some degree. Pellets were considered fresh when they were of dark

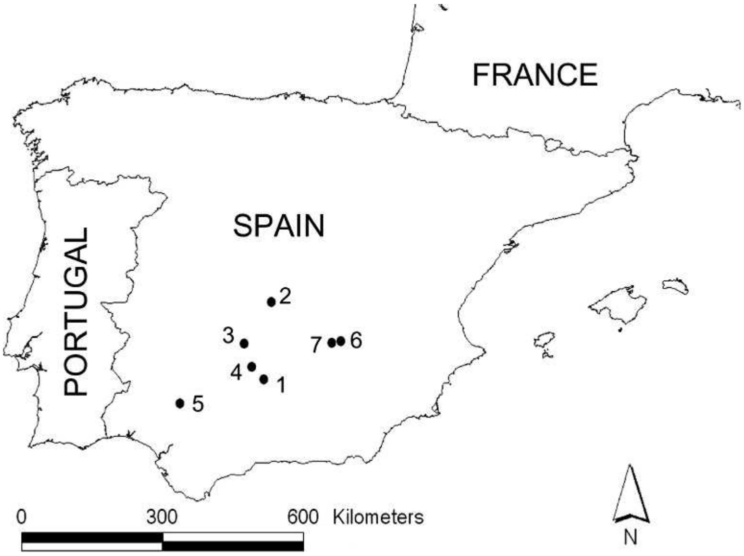

Figure 1. Location of the study areas 1-7 on the Iberian Peninsula.

outer colour, relatively soft and had a glossy patina and no cracks (Hibert et al., in press). Fresh pellets were collected in the surroundings of the grid zone except when enough fresh pellets could not be found; in such cases, we used pellets from a different zone or study area. This only occurred regularly in study area 3 (see Fig. 1). Initially, we placed 10 marked pellets at each of five plots (totalling 50 pellets/month and study area), after having moved any old pellets. We commenced with the first five plots on the grid, and in the following month, we placed pellets at the next five plots and so on. Eight months after placement, we removed the remaining marked pellets in a given plot, and we placed new marked pellets in the plots. Rabbit pellets may last for more than six months in Mediterranean environments (Palomares 2001), but we observed that after eight months, a low proportion still persisted. Although this could affect the estimates of maximum or average persistence, our main interest in this study was to identify the factors affecting pellet persistence rather than estimating maximum or average persistence time. We selected this procedure because of its simplicity, though other options might also have been adequate to sample the variability of factors of the grid (e.g. a spatially random procedure).

We counted the marked pellets remaining after each month at each plot. We defined our persistence index as the proportion of marked pellets that remained intact at the end of each period, related to the number of marked pellets counted in the previous visit. We calculated the persistence index for each locality, month and permanent plot, with the pellet age defined as the number of days since initial placement. We preferred to use this value instead of other options (e.g. persistence rate) and the number of days between counts (ND) as one of the variables (Table 1) to be related to the rabbit pellet persistence.

In autumn 2007, we measured the percentage maximum slope (S) at each permanent plot individually using a digital inclinometer (Bosch DNM 60 L Professional; Bosch, Leinfelden-Echterdingen, Germany). We visually estimated the percentage of woody vegetation cover within a 1-m radius circle with the plot as the centre, considering three height categories: < 50 cm (LW), 50 cm - 2 m (MW) and > 2 m (HW). Moreover, we measured the average vegetation height (VH) within a distance of 5 m from each plot in 20 points, at 1-m intervals following four directions from the plot: forward, behind, left and right. For heights < 2 m, measures were taken using a precision of 0.1 m, and for heights > 2 m, the precision was 1 m. The average of these 20 height measurements for each plot was considered as the variable VH.

To detect possible effects on persistence due to activity (stepping, digging) of ungulates and rabbits at the experimental zones, we used monthly counts of fresh pellets as indices of rabbit and ungulate activity. At each monthly visit, we counted and removed all intact (unmarked) pellets within each 0.5-m^2 plot (see above). The ungulate index may provide an indirect measure at each plot of pellet damage caused by

Table 1. Variables involved in the persistence of rabbit pellets at permanent plots. Steps 1, 2 and 3, respectively, correspond to the questions: 1) Variables correlated with persistence, 2) Variables considered to develop a multivariate model and 3) Variables included in the multivariate model of pellet persistence. In step 1, the Spearman correlation index (R_s) of significant ($P < 0.05$) correlations is shown. '+' indicates a positive correlation, '-' a negative correlation and italics show $P \leq 0.001$. In steps 2 and 3, asterisks show the variables selected in these steps.

Code	Variables	Step 1	Step 2	Step 3
S	Maximum slope (in %)	*0.17*$^{-}$	*	*
	Vegetation variables			
LW	Woody vegetation < 50 cm (in %)	0.09^{-}	*	
MW	Woody vegetation > 50 cm (in %)	0.06^{-}		
HW	Woody vegetation > 2 m (in %)			
VH	Mean vegetation height (in m)			
	Rabbit and ungulate activity variables			
RP	Rabbit pellets (pellets m^{-2} day^{-1})			
UP	Ungulate pellets (pellets m^{-2} day^{-1})			
	Meteorological variables			
TR	Total rainfall (in mm)	*0.33*$^{-}$	*	*
RI	Number of days with rainfall > 10 mm	*0.32*$^{-}$		
MinT	Mean minimum temperature (in °C)	0.08^{+}		
MaxT	Mean maximum temperature (in °C)	0.09^{+}		
TA	Mean daily thermal amplitude (in °C)	*0.14*$^{+}$		
FD	Number of days below 0°C			
WD	Number of days above 25°C	0.08^{+}		
MT	Mean temperature (in °C)	0.08^{+}		
	Temporal variables			
Age	Age of pellets (in number of days)			
ND	No. of days between visits	0.07^{-}	*	*

ungulate behaviour (Massei et al. 1998). The rabbit index may provide a direct measure at each plot of the increase of persistence produced by the accumulation of pellets and then lesser influence of climatic factors (Iborra & Lumaret 1997).

For meteorological information (see Table 1), we used data from the meteorological station (Spanish Agency of Meteorology) located closest to each of the experimental locations (mean distance = 15 km, range: 5-28.6 km).

Statistical analyses

Does persistence vary with locality, season or their interaction?

We calculated the mean monthly persistence of rabbit pellets for each locality and month, and analysed the effects of locality (random factor), season and their interaction by performing a generalised linear mixed model (GLMM). We only considered pellets aged ≤ 3 months in order to avoid an excessive number of plots with no data because of the disappearance of all marked pellets. As the residuals of the model were normally distributed according to the Normal P-plots (Zar 1974), we did not transform the dependent variable. We conducted Tukey's *post hoc* test within the GLMM application to find differences between pairs of localities or seasons.

Variables correlated with persistence

We performed Spearman correlations using the pellet persistence index for each locality, month and permanent plot, against the parameters mentioned above (see Table 1). We selected again the data sets involving pellets of ≤ 3 months of age. We performed correlations with pooled data from all localities and seasons as the range of variation of the independent variables are larger when pooling data. Association between variables was assessed using the Spearman correlation index (R_s) and was considered significant when $P < 0.05$.

Variables considered to develop a multivariate model

To control for multicollinearity (Graham 2003), we tested correlations of pairs of variables of the same type (e.g. meteorological variables) which significantly correlated to the persistence index (see above). Again Spearman correlations (R_s coefficient) with $P < 0.05$ were considered significant. When correlated, we used those variables with higher levels of significance and greater R_s in the correlations against the persistence index (see above).

Variables included in the multivariate model of pellet persistence

Again, a generalised linear mixed model (GLMM) was built using the pellet persistence index for each locality, month and plot (again based on pellets of ≤ 3 months of age) as dependent variable and the variables selected from the previous step and their interactions. Again, the residuals of the model were normally distributed according to the Normal P-plots (Zar 1974), hence no transformation was needed. The locality (L) and the permanent plot (PP) were included as random variables, which implies a multilevel ordination in GLMM (Goldstein 1995), so we did not nest PP within L. For model selection, the backward stepwise deletion of least significant terms based on P-value was performed. The coefficient of determination (R^2) expressed the ability of the factors (independent variables) used in the model to explain the variation in persistence (dependent variable). All analyses were carried out using the software STATISTICA 6.0 (StatSoft Inc. 2001).

Results

Does persistence vary with locality, season or their interaction?

According to the GLMM, locality, season and their interaction significantly affected mean monthly pellet persistence (locality: $F_{6,\ 1153} = 5.17$, $P = 0.003$; season: $F_{3,\ 1153} = 5.26$, $P = 0.009$; locality*season: $F_{18,\ 1153} = 6.89$, $P \leq 0.001$; Fig. 2). The mean monthly persistence index (% ± SE) was highest in locality 5 (92.85 ± 0.95) and lowest in locality 1 (45.99 ± 3.86), being both significantly different to the rest of the localities ($P \leq 0.001$; see Fig. 2). Summer obtained the highest mean monthly persistence index (84.44 ± 1.47) and spring obtained the lowest (59.31 ± 2.29), both being significantly different to the rest of the seasons ($P < 0.05$; see Fig. 2).

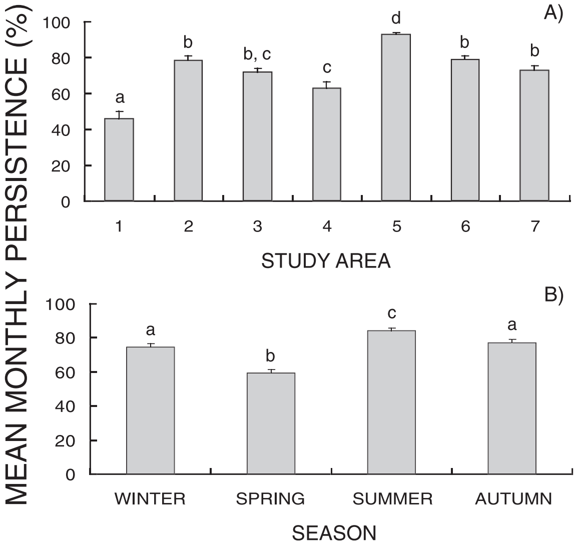

Figure 2. Mean monthly persistence (in %) of rabbit pellets ≤ 3 months of age considering the seven different localities (A) and the four seasons (B). Means (with SE indicated) marked with a common letter above the bars are not significantly different from each other ($P < 0.05$; Tukey's *post hoc* test).

Variables correlated with persistence

Slope steepness (mean = 16.8%, range: 0 - 46.6%) was negatively correlated with the persistence index ($R_s = 0.17$, $N = 1{,}056$, $P \leq 0.001$). Between the vegetation variables, LW ($R_s = 0.09$, $N = 1{,}056$, $P = 0.003$) and MW ($R_s = 0.06$, $N = 1{,}056$, $P = 0.04$) significantly and negatively correlated with pellet persistence. Among rabbit and ungulate activity variables, none of the variables were correlated with the pellet persistence index. Most meteorological variables showed significant correlations with persistence. Correlations were negative in the case of TR ($R_s = 0.33$, $N = 1{,}217$, $P \leq 0.001$) and RI ($R_s = 0.32$, $N = 1{,}217$, $P \leq 0.001$), and positive in the case of TA ($R_s = 0.14$, $N = 1{,}217$, $P \leq 0.001$), MaxT ($R_s = 0.09$, $N = 1{,}217$, $P = 0.002$), MT ($R_s = 0.08$, $N = 1{,}217$, $P = 0.003$), MinT ($R_s = 0.08$, $N = 1{,}217$, $P = 0.007$) and WD ($R_s = 0.08$, $N = 1{,}217$, $P = 0.007$). With respect to temporal variables, ND showed a significant negative correlation with the pellet persistence index ($R_s = 0.07$, $N = 1{,}202$, $P = 0.02$). The variables significantly correlated with persistence in decreasing order of correlation coefficients were TR, RI, S, TA, MaxT, LW, MT, MinT, WD, ND and MW (see Table 1).

Variables considered to develop a multivariate model

Woody vegetation < 50 cm (LW) was significantly and positively correlated with MW ($R_s = 0.37$, N = 1,056, $P \leq 0.001$). Total rainfall (TR) was significantly correlated with the rest of meteorological variables, positively with RI ($R_s = 0.92$, N = 1,217, $P \leq 0.001$) and negatively with TA ($R_s = 0.49$, N = 1,217, $P \leq 0.001$), MaxT ($R_s = 0.27$, N = 1,217, $P \leq 0.001$), WD ($R_s = 0.22$, N = 1,217, $P \leq 0.001$), MT ($R_s = 0.22$, N = 1,217, $P \leq 0.001$) and MinT ($R_s = 0.15$, N = 1,217, $P \leq 0.001$). Therefore, we selected four variables as fixed factors for the model: S, LW, TR and ND (see Table 1).

Variables included in the multivariate model of pellet persistence

After the backward model selection procedure, the model included the following variables (see Table 1): total rainfall (TR; $F_{1, 796} = 16.08$, $P \leq 0.001$), days between visits (ND; $F_{1, 796} = 7.11$, $P = 0.008$), slope (S; $P = 0.52$), and the interactions ND*TR ($F_{1, 796} = 12.67$, $P \leq 0.001$) and TR*S ($F_{1, 796} = 3.9$, $P = 0.048$). The model significantly explaining the pellet persistence index ($R^2 = 0.48$, $F_{244, 796} = 3.05$, $P \leq 0.001$) and is expressed as: Persistence = 0.68 - 0.01 × TR - 0.01 × ND + 0.01 × S + 0.001 × ND*TR - 0.001 × TR*S.

Discussion

In our study, rabbit pellet persistence varied significantly with season, locality and their interaction. In this sense, Putman (1984) noted that dung persists at different rates depending on the time of the year, the habitat and the climatic conditions. According to our results, where pellet counts are to be used to estimate rabbit abundance in Mediterranean habitats, pellet persistence should be estimated in the relevant study areas and the seasons during which surveys are planned. Furthermore, identifying the factors affecting such persistence is also necessary for correcting the density estimates (Murray et al. 2005). In our case, the multivariate model showed that total rainfall and its interaction with number of days between counts were the significant variables most affecting rabbit pellet persistence. The negative relationship between rainfall and persistence is consistent with another study on lagomorphs (Iborra & Lumaret 1997). Then, pellets counts obtained in the same months but different years may not be comparable because different rainfall affecting the persistence would require correcting the number of pellets found for persistence. If this is not possible, and rabbit monitoring of Mediterranean habitats with yearly periodicity is the unique alternative, it is advisable to obtain the pellet-count index during early summer, at the start of the dry season. On the other hand, the number of days between counts was significantly and negatively related to persistence in the multivariate model, suggesting that regular counts (as recommended by Murray et al. 2005) are desirable to avoid pellet loss. This may be achievable in small-scale projects with good access to the study areas, but in large-scale projects where resources are limited, we recommend ongoing monitoring of persistence index to enable correction of pellet count data at any given time. Related to the significant interaction between rainfall and slope obtained in the multivariate model, it may be difficult to control for the effect of these factors when sampling mountainous areas, apart from selecting zones with a gentle slope. On the other hand, locating the plots in ecotone areas near croplands and pastures (as suggested by Delibes-Mateos et al. 2008b) will also increase the probability of selecting areas with a gentle slope.

Several variables were not measured (e.g. coprophagy; Lumaret et al. 1992, diet; Murray et al. 2005 and soil type), and furthermore, several of the variables considered did not show an overall effect on persistence, despite previous reports of such associations (e.g. rabbit and ungulate activity; Iborra & Lumaret 1997, Massei et al. 1998). Overall, persistence is affected by a large number of variables, and their effects may vary between localities and seasons. This complexity of factors may be the reason for the moderate variance explained by the model (48%). Future studies should consider these topics in detail, although these results allow wildlife researchers in Mediterranean areas to consider factors that may bias their pellet-count sampling designs. Previous studies have shown that it is necessary to simultaneously consider pellet persistence and defecation rates when using pellets counts to estimate animal densities (Marques et al. 2001, Laing et al. 2003, Campbell et al. 2004). In our study, we have provided the first report of persistence of European rabbit pellets at a regional scale in Mediterranean areas of the Iberian Peninsula. There is only one study measuring defecation rates of rabbits from the Iberian Peninsula (Gonzalez-Redondo 2009). Future research should investigate further in these areas and also in quantifying the relationship between the census method and the current density of the species (Homyack et al. 2006). In central southern Spain, clearance pellet counts corrected for pellet persistence, estimated as described in our paper, was the index best related to rabbit density estimates in summer (Fernandez-de-Simon et al., in press). This indicates the suitability of the method as a standardised index of rabbit abundance for this area.

Implications for rabbit density estimates

Our persistence estimates will enable corrections to be made to pellet counts from experimental plots, providing an unbiased index of rabbit abundance. Future studies should include measurements of pellet persistence if the clearance plot pellet count method is to be used. This can easily be performed using the methods described in our study. Where estimates of pellet persistence are not available, correction factors estimated simultaneously in similar localities (if available) should be used to correct pellet counts. However, the high variability observed suggests that individual estimates of persistence for each locality and season are highly advisable, and that failure to incorporate correction factors from persistence may lead to biased estimates of rabbit abundance.

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