Acta Theriologica 48 (3): 385–398, 2003.
PL ISSN 0001–7051

Effect of vegetation type and environmental factors on European wild rabbit *Oryctolagus cuniculus* counts in a southern Portuguese montado

Helena MARTINS*, Helena BARBOSA, Matthew HODGSON,
Rui BORRALHO and Francisco REGO

Martins H., Barbosa H., Hodgson M., Borralho R. and Rego F. 2003. Effect of vegetation type and environmental factors on European wild rabbit *Oryctolagus cuniculus* counts in a southern Portuguese montado. Acta Theriologica 48: 385–398.

This study assesses the effect of vegetation and variables related to weather and light conditions on the efficacy of rabbit *Oryctolagus cuniculus* (Linnaeus, 1758) counts carried out in the south of Portugal. Counts were carried out in two years using driven line transects, and correlated with vegetation type and the variables using generalised linear models. The offset was a surveyed area estimated using Distance Sampling Theory as a means of correcting for detectability bias. More rabbits were observed in dense vegetation during day-time counts and in crops during night-time counts. In 1998, day-time counts were higher with higher average daily temperatures, whilst the night-time counts were higher with higher minimum daily temperatures. In 1999, day-time counts decreased with the amount of rainfall in the previous month, and the night-time counts decreased with the accumulated rainfall in the previous two months and with the higher wind speeds. In order to increase efficacy, counts should be carried out either at dawn or at dusk during the post-breeding season, and with greater intensity in dense scrub or open vegetation with high tree cover. During the breeding season and winter, counts should be carried out after dusk and with greater intensity in arable crops.

Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen, AB15 8QH, Scotland, United Kingdom, e-mail: hmartins@mluri.sari.ac.uk (HM); Applied Ecology Centre Prof. Baeta Neves, Agronomy Institute of Lisbon, Tapada da Ajuda, 1349-018 Lisboa Codex, Portugal (HM, HB, FR); Biomathematics and Statistics Scotland, Craigiebuckler, Aberdeen, AB15 8QH, Scotland, United Kingdom (MH); Erena, Lda. Management of Natural Resources, Av. Visconde Valmor, 11-3ş, 1000-289 Lisbon, Portugal (RB)

Key words: *Oryctolagus cuniculus*, population density, efficacy of counts, habitat use, Portugal

Introduction

The wild rabbit *Oryctolagus cuniculus* (Linnaeus, 1758) is a popular game species in the Iberian Peninsula and, particularly in Portugal, its game exploitation

* Present address and address to which correspondence should be sent: Applied Ecology Centre Prof. Baeta Neves, Agronomy Institute of Lisbon, Tapada da Ajuda, 1349-018 Lisboa Codex, Portugal, e-mail: ceabn@isa.utl.pt

is an important source of income (Bugalho and Cipriano 1999). It is also a key species in Mediterranean food webs, being the main prey of several predators, some of which are classed as endangered species (Jaksic and Soriguer 1981, Iborra *et al*. 1990, Palomares and Delibes 1991, Ontiveros and Pleguezuelos 2000).

Specific management of the species has been required in some areas of its range, especially because high population densities can cause significant damage to arable crops and pastures (ONC 1984, Carvalho and Bugalho 1986, Bell *et al*. 1999), regeneration of forest stands (Stevens and Weisbrod 1981) and natural vegetation (Jaksic and Fuentes 1980, Chapuis 1986, Thompson 1994). In Iberian regions, wild rabbit populations have decreased in the past decades due to habitat changes, diseases and excessive predation and hunting (Moreno and Villafuerte 1995, Moreno *et al*. 1996, Palomares *et al*. 1996). The principal current management objective is, therefore, to restore their populations.

Most research concerning variation of rabbit numbers with environmental factors has been done in areas where the wild rabbit has been introduced and where the different environmental conditions might have determined changes in its biology and behaviour (Wallage-Drees 1989, Villafuerte *et al*. 1993). In Mediterranean areas, where it is a native species, research has been done on the effects of vegetation type, weather and light conditions on rabbit counts at each habitat (eg Soriguer and Rogers 1981, Béltran 1991, Villafuerte *et al*. 1993), but has not taken an integrated approach. In Portugal, this subject has never been clarified, although their understanding is essential for the development of appropriate population and habitat management strategies. It is, therefore, important to undertake counts in Portuguese habitats under different environmental conditions in order to capture this variation and understand its driving factors.

The aim of this study is to characterise the spatial and temporal variation of rabbit counts in relation to vegetation type, weather and light conditions in a southern Portuguese montado, ie a savannah-like ecosystem dominated by cork oak and holm oak stands spatially characterized by an open structure. We predicted that these environmental variables affect efficacy of counts differently along the year in close correlations with the reproduction cycle.

Study area

The study area was a 270 ha hunting estate in south-east Portugal (38°47'N, 7°25'W), comprising a rolling landscape between 300 and 420 m in altitude. The climate was Mediterranean with strong seasonality, being characterised by hot and dry summers (average temperature of 25°C and average rainfall 2 mm, in August) and rainy and mild winters (average temperature of 9°C and average rainfall 100 mm, in January) (Rosário *et al*. 1983).

The vegetation consisted mainly of cork oak (*Quercus suber* L.) and holm oak (*Quercus rotundifolia* L.) open stands, herein referred as montados, some of them undersown with crops of triticale (X *Triticosecale* Wittmack) and oats (*Avena sativa* L.). The remaining understorey was dominated either by patches of gum cistus or natural pasture.

Material and methods

Rabbit counts

Counts followed the line transect method (Buckland *et al*. 1993) and were carried out in three different seasons in the year, which reflect different stages of the reproductive biology of the studied population (Alves and Moreno 1996), its size and the dispersion of individuals. These seasons were: (a) breeding season (January–June), (b) the post-breeding season (July–September), and (c) winter (October–December).

The observers went through a previous training in order to standardise the counts procedure. In order to minimise the drawbacks associated with the transect sampling design adopted (Buckland 1985, Buckland *et al*. 1993), it was ensured that the transect centre line was well defined, and only detections made in straight sections of the track were considered. Since corners and loops were cut, only 5925 m were surveyed at each count in total, and the individual transect lengths varied from 49 to 842 m.

The counts were performed by two observers driving a car along dirt tracks, on 3 consecutive days, in two occasions in each season, separated by at least 3 weeks, and over 2 years (1998 and 1999). Moreover, at each one of the surveyed days, potential activity peaks within the day were chosen to carry out counts, namely shortly after sunrise under good light conditions (Villafuerte *et al*. 1993, Moller *et al*. 1996), 1 hr before sunset (Villafuerte *et al*. 1993, Villafuerte and Moreno 1997) and shortly after dusk under total darkness conditions (Rogers 1981, Villafuerte *et al*. 1993, Moller *et al*. 1996). Field observations suggested the relevance of the inclusion of two extra counts, one 2 hr after sunrise and the other 2 hr after dusk. These times were selected to cover situations of occurrence of rainfall or strong wind in the previous count, that could delay emergence from warrens (Rowley 1957). The interval of 1 hr between these extra counts and the precedent ones was accepted as sufficient to insure the reestablishment of a normal behaviour of the population after disturbance, on the basis of field observations.

Each count took approximately 1 hr. The speed of the vehicle was maintained at 10–20 km/hr. Night-time counts used a hand-held 100 W, 12 V quartz-halogen spotlight, directed regularly at approximately 45° either side of the transect line (Rogers 1981). Prior training in visually estimating distances was carried out. The direction along which transects were driven was alternated to compensate for possible different activity levels in different survey sections at different times (Rogers 1981).

When more than one individual was present within a distance not exceeding 10 m (Villafuerte and Moreno 1997), the detection was considered as a group and its size was recorded. The perpendicular distance, either from individuals or from the geometric centre of groups, was visually estimated. A pilot study, based on the pattern of variation of the mean error between actual measured and visually estimated distances, led to the definition of six distance classes: 0–5 m, 5–15 m, 15–25 m, 25–40 m, 40–60 m and 60–100 m.

At each detection, the vegetation type that the detected individuals were on was recorded. Six different vegetation types were considered: (a) cleared scrub: oak stands where scrub clearance had been undertaken, characterised by a disrupted scrub and herbaceous layer; (b) pasture: oak stands with pasture as the understorey, and without scrub; (c) arable crops: unfenced areas either with triticale or oats, and with a reduced number of trees, which are not harvested and are aimed at providing food for the game populations; (d) tall scrub: oak stands where the vegetation cover is dominated by tall and dense scrub, with a reduced herbaceous layer; (e) medium scrub: oak stands covered by tall shrubs but sparsely distributed, leaving reasonable open patches of herbaceous vegetation; (f) low scrub: oak stands with low shrubs very sparsely distributed and interspersed with natural pasture.

The environmental variables, whose effect on counts was investigated, were selected as being those that potentially affect wild rabbit activity, behaviour and consequent dispersion (Southern 1940, Rowley 1957, Kline 1965, Gibb *et al*. 1978, Fraser 1992, Kolb 1992, Villafuerte *et al*. 1993) and are given in Table 1. Complete records of temperature, wind intensity, relative humidity and barometric pressure were obtained from the Évora meteorological station (altitude: 309 m, longitude: 7°54'W, latitude: 38°34'N), 20 km from the study site. Rainfall values were measured at the study area.

Table 1. The environmental variables whose effect on rabbit counts was assessed.

Variable	Categories/Units
Daily maximum temperature	°C
Daily minimum temperature	°C
Daily average temperature	°C
Nearest temperature to the count	°C
Rainfall within the previous 60 days	mm
Rainfall within the previous 30 days	mm
Rainfall within the previous 15 days	mm
Rainfall within the previous 7 days	mm
Rainfall in the previous day	mm
Number of days since last rainfall	*n*
Occurrence of rainfall during count	0 – no rain
	1 – raindrops
	2 – heavy rain
Cloudiness	0 – clear sky
	1 – some clouds
	2 – cloudy
	3 – total cloud cover
Relative humidity	%
Barometric pressure	hPa
Wind speed	0 – no wind
	1 – moderate wind speed
	2 – high wind speed
Sun height	° (degrees)
Illuminated fraction of the moon	%
Order	1 – shortly after sunrise
	2 – 2 hr after sunrise
	3 – 1 hr before sunset
	4 – shortly after dusk
	5 – 2 hr after dusk

Modelling of counts

Log-linear modelling was used to fit explanatory linear models correlating rabbit counts with the environmental factors (McCullagh and Nelder 1991). The rabbit counts were assumed to follow a Poisson distribution of mean μ calculated as:

$$\mu_i = \mathrm{A}_i \times \lambda_i$$

and hence

$$\log \mu_i = \log \mathrm{A}_i + \log \lambda_i$$

where the surveyed area is calculated by $A_i = 2xL_ixESW_i$, i is the vegetation type crossed by transect replicates of total length L_i(m) and ESW_i (Effective Strip Width, metres) was estimated using Distance 3.5 after data truncation (Thomas *et al*. 1998); and λ_i is an index of rabbits' abundance (number of animals/ha of *ESW*), which was regressed against environmental variables. *ESW* was estimated considering the detection unit as the group, and corrected for detectability bias due to group size by regressing *ln*(*group size*) against the detection function, $g(y)$, in cases where their correlation was significant. The detection function represents the probability of detection of an object or object cluster at a distance y from the transect line (Buckland *et al*. 1993).

The *ESW* is defined as the distance from the line such that the number of unseen animals located closer to the line equals the number of animals seen further away (Gates 1979). Thus, *ESW* is the distance from the transect line such that the number of rabbits in the area *A* would equal the total number of detected animals according to the detection probability associated with the vegetation type (Buckland *et al*. 1993). Using the *ESW* in the calculation of the index of rabbits' abundance makes the counts conditional on the detection probability allowed by each vegetation type. Therefore, it is possible to compare counts in different vegetation types, since the detection functions correct for differences in detectability.

To estimate the *ESW*s, different detection functions were tested for each vegetation type, in each season and under day-time and night-time conditions. The most accurate model for each combination of vegetation type, season and light conditions was selected on the basis of the lowest Akaike's Information Criterion (AIC; Burnham and Anderson 1998). The fact that the counts were repeated on the same day and consecutive seasons makes them pseudoreplicates (Hurlbert 1984). This leads to a situation where the sampling variance exceeds the model-based Poisson variance, and this was taken into account by allowing the estimation of a dispersion parameter from the residual mean square of the fitted models (McCullag and Nelder 1991, Burnham and Anderson, 1998).

The environmental variables tested in the models were organised into four functional groups, related to temperature, rainfall, other weather variables and comfort or risk of predation. The latter did not take into consideration changes in predation pressure (Palomares and Delibes 1997) since this was considered stable during the study period. From each group, variables were included in sub-models either for being highly correlated with the observed rabbit abundance (λ_i), or after being selected by a stepwise procedure. The inclusion process, as well as the definition of the functional groups, were carefully conducted in order to avoid collinearity and produce the most reasonable sub-models in terms of interpretation and ecological meaning. The interaction between cloudiness and illuminated fraction of the moon was also analysed. Besides these sub-models, a model with all the variables and a model with only vegetation type were also included in the comparison. All the models were obtained using Genstat 5 (Genstat 5 Committee 1993). Different models were fitted for each year, because the proportion of tall scrub changed between years due to scrub clearance and hence λ_i would reflect both the change in rabbit counts and in habitat area. The criterion used to select the best model was the maximisation of the amount of variance explained by the variables included in the model divided by the number of degrees of freedom in order to be parsimonious (Mean Regression Deviance). It is a criterion that simplifies the use of analyses of deviance to identify the important terms, without attempting to assign precise significance (McCullagh and Nelder 1991). It also allows the comparison of exploratory models that are not necessarily nested. Comparison was made with the models others than the best to check if the increase in Mean Regression Deviance was significant or if important ecological information was not being omitted by not selecting them.

Results

The sampling effort was not strictly proportional to habitat availability due to the use of the dirt tracks present (in 1998 the correlation was $r_P = 0.74$ and in 1999 was $r_P = 0.71$). Therefore, the number of counted rabbits was affected by both survey effort and habitat selection, conditional on seasonal, weather and light conditions. Interpretation of the models in terms of habitat use is nonetheless possible if the effect of survey effort is minimized, which was achieved by fitting different models for each year since the proportion of tall scrub decreased due to scrub clearance between years.

The seasonal changes in the number of rabbits counted during day-time and night-time counts are presented in Fig. 1. The highest number was observed during the post-breeding season. During the breeding season and the winter, the observed night-time numbers were higher than the day-time ones, but in the post-breeding season day-time numbers were higher than the night-time ones. There was occasionally an inversion in the pattern of counts between day-time and night-time.

The probability of detection for each vegetation type, within the same season and for day-time and night-time surveys, was assumed constant between years and periods. Thus day-time and night time counts within each season were obtained by pooling counts across periods of the same season and across the same season of both years. In spite of this, it was not possible to obtain a sample size sufficient (n of counts < 20) to accurately estimate *ESW* for cleared scrub. Aggregation of this habitat type with another was not possible due to its characteristically disrupted herbaceous and scrub layers. Therefore, this vegetation type was excluded from the analysis.

The negative exponential model had the lowest AIC value on several occasions. There was evidence of spiked data, which is considered to be inadequate for reliable modelling. In these cases, the hazard-rate model was applied (Buckland *et al*. 1993).

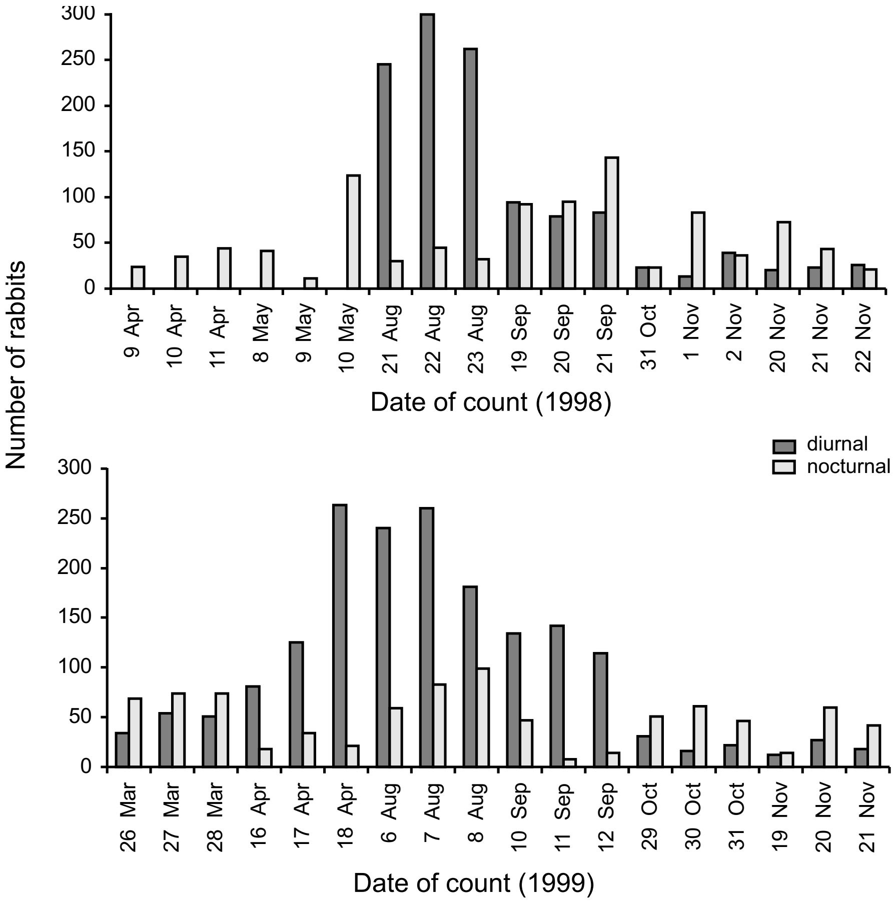

Fig. 1. Patterns of change of rabbit detections during the surveys in 1998 and 1999.

Table 2. Effective Strip Width (ESW) estimates and coefficients of variation (CV).

Vegetation type		Season					
		Breeding season		Post-breeding season		Winter	
		Day-time	Night-time	Day-time	Night-time	Day-time	Night-time
Arable crop	ESW (m)	9.03	7.57	35.98	9.97	34.17	12.70
	CV (%)	12.3	19.8	3.4	6.8	27.8	9.2
Pasture	ESW (m)	23.19	3.15	10.16	4.94	3.47	3.38
	CV (%)	15.4	26.0	28.0	14.1	29.1	27.1
Tall scrub	ESW (m)	7.22	6.39	9.01	6.31	5.53	6.86
	CV (%)	13.0	18.4	10.0	21.7	15.6	20.3
Medium scrub	ESW (m)	9.87	7.08	7.79	5.36	10.18	6.93
	CV (%)	10.5	13.4	8.5	13.9	9.5	11.4
Low scrub	ESW (m)	13.93	9.32	14.69	7.60	15.27	10.91
	CV (%)	15.8	14.8	13.1	15.5	7.6	9.5

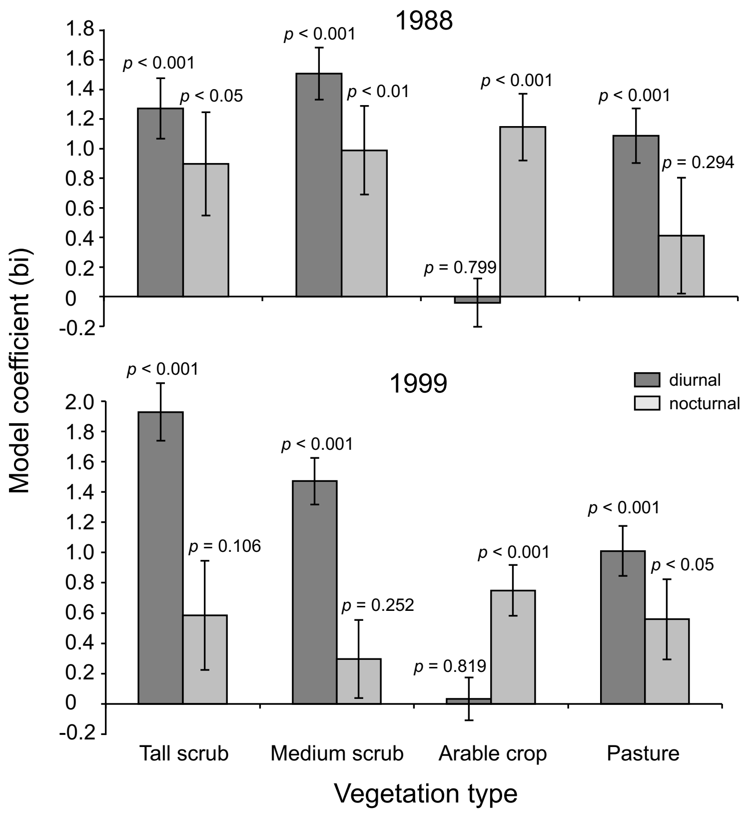

Fig. 2. Relative comparison of the results of the counts with the vegetation type, in relation to low scrub, for 1998 and 1999. This comparison is made by the size of the bars, ie the value of the coefficients associated with the vegetation type in models explaining the results of the performed counts (± SE of the coefficient estimates).

Table 3. Models to explain the results of the counts performed during the study period in terms of interaction between vegetation type and season (* no data collected during day-time). The model coefficients represent the change in counts in relation to breeding season and low scrub, respectively, categories left out to guarantee independence. Only for models to explain day-time counts in 1998, the coefficient for winter represents the change in relation to post-breeding season.

Vegetation type	Time	Variables	Year and season			
			1998		1999	
			Post-breeding*	Winter	Post-breeding	Winter
Arable crop	Day-time	Coefficient	–	−2.666	0.263	−2.015
		t value	–	−2.93	0.86	−2.29
		p level	–	< 0.01	NS	< 0.05
	Night-time	Coefficient	2.060	1.134	1.676	0.783
		t value	4.08	2.28	3.66	1.94
		p level	< 0.001	< 0.05	< 0.001	< 0.05
Pasture	Day-time	Coefficient	–	−0.628	−0.149	0.310
		t value	–	−0.96	−0.42	0.53
		p level	–	NS	NS	NS
	Night-time	Coefficient	0.502	−0.650	−0.436	−0.857
		t value	0.66	−0.55	−0.66	−1.21
		p level	NS	NS	NS	NS
Tall scrub	Day-time	Coefficient	–	0.463	−1.176	−1.544
		t value	–	0.88	−3.03	−1.83
		p level	–	NS	< 0.01	NS
	Night-time	Coefficient	−0.753	0.995	−0.133	−0.850
		t value	−0.84	1.46	−0.16	−0.81
		p level	NS	NS	NS	NS
Medium scrub	Day-time	Coefficient	–	−0.796	0.188	−0.273
		t value	–	−1.64	0.57	−0.52
		p level	–	NS	NS	NS
	Night-time	Coefficient	1.167	2.315	0.871	0.088
		t value	1.54	3.67	1.35	0.14
		p level	NS	< 0.001	NS	NS

The two smallest distance classes were pooled for detections made in arable crops during day-time counts in winter, because the number of detections increased with the distance from the line, pointing to a situation of not detecting objects laying on the line [$g(0) < 1$; Buckland *et al*. 1993]. The values of *ESW* estimated by the detection models, and the respective coefficients of variation, are presented in Table 2. In general, the *ESW* was lower in the night-time conditions, and it did not change substantially with season in the scrub vegetation types. In arable crops under day-time conditions, *ESW* was lowest in the breeding season, whilst in pasture was lowest in winter. The Coefficients of Variation indicate that some estimates of *ESW* are not precise. However, with the exception of pasture in winter, in the rest of the cases the *ESW* varies with season and time of day as expected. Results concerning the use of pasture will, therefore, be interpreted cautiously.

The models with the highest Mean Regression Deviance showed that more rabbits were observed in dense vegetation, such as tall scrub and average scrub, during day-time counts and in arable crops during night-time counts (Fig. 2). Rabbit numbers during day-time counts were significantly higher in average scrub, tall scrub and pasture in relation to low scrub, both in 1998 and 1999. In both years, arable crop and low scrub were the vegetation types where significantly fewer rabbits were counted during the day-time counts. For night-time counts, arable crop was the vegetation type with highest and less variable number of counts. These general trends in habitat use were not affected by season greatly, as demonstrated in Table 3, except for the following cases. The number of rabbits in arable crops during day-time counts was statistically significantly reduced from the post-breeding season to winter in both years. Simultaneously, the number of rabbits counted in the same vegetation type during night-time counts significantly increased from the breeding season to winter in 1998, and from the breeding season to the post-breeding season in 1999. In average scrub, the results of the night-time counts decreased during winter in 1998 whereas in tall scrub the results of the day-time counts were lower during the post-breeding season in 1999.

The model coefficients in relation to other variables are presented in Table 4. In 1998, significantly higher day-time counts were associated with higher average daily temperatures. Similarly, the night-time counts were significantly higher with higher minimum daily temperatures. In 1999, the rabbit counts were more affected by rainfall than by temperature. Day-time counts were significantly lower with higher rainfall in the previous month. The night-time counts were significantly and negatively related to the accumulated rainfall in the previous 2 months and to wind speed.

Table 4. Models selected to explain the results of the counts performed during the study period in terms of variables other than vegetation type.

Model parameters	df	*F*	*p*	Antilog of estimate	SE	*p*
1998 day-time counts	5,174	82.65	< 0.001			
Average temperature				1.160	0.009	< 0.001
1998 night-time counts	5,169	10.70	< 0.001			
Minimum temperature				1.068	0.014	< 0.001
1999 day-time counts	5,264	83.98	< 0.001			
Accumulated rainfall in the last month				0.986	0.001	< 0.001
1999 night-time counts	8,172	11.24	< 0.001			
Accumulated rainfall in the last 2 months				0.996	0.001	< 0.001
Moderate wind speed				0.856	0.140	NS
High wind speed (0 no wind)				0.171	0.391	< 0.001

Discussion

Distribution and number of rabbits

The results obtained show that higher rabbit numbers were observed in scrub during the day-time surveys. This can be explained in terms of predator avoidance since dense scrub cover offers protection from visually oriented birds of prey (Gibb 1993, Moreno *et al*. 1996). Seeking open vegetation only during the night restricts foraging activity but may be the response to a trade-off between maximising energy gain and minimising predation risk. The observation that pasture was more used during the day might be considered to contradict this suggestion. However, there was a difference between pasture and arable crops in tree density. In pastures, the higher tree density offers protection from birds of prey, which could explain why rabbits risk foraging there during day-time activity periods. Furthermore, the higher tree cover in pastures offers shade, which is of great importance in the Mediterranean regions during the summer, coincident with the post-breeding season when diurnal activity is increased.

The general pattern of habitat use did not change much from season to season. Scrub cover was selected during the day, whilst arable crops were avoided with their attractiveness increasing after dusk. The significant changes from season to season were due to ploughing in the arable crops in winter, and to disturbance of areas with tall scrub due to cork harvesting and hunting activities at the end of the breeding season.

In what concerns the other variables, the results of the counts were mainly explained by temperature and the accumulated rainfall. Both play an important role in determining the amount of food available and the reproductive activity of the wild rabbit in Mediterranean areas (Wood 1980, King and Wheeler 1981, Soriguer and Rogers 1981, Stevens and Wiesbrod 1981, King *et al*. 1983, Wheeler and King 1985). A previous study on the same rabbit population by Alves and Moreno (1996) showed that the start of the reproductive activity is positively correlated with accumulated rainfall in the previous month and negatively correlated with temperature. Similarly these conditions would also coincide with the breeding season, as defined in this study, what can be explained by the fact that those are the weather conditions that preclude the appearance of green vegetation (Myers and Poole 1961). The peak of observed rabbit numbers in the post-breeding season coincided with summer and with an increase in temperature and a decrease in the accumulated rainfall (Fig. 3). There was a time lag of about 2 months, between the breeding season and the post-breeding season time required for the emergence of the kittens (Künkele and von Holst 1996). The low dispersal of the juveniles in the first weeks of life also contributes to lower detectability, and consequently lower counts (Béltran 1991). The numbers observed fell during winter, according to some authors due to an increase in the incidence of diseases (eg Orueta *et al*. 1995). This pattern of population dynamics has also been observed in Spain by Soriguer and Rogers (1981), Béltran (1991) and Orueta *et al*. (1995).

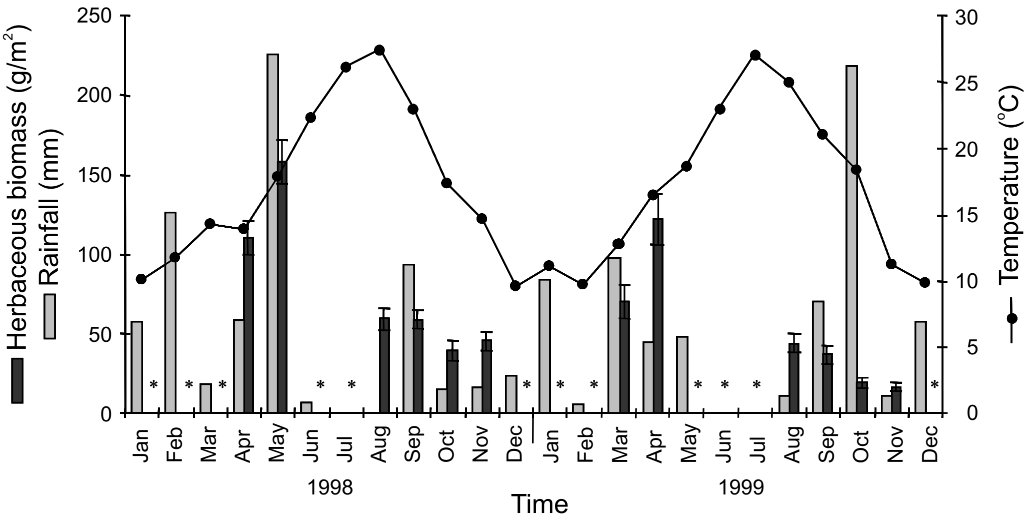

Fig. 3. Herbaceous biomass in terms of standing crop (± SE of biomass recorded at all sampled quadrats; * indicate missing data on standing crop), mean monthly temperature and monthly total rainfall during the period of the study. The rainfall was recorded in the study area and the temperature at the Meteorological Station of Évora.

Rainfall appeared to play more important role in explaining the variation in observed rabbit numbers in 1999 than in 1998. During the breeding season in 1999 the accumulated rainfall was lower than in the previous year and might have been more limiting to plant growth than temperature, reducing the duration of the breeding season.

Night-time counts were higher than day-time counts during the breeding season and winter, as opposed to the post-breeding season, which was also observed in south-western Spain (Villafuerte *et al.* 1993). The post-breeding season is associated with a depletion of feeding resources, in terms of quantity (Fig. 3) (Martins *et al.* 2002) and quality (Alves and Moreno 1996). This, in association with a population increase, can lead to an extension of the foraging activity throughout the day-time activity peaks to compensate for lower food intakes (Gibb *et al.* 1978, Fullagar 1981, Gibb 1993). Rowley (1957) also suggested that the longer winter nights allow the extension of grazing activity, making daylight emergence unnecessary. Thermoregulatory reasons might also explain such behaviour, since the ambient temperature is higher at night than at dawn causing an increase of nocturnal activity at this time (Villafuerte *et al.* 1993). The fact that minimum temperature was a limiting factor for night-time surveys in 1998, but not in 1999, supports the hypothesis that both food availability and thermoregulatory strategies might be acting either individually or together.

An inversion in the pattern of results of counts between day and night was also recorded by Kline (1965) during roadside counts of cottontails and was explained as a thermoregulatory strategy to cope with strong winds and a decrease in temperature. Wind speed and temperature have also been pointed out as being responsible for considerable daily fluctuations in emergence from the warrens (Rowley 1957, Fraser 1992), and in restricting foraging activity (Southern 1940, Gibb *et al*. 1978). This could explain the negative effect of wind speed on night-time rabbit numbers in 1999.

Implications for counting

The results of this study can be used when planning wild rabbit counts in southern Portuguese montados. If the aim is monitoring population dynamics and obtaining more accurate density estimates for the whole area, counts should be restricted to the most favourable conditions. Counts are expected to be higher and less variable at dawn or at dusk during the post-breeding season and at the beginning of the night during the breeding season and winter. Moreover, if possible allocation of transect replicates should be proportional to both habitat availability and selectivity (Buckland *et al*. 1993). Thus, counts should be intensified at dense scrub or open vegetation with high tree cover during the day, and at feeding areas such as arable crops during the night. Counts should be avoided at high wind speed and low temperatures.

Acknowledgements: We are grateful to Direcç□o Geral de Florestas for allowing the data collection at Tapada Pequena de Vila Viçosa, and to Dr J. A. Milne and Dr G. R. Iason for kindly commenting on drafts of the manuscript. This study was funded by European Commission Programme PRAXIS XXI (BD9396/96).

References

Alves P. C. and Moreno S. 1996. Study of the reproduction of wild rabbit (*Oryctolagus cuniculus*) in Portugal. Revista Florestal 91: 149–166. [In Portuguese]

Bell A. C., Byrne P. M. and Watson S. 1999. The effect of rabbit (*Oryctolagus cuniculus*) grazing damage on the growth, botanical composition and yield of a ryegrass re-seed. Annals of Applied Biology 1351: 417–424.

Béltran J. F. 1991. Temporal abundance pattern of the wild rabbit in Don□na, SW Spain. Mammalia 554: 591–599.

Buckland S. T. 1985. Perpendicular distance models for line transect sampling. Biometrics 41: 177–195.

Buckland S. T., Anderson D. R., Burnham K. P. and Laake J. L. 1993. Distance sampling. Estimating abundance of biological populations. Chapman and Hall, London: 1–446.

Bugalho J. F. F. and Cipriano R. 1999. The assessment of the importance of hunting in Portugal through a query to hunters. Expresso (Dossiers promocionais) 1408: 6–7. [In Portuguese]

Burnham K. P. and Anderson D. R. 1998. Model selection and inference. A practical information--theoretic approach. Springer-Verlag, Berlin: 1–353.

Carvalho J. C. S. and Bugalho J. F. F. 1986. Dégats du lapin de garenne au Portugal. [In: Proceedings of the Symposium International "Le lapin dans la chasse, l'agriculture et la sylviculture"]. Conseil International de la Chasse et de la Conservation du Gibier, Montpellier: 45–53.

Chapuis J. L. 1986. Preferences alimentaires du lapin de garenne, *Oryctolagus cuniculus*, dans diferents types d'habitats. [In: Proceedings of the Symposium International "Le lapin dans la chasse, l'agriculture et la sylviculture"]. Conseil International de la Chasse et de la Conservation du Gibier, Montpellier: 94–116.

Fraser K. W. 1992. Emergence behaviour of rabbits, *Oryctolagus cuniculus*, in Central Otago, New Zealand. Journal of Zoology, London 228: 615–623.

Fullagar P. J. 1981. Methods for studying the behaviour of rabbits in a 33 ha enclosure at Camberra and under natural conditions at Calindary, N.S.W. [In: Proceedings of the World Lagomorph Conference, Guelph, University of Guelph, 1979. K. Myers and C. D. MacInnes, eds]. University of Guelph, Ontario: 240–255.

Gates C. E. 1979. Line transect and related issues. [In: Sampling biological populations. R. M. Cormack, G. P. Patil and D. S. Robson, eds]. International Co-operative Publishing House, Fairland: 71–154.

Genstat 5 Committee 1993. Genstat 5 Reference Manual. Claredon Press, Oxford: 1–796.

Gibb J. A., Ward C. P. and Ward G. D. 1978. Natural control of a population of rabbits (*Oryctolagus cuniculus* L.) for ten years in the Kourdrau exclosure. DSRI Bulletin 223: 1–89.

Gibb J. A. 1993. Sociality, time and space in a sparse population of rabbits *Oryctolagus cuniculus*. Journal of Zoology, London 229: 581–607.

Hurlbert S. T. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 542: 187–211.

Iborra O., Arthur C. P. and Bayle P. 1990. Importance trophique du lapin de garenne pour les grandes rapaces provençaux. Vie Milieu 402: 177–188.

Jaksic F. M. and Fuentes E. R. 1980. Why are native herbs in the Chilean matorral more abundant beneath bushes: microclimate or grazing? Journal of Ecology 68: 665–669.

Jaksic F. M. and Soriguer R. C. 1981. Predation upon the European rabbit (*Oryctolagus cuniculus*) in Mediterrranean habitats of Chile and Spain: a comparative analysis. Journal of Animal Ecology 50: 269–281.

King D. R. and Wheeler S. H. 1981. Ecology of the rabbit in western Australia. [In: Proceedings of the World Lagomorph Conference, Guelph, University of Guelph, 1979. K. Myers and C. D. MacInnes, eds]. University of Guelph, Ontario: 858–869.

King D. R., Wheeler S. H. and Schmidt G. L. 1983. Population fluctuations and reproduction of rabbits in a pastoral area on the coast north of Carnarvon, W.A. Wildlife Research 10: 97–104.

Kline P. D. 1965. Factors influencing roadside counts of cottontails. The Journal of Wildlife Management 294: 665–671.

Kolb H. H. 1992. The effect of moonlight on activity in the wild rabbit (*Oryctolagus cuniculus*). Journal of Zoology, London 228: 661–665.

Künkele J. and von Holst D. 1996. Natal dispersal in the European wild rabbit. Animal Behaviour 51: 1047–1059.

Martins H., Milne J. A. and Rego F. 2002. Seasonal and spatial variation in the diet of the wild rabbit (*Oryctolagus cuniculus* L.) in Portugal. Journal of Zoology, London: 258: 395–404.

McCullagh P. and Nelder J. A. 1991. Generalized linear models. Monographs on Statistics and Applied Probability 37. Chapman and Hall, Cambridge: 1–511.

Moller H., Newton K. and McKinlay B. 1996. Day-time transect counts to measure abundance of rabbits (*Oryctolagus cuniculus*). Journal of Zoology, London 239: 406–410.

Moreno S. and Villafuerte R. 1995. Traditional management of scrubland for the conservation of rabbit and their predators in Do□ana National Park Spain. Biological Conservation 731: 81–85.

Moreno S., Villafuerte R. and Delibes M. 1996. Cover is safe during the day but dangerous at night: the use of vegetation by European wild rabbits. Canadian Journal of Zoology 74: 1656–1660.

Myers K. and Poole W. E. 1961. A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.) in confined populations. II. The effects of season and population increase in behaviour. Wildlife Research 6: 1–41.

Organizatier National de la Chasse 1984. Méthode d'inventaire des dégâts de lapin sur cultures agricoles. Bulletin Mensuel 86(20): 1–45.

Ontiveros D. and Pleguezuelos J. M. 2000. Influence of prey densities in the distribution and breeding success of Bonelli's eagle (*Hieraaetus fasciatus*): management implications. Biological Conservation 931: 19–25.

Orueta J. F., Aranda Y., Gomez T. and Tapia G. G. 1995. Evolución annual de las densidades de una población de conejo (*Oryctolagus cuniculus*) en ambiente semiárido. [In: Proceedings of the II Jornadas Españolas de Conservación y Estudio de Mamíferos, Zaragoza, 1994]. SECEM, Saragoza: 1–65.

Palomares F. and Delibes M. 1991. Alimentation del meloncillo (*Herpestes ichneumon*) y de la gineta (*Genetta genetta*) en la reserva biologia de Doñana, SO de la Peninsula Ibérica. Doñana, Acta Vertebrata 181: 5–20.

Palomares F., Calzada J. and Revilla E. 1996. El manejo del habitat y la abundancia de conejos: diferencias entre dos areas potencialmente identicas. Revista Florestal 91: 201–210.

Palomares F. and Delibes M. 1997. Predation upon European rabbits and their use of open and closed patches in Mediterranean habitats. Oikos 802: 407–410.

Rogers P. M. 1981. Ecology of the European wild rabbit (*Oryctolagus cuniculus* L.) in Mediterranean habitats. II. Distribution in the landscape of the Camargue, S. France. Journal of Applied Ecology 18: 355–371.

Rosário L., Marques A., Bugalho M. F. and Lopes F. 1983. Management plan for Tapada Pequena de Vila Viçosa. Ministério da Agricultura Comércio e Pescas – Direcção Geral das Florestas, Lisbon: 1–67. [In Portuguese]

Rowley I. 1957. Observations on evening rabbit activity in relation to weather and sunset. Wildlife Research 2: 168–169.

Soriguer R. C. and Rogers P. M. 1981. The European wild rabbit in Mediterranean Spain. [In: Proceedings of the World Lagomorph Conference, University of Guelph, Guelph, 1979. K. Myers and C. D. MacInnes, eds]. University of Guelph, Ontario: 600–613.

Southern H. N. 1940. The ecology and the population dynamics of the wild rabbit (*Oryctolagus cuniculus*). Annals of Applied Biology 27: 509–526.

Stevens W. F. and Weisbrod A. R. 1981. The biology of the European rabbit on San Juan Island, Washington, U.S.A. [In: Proceedings of the World Lagomorph Conference, Guelph, University of Guelph, 1979. K. Myers and C. D. MacInnes eds]. University of Guelph, Ontario: 870–879.

Thomas L., Laake J. L., Derry J. F., Buckland S. T., Borchers D. L., Anderson D. R., Burnham K. P., Strindberg S., Hedley S. L., Bust M. L., Marques F., Pollard J. H. and Fewster R. M. 1998. Distance 3.5. Research Unit for wildlife population assessment. University of St. Andrews, UK: 1–259.

Thompson H.V. 1994. The rabbit in Britain. [In: The European rabbit. The history and biology of a successful colonizer. H. V. Thompson and C. M. King, eds]. Oxford University Press, London: 83–107.

Villafuerte R., Kufner M. B., Delibes M. and Moreno S. 1993. Environmental factors influencing the seasonal daily activity of the European rabbit (*Oryctolagus cuniculus*) in a Mediterranean area. Mammalia 573: 341–347.

Villafuerte R. and Moreno S. 1997. Predation risk, cover type, and group size in European rabbits in Doñana, SW Spain. Acta Theriologica 422: 225–230.

Wallage-Drees J. M. 1989. A field study on seasonal changes in the circadian activity of rabbits. Zeitschrift für Säugetierkunde 54: 22–30.

Wheeler S. H. and King D. R. 1985. The European rabbit in south-western Australia. II. Reproduction. Wildlife Research 12: 197–212.

Wood D. H. 1980. The demography of a rabbit population in an arid region of New South Wales, Australia. Journal of Animal Ecology 49: 55–79.

Received 25 February 2002, accepted 6 January 2003.

Associate Editor was Leszek Rychlik.