
ELSEVIER
Mammalian Biology
Zeitschrift für Säugetierkunde
DEUTSCHE GESELLSCHAFT FÜR SÄUGETIERKUNDE E.V. BERLIN
www.elsevier.de/mambio
ISSN 1616-5047
Mamm. biol. · 77(2012)2
S. 75–152
2·2012

Mammalian Biology 77 (2012) 140–146

Contents lists available at SciVerse ScienceDirect

Mammalian Biology

journal homepage: www.elsevier.de/mambio

Original Investigation

Life at the edge: Roe deer occurrence at the opposite ends of their geographical distribution, Norway and Portugal

Rita Tinoco Torres[a,c,*], Emílio Virgós[b], Manuela Panzacchi[c], John D.C. Linnell[c], Carlos Fonseca[a]

[a] CESAM & Department of Biology, University of Aveiro, Campus de Santiago, 3810-193 Aveiro, Portugal
[b] Biodiversity and Conservation Area, University of Rey Juan Carlos, c/Tulipán s/n, E-28933 Móstoles (Madrid), Spain
[c] Norwegian Institute for Nature Research, PO Box 5685 Sluppen, NO-7485 Trondheim, Norway

ARTICLE INFO

Article history:
Received 22 March 2011
Accepted 2 November 2011

Keywords:
Distribution edge
Mediterranean forest
Boreal forest
Capreolus capreolus
Human activities

ABSTRACT

In the face of climate change and habitat fragmentation there is an increasingly urgent need to learn more about factors that influence species distribution patterns and levels of environmental tolerance. Particular insights can be obtained by looking at the edges of a species range, especially from species with wide distributions. The European roe deer was chosen as a model species due to its widespread distribution. By using pellet group counts, we studied summer and winter habitat use of this herbivore at two of the extreme edges of its distribution – southwest of Portugal, and northeast of Norway – in relation to a range of fine-scale environmental factors including forest structure, vegetation characteristics and human disturbance. Our first prediction that roe deer would respond differently to human activity in both counties was supported. While in Norway roe deer are always close to houses, in Portugal they are either far (in summer) or indifferent (winter). However, everywhere and in every season, roe deer are far from roads. Our second prediction that roe deer better tolerate anthropogenic disturbances in the area where the importance of limiting factors is higher (Norway) was validated. However, our third prediction that anthropogenic disturbance would be less tolerated by roe deer outside the limiting seasons in each country was not supported. Our results suggest that roe deer perceive human activities differently in the two countries and that roe deer better tolerate anthropogenic disturbances in Norway.

Introduction

There is now an emerging consensus that human driven habitat fragmentation is dramatically changing the geographic distributions of species (Parmesan and Yohe 2003). These changes are expected to have a stronger effect on marginal populations since these so-called edge populations, already living near the environmental limits for the species, are expected to be particularly susceptible to environmental change (Hoffmann and Blows 1994; González-Megías et al. 2005). Despite a long interest in how species are distributed spatial and temporally, only few studies have compared basic ecological requirements of the same species at different edges of their distribution.

Since environmental conditions are not the same throughout a species' range (Gaston 2003), observations made in one part of the range are not always applicable in another part of a species' distribution (Randall 1982). A suitable approach to begin exploring this topic is to evaluate how the same suit of environmental factors, affects the same species in different locations across their geographic range (Gaston 2003).

The European roe deer (*Capreolus capreolus*) currently has a distribution range that stretches from the Mediterranean scrublands of Portugal, on the southwest of its distributional range, to the boreal forests of central Norway, on the northwest of its distributional range (Apollonio et al. 2010). Roe deer were chosen as a model species because of their widespread distribution (Apollonio et al. 2010). Within the distribution range, roe deer occurrence is influenced by a variety of factors including food availability (Virgós and Telléria 1998), cover (Mysterud and Østbye 1999; Borkowski and Ukalska 2008), human disturbance (Hewison et al. 2001; Torres et al. 2011), terrain characteristics (Mysterud and Østbye 1999), climatic factors (Brewka and Kossak 1994) and predation (Melis et al. 2010). We explored which environmental factors influence roe deer distribution at the southern and northern limits of their geographic range; more specifically we examined species' occurrence with respect to habitat parameters and anthropogenic factors. Furthermore, the Mediterranean climatic patterns of Portugal strongly contrast with the boreal climate of Norway. In Norway, winter is the most critical season for roe deer, as deep snow can impede locomotion and make roe deer vulnerable to starvation (Mysterud et al.

* Corresponding author at: CESAM & Department of Biology, University of Aveiro, Campus de Santiago, 3810-193 Aveiro, Portugal. Tel.: +351 234 370975; fax: +351 234 372587.
E-mail address: rita.torres@ua.pt (R.T. Torres).

1616-5047/$ – see front matter © 2011 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.
doi:10.1016/j.mambio.2011.11.002

1997) and predation (Jędrzejewski et al. 1992). In this season, artificial feeding sites, which are often situated close to houses, can be essential for roe deer survival in particularly snowy winters. As roe deer are income breeders (Andersen et al. 2000), females have to rapidly gain energy during the fawning season (in spring) and for this reason they have to utilize high-quality resources, which can be found mostly in agricultural landscapes such as man-made meadows and field-forest edges (Panzacchi et al. 2010). According to Tufto et al. (1996), roe deer perceives humans, domestic dogs and other human activities as potential predators. Therefore, in areas inhabited by predators, it is expected that when predation rates are higher in the same areas providing high-quality forage, the potential fitness advantages arising from feeding in productive areas can be offset by higher individual mortality (Panzacchi et al. 2010).

In Portugal the hot and dry summer represents the limiting factor for the species (Tellería and Virgós 1997). Overall, it has been suggested that roe deer are maladapted to the consumption of sclerophyllous vegetation (Tellería and Virgós 1997), which is common in the Mediterranean area. However, the overall importance of limiting factors seems to be much higher in Norway compared to Portugal because extreme snow depth in winter can set a much more absolute constraint on roe deer occurrence than subtle differences in the degree of digestibility of vegetation. Based on this we expect that the effect of anthropogenic factors such as distance to houses and to field-forest edges on roe deer occurrence would differ between the two countries, while we expect in both countries that the species' occurrence would be higher further from roads (Prediction 1). Specifically, we predict that while roe deer in Norway will show a higher degree of tolerance to human-dominated landscapes, which may provide important resources especially during the most critical season, in Portugal the lower magnitude of the critical season makes it possible for roe deer to avoid human-dominated landscapes and show "human-shyness" (Prediction 2). Also, we predict that anthropogenic disturbance would be less tolerated outside the limiting seasons: while in Portugal roe deer would be most often found in areas far from anthropogenic factors during summer, in Norway this species would make more use of areas closer to field-forest edges and settlements in winter than in summer (Prediction 3).

Material and methods

Study areas

The study was conducted in two areas that differed in climate and demographic characteristics of the roe deer populations. Populations of roe deer have increased considerably during the last century in Norway (Andersen et al. 1998, 2004), whereas in Portugal, numbers have remained stable at generally low densities despite the lack of a legal harvest (Vingada et al. 2010).

Norway

In Norway, the study area was located in the southeastern part of the country, in the counties of Østfold and Akershus (59–60°N; 11–12°E), covering an area of approximately 910.000 ha. Mean annual temperature varies between −2.8 °C in winter and 16.2 °C in summer and in winter snow cover accumulates to an average depth of 13.3 cm and mean precipitation in summer is 74.7 mm. The study area is dominated by commercially exploited boreal forests, mainly composed of Norway spruce *Picea abies*, Scots pine *Pinus sylvestris* and birch *Betula pubescens*. Other species present are the bird cherry *Prunus padus*, hoary alder *Alnus incana* and linden *Tilia cordata*. The forests are harvested by clearcutting and the average size of clear cuts is small, typically in the order of a few hectares. All the area is fragmented by farmlands, especially along valley bottoms. Roe deer recolonised the area around 1920, after being absent from this area since the seventeenth century (Andersen et al. 2004). In the hunting season 2001/2002, approximately 6.342 roe deer were felled in the study area (Statistics Norway). The other wild ungulate present is the moose *Alces alces*, which is hunted. Roe deer constitutes the main part of lynx *Lynx lynx* diet, representing up to 83% of ingested biomass by lynx in winter (Odden et al. 2006). The density of lynx in the study area has been estimated to be *ca.* 0.4/100 km^2 (Odden et al. 2006). However, lynx are not the only predator of roe deer in the study area: red foxes prey upon on roe deer fawns (Panzacchi et al. 2008). Human population density in the municipalities within the study area, measured on 1 January 2009, varied between 64 people km^{-2} and 107 people km^{-2}, living in a dispersed manner throughout the landscape (Statistics Norway). Roads in the study area consist of one Highway, National roads with daily high traffic density, and smaller roads.

Portugal

In Portugal, the study was carried out in Montesinho Natural Park and Serra da Nogueira, Trás-os-Montes, northeast Portugal (6°30′–7°12′W and 41°43′–41°59′N), covering an area of 75.000 ha. The terrain consists of rolling hills with elevation ranges from 438 to 1481 m. The climate is Mediterranean with the mean annual temperature varying between 3 °C in the coldest month and 21 °C in the warmest month and mean precipitation between 1000 and 1600 mm. The vegetation is varied and characterized by Pyrenean oak *Quercus pyrenaica*, sweet chestnut *Castanea sativa*, Scots pine *Pinus sylvestris*, *Pinus pinaster*, and holm oak *Quercus rotundifolia*. Main understorey species are *Erica australis*, *Pterospartum tridentatum* and *Halimium alyssoides*, *Cistus ladanifer* and *Lavandula sampaioana*. The area is crossed by a number of rivers and small streams and the associated vegetation is mainly common alder *Alnus glutinosa*, *Fraxinus angustifolia*, black poplar *Populus nigra* and *Salix salviifolia*, which, in the study area, are strongly linked to mountain meadows. The area exhibits a mosaic of deciduous and coniferous forest, fragmented by small-cultivated fields. Roe deer is a native species in the north of Portugal, where populations have always persisted in a few patches. Due to its low abundance, hunting is very restricted, occurring only in a few touristic hunting grounds (Vingada et al. 2010). Vingada et al. (2010) estimated that current distribution of wild roe deer should vary between 3000 and 5000 animals throughout all Portugal. Unfortunately, poaching is common. Other wild ungulates present in the area are the red deer *Cervus elaphus* and wild boar *Sus scrofa*, both are hunted. In the study area, wolves have been present since historical times and densities have been calculated to be 1.6–3.1 wolves/100 km^2 (Moreira et al. 1997). The area has a low human population density of 9.5 inhabitants km^{-2}, living in small villages. A number of national roads, which provide connection between Portugal and Spain, cross the study area.

Data collection

General description

Field work was carried out during three years – 2007, 2008 and 2009 – using pellet group counts. This method is widely applied in studies of ungulate habitat use (*e.g.* Neff 1968; Tellería and Virgós 1997; Borkowski and Ukalska 2008) and provides a valid approach to allow an initial coarse scale assessment of habitat use. Although it has been criticized by some authors (Collins and Urness 1981), when it is compared with other methods to infer habitat use patterns (*e.g.* such as radio-telemetry), it has been found that the results are similar (Guillet et al. 1995). Furthermore, other authors (Loft and Kie 1988; Edge and Marcum 1989) have found that pellet group counts accurately indicate which habitat receive the greatest and least amount of use. In any case, this was the only methodology available for this comparative study.

Sampling plots were distributed along triangular transects both in Norway and Portugal. Each transect consisted of a 1 km × 1 km × 1 km triangle (3 km in total), which is an efficient field design as the start point and end point are on the same place (Lindén et al. 1996). In order to maximize spatial coverage and to reduce sampling dependence, plots were evenly spaced along the line. Both in Portugal and Norway, at each plot, the presence of roe deer pellet groups was firstly assessed, and then, the habitat variables that potentially could affect their distribution were recorded in a 10 m radius circle. A pellet group was defined as containing six or more individual pellets, and identified as being produced at the same defecation (similar size, shape, texture and colour) (Mayle et al. 2000). Pellet groups lying on the boundary of plots were alternately counted and ignored (Mayle et al. 2000). We used the presence and non-presence of roe deer pellets groups within each plot in both countries as our index of habitat use.

Norway

In Norway, the triangular transects were placed randomly in the landscape, stratified by altitude; plots that felt on lakes and agricultural fields were avoided by field workers and were not included in the analysis. In total, 32 plots were rejected (5% of the total plots). Data were collected over 21 triangular transects and at each 100 m interval we delimited a circular 10 m^2 plot to record the number of roe deer pellet groups (Wahlström and Liberg 1995). A total of 598 plots per season were examined. Each plot was visited five times throughout the field survey: pellets were counted in spring (April–May) 2007–2009 (reflecting winter habitat use) and end of summer (September) 2007 and 2008 (reflecting summer habitat use). With this, we avoided the period when vegetation was too high in summer and the ground being covered by snow in winter. Plots were cleaned after inspection, overcoming the need for any assumption regarding faecal persistence period.

Portugal

In Portugal, transects were randomly located with the help of technical staff from the Natural Park and were drawn on a 1:10,000 map scale, distributed to provide an adequate coverage of all the habitat types in the study area (Mayle et al. 2000). The methodology used in the two countries is different since the method used in Norway was difficult to implement in Portugal because roe deer densities are (very) low when compared to those in Norway. In order to overcome these problems, and maximize the pellets detection in Portugal, we replaced the circular plots with line-transect furthermore, by selecting long narrow plots (2 m wide) the task of systematically searching the plots is made easier and estimates with poor precision in areas of low deer density are avoided (Buckland 1992). In Portugal, a total of 120 rectangular plots (50 m × 2 m), distributed evenly along the transect line, were examined and both fresh and old pellets were counted; this method is expected to improve precision (Campbell et al. 2004), particularly when roe deer density, and consequently pellet group density, is very low, such as in our study area. Pellets were counted in November 2007, February 2008 and May 2009 (reflecting winter habitat use) and October 2008 and August 2009 (reflecting summer habitat use). To avoid any complication regarding different faecal decay rates, a pilot study on the study area was conducted to determine decay rates and the mean number of days needed for pellets to disappear was 182.5 ± 49.4 (S.E.) (Torres RT unpl. data). Therefore, the length of time between visits was chosen to be smaller than the disappearance days.

Table 1
Description of the variables used to model roe deer occurrence in Østfold and Akershus counties, southeastern Norway and northeast of Portugal, Trás-os-Montes, on winter and summer (2007–2009).

Abbreviation	Variable description
Patch-scale variables (in 10-m radius circle)	
TREECOV (height > 150 cm)	Tree cover classified as no understorey, sparse, medium-density and dense
SHRUBCOV (height 50–150 cm)	Shrub cover classified as no understorey, sparse, medium-density and dense
GROUNDCOV (height < 50 cm)	Ground cover classified as no understorey, sparse, medium-density and dense
VISINDEX	Measure of lateral visibility (m)
CANOPCOV	Canopy cover
Broad-scale variables	
DROAD	Distance (m) to the closest road
DHOUSE	Distance (m) to the closest settlement
DEDGE	Distance (m) to the closest edge field/forest

Environmental variables

For each sampling plot, a series of patch-scale and landscape scale variables were quantified. Patch-scale variables were collected in the field, while landscape variables were derived from digital maps with the help of a geographic information system (ArcGIS 9 ESRI Inc, Redlands, CA, USA). Variables that could potentially influence the occurrence of roe deer were selected based on previous studies (Virgós and Telléria 1998) and the author's predictions (Table 1). During the sampling survey we estimated variables related to habitat structure: tree cover (>2 m), shrub cover (0.5–2 m) and ground cover (<0.5 m). Tree cover (TREECOV), shrub cover (SHRUBCOV) and ground cover (GROUNDCOV) were classified based on visual estimations into four classes: no cover, sparse, medium and dense (Borkowski and Ukalska 2008). Visual concealment provided by vegetation might be important for protection against human and non-human predators. Hence, we measured a *hiding cover index* (VISINDEX) by placing a cover board, of roe deer size (~80 cm, Mysterud et al. 1997), in the centre of the plot. With the help of a compass, in a random direction, the minimum distance required for the board to be completely hidden was noted. Cover might be also important to provide thermal cover (*e.g.* protection against snow during winter in Norway, Ratikainen et al. 2007, and against the heat during summer in Portugal). Hence, we calculated a *thermal cover index* (CANOPCOV) as the average amount of canopy cover measured in the north, south, east and west, by using Lemmon's densiometer (Lemmon 1956). In contrast to Portugal, roe deer populations experience a strong harvest pressure in Norway, and it is likely that hunting can induce responses similar to non-human predation risk in Norway (Frid and Dill 2002). Furthermore, human disturbance factors can influence roe deer distribution as they may be considered as analogues to predation risk. As human activities are expected to affect roe deer, we included variables related to human disturbance in our analyses. To analyze these effects, distances were measured from the centre of each plot to the nearest border of the following features: the nearest settlement (DHOUSE), the nearest pavement roads (DROAD) and the nearest edge between a forest and a field (DEDGE). The variables were obtained from the CORINE Land Use/Land Cover database (European Environment Agency) and from the official Norwegian Mapping Authority (Statens Kartverk).

Statistical analyses

Roe deer occurrence was estimated through Generalized Linear Mixed Models (GLMM) (Faraway 2006). Continuous variables were square root transformed in order to mitigate the effects of extreme values, and standardized (giving zero mean and variance of one), to avoid the effect of different measurement scales and to

Table 2
Candidate models describing roe deer occurrence in northeast of Portugal, Trás-os-Montes, on winter and summer (2007–2009), with the number of parameters used (*k*), the Akaike information criterion (AIC) and the difference between each selected model and the best model (ΔAIC).

Models	*k*	AIC	ΔAIC
Portugal			
Winter			
(*i*) TREECOV + SHRUBCOV + DROAD	3	460.7	0
(*ii*) TREECOV + SHRUBCOV + DROAD + DHOUSE	4	462.3	1.6
(*iii*) TREECOV + SHRUBCOV + DROAD + DHOUSE + CANOPCOV	5	464.3	3.6
(*iv*) TREECOV + SHRUBCOV + DROAD + DHOUSE + CANOPCOV+ VISINDEX	6	466.3	5.6
(*v*) TREECOV + SHRUBCOV + DROAD + DHOUSE + CANOPCOV + VISINDEX + GROUNDCOV[a]	7	469.5	8.8
Summer			
(*vi*) GROUNDCOV + DHOUSE	2	329.4	0
(*vii*) GROUNDCOV + DHOUSE + DROAD	3	330.8	1.4
(*viii*) GROUNDCOV + DHOUSE + DROAD + SHRUBCOV	4	335.4	6
(*ix*) GROUNDCOV + DHOUSE + DROAD + SHRUBCOV + TREECOV	5	336.3	6.9
(*x*) GROUNDCOV + DHOUSE + DROAD + SHRUBCOV + TREECOV + VISINDEX	6	338.1	8.7
(*xi*) GROUNDCOV + DHOUSE + DROAD + SHRUBCOV + TREECOV + VISINDEX + CANOPCOV[a]	7	340.1	10.7

For explanation of variables see Table 1. Models were ordered from the lowest (best model) to the highest AIC values.
[a] Full model.

facilitate direct comparison. Multicollinearity was limited by computing pairwise Pearson correlations. Whenever a correlation exceeded 0.5, the variable with lower biological meaning was dropped. The model assumed a binomial error structure, and a logit link function, as the response variable was binary (*i.e.* occurrence or non occurrence of roe deer pellet groups in each sampling plot). Transect identity was included as random factor, to control for the lack of independence of segments within them and to avoid pseudoreplication arising from repeated sampling of the same transect. The models were fitted using the lmer function in lme4 library (Bates and Sarkar 2006) in the R software package. We used a backward stepwise procedure for model simplification. In order to select the best model, we evaluated the parsimony relative to predictive efficiency of all possible subsets of uncorrelated candidate variables using an information theoretical-approach (Burnham and Anderson 1998). In this framework, we generated models and they were ranked according to Akaike information criterion (AIC) values, where model with the lowest AIC is the best one. We also reported the ΔAIC value in order to compare the difference between each model and the best model. As a rule of thumb, a ΔAIC < 2 suggests substantial evidence for the model (and consequently for the variables included) (Burnham and Anderson 1998). Separate models were conducted for each of these two populations and for each of the seasons. Thereafter, we related the variables emerged from the best models to the response variable by performing an ANOVA. Such proceeding will give the significance of the whole factor. The level of significance was set at 0.05 for all statistical tests.

Results

Portugal

Winter

The model with the lowest AIC (*i*, Table 2) retained 3 environmental variables: tree cover (TREECOV, *F*-value = 4.849, *P* = 0.003), shrub cover (SHRUBCOV, *F*-value = 3.331, *P* = 0.020), and distance to the closest asphalt road (DROAD, *F*-value = 18.611, *P* < 0.001). In particular, roe deer occurrence was positively related with areas of sparse tree cover (GLMM parameter estimate: 1.790, *z-value* = 2.654, *P* = 0.008), sparse shrub cover (GLMM parameter estimate: 1.104, *z-value* = 2.518, *P* = 0.012) and increasing distance to a road (parameter estimate: 0.586, *z-value* = 2.844, *P* = 0.004).

Summer

The model with the lowest AIC (*iii*, Table 2) retained 2 environmental variables: ground cover (GROUNDCOV, *F*-value = 3.403, *P* = 0.018) and distance to the closest house (DHOUSE, *F*-value = 2.392, *P* = 0.123). In particular, roe deer occurrence was positively related to areas of sparse ground cover (GLMM estimate parameter: 1.447, *z-value* = 2.945, *P* = 0.003) and with increasing distance from settlements (GLMM estimate parameter: 0.222, *z-value* = 1.528, *P* = 0.126).

Norway

Winter

The model with the lowest AIC (*v*, Table 2) retained 4 environmental variables: ground cover (GROUNDCOV, *F*-value = 2.590, *P* = 0.051), distance to the closest house (DHOUSE, *F*-value = 2.590, *P* = 0.051), distance to the closest asphalt road (DROAD, *F*-value = 0.502, *P* = 0.479) and distance to the closest edge between field and forest (DEDGE, *F*-value = 10.553, *P* = 0.001). In particular, roe deer occurrence was negatively related to sparse ground cover (GLMM parameter estimate: −0.702, *z-value* = −2.794, *P* = 0.005), and was found closer to settlements (GLMM parameter estimate: −0.208, *z-value* = −1.854, *P* = 0.064) and with distance to the closest edge between field and forest (GLMM parameter estimate: −0.222, *z-value* = −1.579, *P* = 0.114), while it was positively related with the distance to the closest asphalt road (GLMM parameter estimate: 0.171, *z-value* = 1.487, *P* = 0.137).

Summer

The model with the lowest AIC (*vii*, Table 2) retained 2 environmental variables: distance to the closest house (DHOUSE, *F*-value = 6.319, *P* = 0.012) and distance to the closest asphalt road (DROAD, *F*-value = 3.998, *P* = 0.084), showed the highest parsimony ranks according to AIC scores (*iii*, Table 3). In particular, roe deer was found closer to settlements (GLMM estimate parameter: −0.283, *z-value* = −2.245, *P* = 0.025) and positively related with the distance to the closest asphalt road (GLMM estimate parameter: 0.297, *z-value* = 1.912, *P* = 0.056).

Discussion

Our results suggest that, in Portugal, roe deer occur in areas farther away from houses. This result indicates that in Portugal, this species is particularly sensitive to human activities. In Norway, roe deer are closely associated with human modified landscapes and the presence of agricultural fields, inhabiting the belt between forest dominated-areas and human dominated-areas (Panzacchi et al. 2010) while in Portugal, they generally avoid such human modified landscapes (Torres et al. 2011). This supports findings from

Table 3
Candidate models describing roe deer occurrence in southeast of Norway, Østfold and Akershus, on winter and summer (2007–2009), with the number of parameters used (*k*), the Akaike information criterion (AIC) and the difference between each selected model and the best model (ΔAIC).

Models	*k*	AIC	ΔAIC
Norway			
Winter			
(*i*) GROUNDCOV + DHOUSE + DROAD + DEDGE	4	990.8	0
(*ii*) GROUNDCOV + DHOUSE + DROAD + DEDGE + VISINDEX	5	991.7	0.9
(*iii*) GROUNDCOV + DHOUSE + DROAD + DEDGE + VISINDEX + CANOPCOV	6	993.6	2.8
(*iv*) GROUNDCOV + DHOUSE + DROAD + DEDGE + VISINDEX + CANOPCOV + SHRUBCOV	7	996.1	5.3
(*v*) GROUNDCOV + DHOUSE + DROAD + DEDGE + VISINDEX + CANOPCOV + SHRUBCOV + TREECOV[a]	8	1001	10.2
Summer			
(*vi*) DHOUSE + DROAD	2	603.6	0
(*vii*) DHOUSE + DROAD + DEDGE	3	605.6	2
(*viii*) DHOUSE + DROAD + DEDGE + CANOPCOV	4	605.8	2.2
(*ix*) DHOUSE + DROAD + DEDGE + CANOPCOV + VISINDEX	5	607.7	4.1
(*x*) DHOUSE + DROAD + DEDGE + CANOPCOV + VISINDEX + GROUNDCOV	6	612.3	8.7
(*xi*) DHOUSE + DROAD + DEDGE + CANOPCOV + VISINDEX + GROUNDCOV + SHRUBCOV	7	617.6	14
(*xii*) DHOUSE + DROAD + DEDGE + CANOPCOV + VISINDEX + GROUNDCOV + SHRUBCOV + TREECOV[a]	8	622.4	18.8

For explanation of variables see Table 1. Models were ordered from the lowest (best model) to the highest AIC values.
[a] Full model.

Spain, where Aragón et al. (1995) showed that roe deer were associated with areas with no human disturbance, and Portugal (Pimenta and Correia 2001; Torres et al. 2011), and it is possible that proximity to human houses increases the risk perceived by roe deer (Mysterud et al. 1999). In particular, in our Portuguese study area, this avoidance may be due to the presence of free ranging domestic dogs, which are widespread throughout our study site, with their activities centred around villages and are a major cause of roe deer disturbance. Another important factor is the high pressure from illegal hunting, which is believed to be commonplace in the study area. Our results also revealed that, during winter, roe deer make more use of areas with sparse tree and shrub cover. These results are somehow puzzling since they might suggest the use of areas with limited food availability. However, it is likely that in a Mediterranean environment, roe deer can easily fulfil their winter nutritional needs in the mosaic of habitats that constitute our study area. In fact, heavy snowfalls are rare and woody plants growing in Mediterranean ecosystems show various morphological adaptations to withstand the stressful periods of winter cold (Larcher 2000), and for this, most of the vegetation is available on the ground layer during this season. Tree cover represents the availability of habitat in terms of shelter and refuge, another parameter essential to roe deer, namely to provide concealment from disturbance/predators and adverse weather conditions, and high percentages of tree cover seems to be selected by roe deer in Portugal (Pimenta and Correia 2001). However, in our case, roe deer use patches with sparse tree cover. Nevertheless, this is in agreement with Gill and Beardall (2001), who reported that roe deer density increased while tree cover was sparse and several studies have shown that high canopy cover areas are avoided by roe deer (Latham et al. 1997). Our results show that during summer, roe deer made more use of areas with sparse ground cover. Such use can be related to the abundance of plant species that grow in this layer and frequently appear in roe deer diet (*e.g. Poa bulbosa*, *Hallimium alyssoides*, Kaluzinski 1982; Faria 1999). Such vegetation is related to deep soils, in small valleys or near rivers or springs, where edaphic water sources persist throughout the dry Mediterranean summer. However, in Mediterranean ecosystems, summers are hot and dry. This is the time of the year where productivity is more restricted, with lower availability of food resources, which is also reflected in the reduction of food resources in the ground layer (Blondel and Aronson 1995).

According to our prediction (Prediction 1) we found that study plots where roe deer were present were positively associated with increasing distance from roads in both countries, a trend already demonstrated in Portugal (Torres et al. 2011) and in different countries and for other deer species (*e.g.* Rowland et al. 2000; Jiang et al. 2009). This was expected since roads are sources of disturbance and a mortality hazard, so roe deer may avoid them because of the risk of collision, as has been shown in elk (Rowland et al. 2000).

In Norway, the use of ground cover is probably related to the availability of food in this layer. Mysterud et al. (1999) showed that the majority of roe deer winter diet in southern Norway is based on deciduous shrubs (*e.g.* aspen, ash and rowan) and also on plants located in the ground cover (*e.g. Vaccinium myrtillus*). During winter, and in agreement with our second prediction, roe deer maximize food intake by using areas closer to human settlements and the ecotones between fields and forests (Panzacchi et al. 2010; Saïd and Servanty 2005; Miyashita et al. 2008). This positive correlation can be related to soil fertility since it has been shown that human settlements are generally situated on more fertile grounds and that agricultural activity tends to further increase fertility through the use of fertilizer (Pautasso 2007). Houses are also generally close to agricultural fields (suggesting high landscape heterogeneity), the later providing extra sources of high-quality forage. Distance to the closest edge forest/field was negatively correlated with roe deer occurrence. Norwegian roe deer tended to be found closer to the forest-field edge. Forest edges bordering agricultural fields are characterized by a high diversity of plant species, therefore partly compensating for the scarcity of preferred forage but also provide protective cover in close proximity. Consequently, edges provide a good interspersion of cover and a diversity of forage. This preference for areas close to the forest edges has been already described earlier (Mysterud and Østbye 1999).

We predicted that human activities would be perceived differently by roe deer in the two countries, which would respond differently to roads, houses, and agricultural areas (Prediction 1). We found our prediction to be fulfilled. In fact, the distance to houses varies: while in Norway, roe deer in both summer and winter are always found close to houses, in Portugal they are either far (summer) or indifferent (winter). Alternative mechanisms seem to be acting in both landscapes and may be the result of contrasting human pressures (*e.g.* hunting, differences on how humans are scattered trough the landscape). At this stage, we do not know which factor(s) contribute most to the generally low densities of roe deer in Portugal and specifically in Trás-os-Montes. Contrasting with this situation, in Norway roe deer populations are often food-provisioned by humans and inhabit the belt between forests and agricultural fields, where they find large food supply reservoirs. Our second prediction, that roe deer would be more tolerant to anthropogenic disturbances in the country where the critical season is stronger *e.g.* Norway, was supported. In fact, winter is a critical period for cervid species that live at high latitudes, and roe deer seems to be constrained by the snow depth (Mysterud et al. 1997). Indeed, in Norway, this species seems to thrive in landscapes with moderate human activities – *i.e.* cultivated fields and houses. We predicted that the degree of tolerance to anthropogenic disturbance would be significantly higher during the most limiting season in each study area (Prediction 3). However, in Norway roe deer were always found close to houses, contrary to our prediction, which stated that roe deer would be close to houses in winter, but far in summer, and in Portugal they are either far (in summer) or indifferent (winter). Thus, our Prediction 3 is not supported. Hence, roe deer appear to adopt a given strategy, and do not change it according to the season. Furthermore, the rejection of Prediction 3, in Norway, is intriguingly. Despite hunting being allowed from 10th August to the 31st December in Norway, which could be expected to induce an avoidance of houses (Stankowich 2008), we found that roe deer were actually associated with houses during this period. This probably reflects the manner of hunting in Norway, which is not conducted close to houses because of safety reasons, and the absence of stray dogs. Furthermore, the intensity of human activity intensity is different in both countries. The human population density in Norway is much higher than in Portugal, but the way human population is distributed throughout the landscape is also different: scattered in Norway and confined to small villages in Portugal. This provides a greater possibly for roe deer to habituate to a well disturbed disturbance in Norway, whereas in Portugal disturbance is less dispersed but more concentrated, which would not favour habituation.

In conclusion, we found that (1) while moderate human activities occurring in agricultural areas are perceived differently in the two countries by roe deer, in both countries roe deer occurrence was always higher far from roads, therefore validating our first prediction; (2) roe deer better tolerate anthropogenic disturbances in Norway, where the importance of the critical season seems to be higher, consequently validating our second prediction and (3) the degree of tolerance to anthropogenic disturbances is not significantly higher during the most limiting season in each country, therefore not supporting our third prediction.

The results of our analysis may suggest implications for conservation and management of roe deer populations in Europe. Roe deer avoidance of roads in both countries and sensitivity towards houses and settlements in Portugal needs to be taken into account in management measures and landscape planning. Roads are persistent components of most landscapes throughout the world. The construction of roads must be carefully planned and managers should investigate efficient mitigation techniques such as roads overpass and fences. Anthropogenic disturbance is better tolerated in Norway, where the importance of the critical season seems to be higher. Human settlements and disturbance may contribute to roe deer habitat loss in Portugal, while roe deer are able to persist close to humans in managed landscapes in Norway. In fact, some of the differences observed could be more due to the impacts of human exploitation, and the precise nature of human disturbance (*e.g.* the presence of free-ranging dogs and the regulation of hunting) rather than the actual human presence or land-use *per se*.

Acknowledgements

We are grateful to A. Gomes, F. Gonçalves, J. van Mil, J. Santos, M. Borges and R. Ramalho (Portugal) and to I. Teurlings, M. Santos and S. Timóteo (Norway) for their valuable field assistance. We thank J.C. Carvalho for his comments on an earlier draft of the manuscript. Several institutions provided invaluable support: Instituto da Conservação da Natureza e Biodiversidade and Autoridade Florestal Nacional, especially the Unidade de Gestão Florestal do Nordeste Transmontano. Rita Torres was supported by Portuguese Foundation for Science and Technology (SFRH/BD/28310/2006). The Norwegian research activity was funded by the Research Council of Norway and the Norwegian Directorate for Nature Management.

References

Andersen, R., Duncan, P., Linnell, J.D.C., 1998. The European Roe Deer: The Biology of Success. Scandinavian University Press, Oslo.

Andersen, R., Gaillard, J.-M., Linnell, J.D.C., Duncan, P., 2000. Factors affecting maternal care in an income breeder, the European roe deer. J. Anim. Ecol. 69, 672–682.

Andersen, R., Herfindel, I., Sæther, B.E., Linnell, J.D.C., Odden, J., Liberg, O., 2004. When range expansion rate is faster in marginal habitats. Oikos 107, 210–214.

Apollonio, M., Andersen, R., Putman, R., 2010. European ungulates and their management in the 21st Century.

Aragón, S., Braza, F., San José, C., 1995. Socioeconomic, physiognomic, and climatic factors determining the distribution pattern of roe deer *Capreolus capreolus* in Spain. Acta Theriol. (Warsz.) 40, 37–43.

Bates, D., Sarkar, D., 2006. lme4: Linear Mixed-effects Models using S4 Classes. R Package Version 0.9975-10, Available at: http://cran.r-project.org/web/packages/lme4/index.html.

Blondel, J., Aronson, J., 1995. Biodiversity and ecosystem function in the Mediterranean basin: human and non-human determinants. In: Mediterranean-type Ecosystems: The Function of Biodiversity. Springer-Verlag, Berlin.

Borkowski, J., Ukalska, J., 2008. Winter habitat use by red and roe deer in pine-dominated forest. For. Ecol. Manag. 255, 468–475.

Brewka, A., Kossak, S., 1994. The influence of atmospheric conditions on the mobility of roe deer (*Capreolus capreolus* L.) in winter. Ekol. Polsk. 40, 225–237.

Buckland, S., 1992. A review of deer count methodology. Report to Scottish Office Agriculture and Fisheries Department, p. 41 (unpublished).

Burnham, K.P., Anderson, D.R., 1998. Model Selection and Inference: A Practical Information – Theoretic Approach. Springer, New York.

Campbell, D., Swanson, G.M., Sales, J., 2004. Methodological insights: comparing the precision and cost-effectiveness of faecal pellet group count methods. J. Appl. Ecol. 41, 1185–1196.

Collins, W.B., Urness, P.J., 1981. Habitat preferences of mule deer as rated by pellet-group distributions. J. Wildl. Manag. 45, 969–972.

Edge, W.D., Marcum, C.L., 1989. Determining elk distribution with pellet-group and telemetry techniques. J. Wildl. Manag. 53, 621–624.

Faraway, J.J., 2006. Extending the Linear Model with R: Generalized Linear Mixed Effects and Nonparametric Regression Models. Chapman and Hall.

Faria, A.M.S., 1999. Dieta de corço (*Capreolus capreolus* L.) no Centro e Nordeste de Portugal. University of Coimbra, Coimbra.

Frid, A., Dill, L.M., 2002. Human-caused disturbance stimuli as a form of predation risk. Conserv. Ecol. 6, 1–16.

Gaston, K.J., 2003. The Structure and Dynamics of Geographic Ranges. Oxford University Press, Oxford.

Gill, R.M.A., Beardall, V., 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. Forestry 74, 209–218.

González-Megías, A., Gómez, J.M., Sanchez-Piñero, F., 2005. Consequences of spatial autocorrelation for the analysis of metapopulation dynamics. Ecology 86, 3264–3271.

Guillet, C., Bergstrom, R., Cederlund, G., Bergstrom, J., Ballon, P., 1995. Comparison of telemetry and pellet-group counts for determining habitat selectivity by roe deer (*Capreolus capreolus*) in winter. Gibier Faune Sauvage 12, 253–269.

Hewison, A.J., Vincent, J.P., Joachim, J., Angibault, J.M., Cargnelutti, B., Cibien, C., 2001. The effects of woodland fragmentation and human activity on roe deer distribution in agricultural landscapes. Can. J. Zool. 79, 679–689.

Hoffmann, A.A., Blows, M.W., 1994. Species borders: ecological and evolutionary perspectives. Trends Ecol. Evol. 9, 223–227.

Jędrzejewski, W., Jędrzejewska, B., Okarma, H., Ruprecht, A.L., 1992. Wolf predation and snow cover as mortality factors in the ungulate community of the Bialowieża National Park, Poland. Oecologia 90, 27–36.

Jiang, G., Ma, J., Zhang, M., Stott, P., 2009. Multiple spatial-scale resource selection function models in relation to human disturbance for moose in northeastern China. Ecol. Res. 24, 423–440.

Kaluzinski, J., 1982. Dynamics and structure of a field roe deer population. Acta Theriol. (Warsz.) 27, 385–408.

Larcher, W., 2000. Temperature stress and survival ability of Mediterranean sclerophyllous plants. Plant Biosyst. 134, 279–295.

Latham, J., Staines, B.W., Gorman, M.L., 1997. Correlations of red (*Cervus elaphus*) and roe (*Capreolus capreolus*) deer densities in Scottish forests with environmental variables. J. Zool. 242, 681–704.

Lemmon, P.E., 1956. A spherical densiometer for estimating forest overstory density. For. Sci. 2, 314–320.

Lindén, H., Helle, E., Helle, P., Wikman, M., 1996. Wildlife triangle scheme in Finland: methods and aims for monitoring wildlife populations. Fin. Game Res. 49, 4–11.

Loft, E.R., Kie, J.G., 1988. Comparison of pellet-group and radio triangulation methods for assessing deer habitat use. J. Wildl. Manag. 52, 524–527.

Mayle, B.A., Putman, R.J., Wyllie, I., 2000. The use of trackway counts to establish an index of deer presence. Mamm. Rev. 30, 233–237.
Melis, C., Basille, M., Herfindal, I., Linnell, J.D.C., Odden, J., Gaillard, J.-M., Høgda, K.-A., Andersen, R., 2010. Roe deer population growth and lynx predation along a gradient of environmental productivity and climate in Norway. Ecoscience 17, 166–174.
Miyashita, T., Suzuki, M., Ando, D., Fujita, G., Ochiai, K., Asada, M., 2008. Forest edge creates small-scale variation in reproductive rate of sika deer. Pop. Ecol. 50, 111–120.
Moreira, L.M., Rosa, J.L., Lourenc, O.J., Barroso, I., Pimenta, V., 1997. Projecto Lobo. Relatório de Progressão 1996 (Cofinanciado pela U. E. – Programa LIFE). Parque Natural de Montesinho, Bragança.
Mysterud, A., Bjornsen, B.H., Østbye, E., 1997. Effects of snow depth on food and habitat selection by roe deer *Capreolus capreolus* along an altitudinal gradient in south-central Norway. Wildl. Biol. 3, 27–33.
Mysterud, A., Lian, L.-B., Hjermann, D.O., 1999. Scale-dependent trade-offs in foraging by European roe deer (*Capreolus capreolus*) during winter. Can. J. Zool. 77, 1486–1493.
Mysterud, A., Østbye, E., 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. Wildl. Soc. Bull. 27, 385–394.
Neff, D.J., 1968. The pellet-group count technique for big game trend, census, and distribution: a review. J. Wildl. Manag. 32, 597–614.
Odden, J., Linnell, J., Andersen, R., 2006. Diet of Eurasian lynx *Lynx lynx*, in the boreal forest of southeastern Norway: the relative importance of livestock and hares at low roe deer density. Eur. J. Wildl. Res. 52, 237–244.
Panzacchi, M., Herfindal, I., Linnell, J., Odden, M., Odden, J., Andersen, R., 2010. Trade-offs between maternal foraging and fawn predation risk in an income breeder. Behav. Ecol. Sociobiol. 64, 1267–1278.
Panzacchi, M., Linnell, J.D.C., Odden, J., Odden, M., Andersen, R., 2008. When a generalist becomes a specialist: patterns of red fox predation on roe deer fawns under contrasting conditions. Can. J. Zool. 86, 116–126.
Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.
Pautasso, M., 2007. Scale dependence of the correlation between human population presence and vertebrate and plant species richness. Ecol. Lett. 10, 16–24.
Pimenta, V., Correia, J., 2001. Distribuição do corço (*Capreolus capreolus*) no Parque Natural do Douro Internacional: análise dos factores ambientais que a condicionam. Inst. Politécnico de Bragança, Portugal.
Randall, M.G.M., 1982. The dynamics of an insect population throughout its altitudinal distribution: *Coleophora alticolella* (Lepidoptera) in Northern England. J. Anim. Ecol. 51, 993–1016.
Ratikainen, I.I., Panzacchi, M., Mysterud, A., Odden, J., Linnell, J., Andersen, R., 2007. Use of winter habitat by roe deer at a northern latitude where Eurasian lynx are present. J. Zool. 273, 192–199.
Rowland, M.M., Wisdom, M.J., Johnson, B.K., Kie, J.G., 2000. Elk distribution and modeling in relation to roads. J. Wildl. Manag. 64, 672–684.
Saïd, S., Servanty, S., 2005. The influence of landscape structure on female roe deer home-range size. Landsc. Ecol. 20, 1003–1012.
Stankowich, T., 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biol. Conserv. 141, 2159–2173.
2009. Statistics Norway, http://www.ssb.no/.
Tellería, J.L., Virgós, E., 1997. Distribution of an increasing roe deer population in a fragmented Mediterranean landscape. Ecography 20, 247–252.
Torres, R.T., Santos, J., Linnell, J.D.C., Virgós, E., Fonseca, C., 2011. Factors affecting roe deer occurrence in a Mediterranean landscape Northeastern Portugal. Mamm. Biol. 76, 491–497.
Tufto, J., Andersen, R., Linnell, J., 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. J. Anim. Ecol. 65, 715–724.
Vingada, J., Fonseca, C., Cancela, J., Ferreira, J., Eira, C., 2010. Ungulates and their Management in Portugal. Cambridge University Press, Cambridge.
Virgós, E., Telléria, J.L., 1998. Roe deer habitat selection in Spain: constraints on the distribution of a species. Can. J. Zool. 76, 1294–1299.
Wahlström, L.K., Liberg, O., 1995. Contrasting dispersal patterns in two Scandinavian roe deer *Capreolus capreolus* populations. Wildl. Biol. 1, 159–164.