Original Investigation

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

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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.

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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.

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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