ECOGRAPHY 20: 247-252. Copenhagen 1997

Distribution of an increasing roe deer population in a fragmented Mediterranean landscape

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Telleria, J L and Virgos, E 1997 Distribution of an increasing roe deer population in a fragmented Mediterranean landscape - Ecography 20 247-252

This paper describes roe deer *Capreolus capreolus* distribution in central Spain, where the species has spread from the mountains into peripheral agricultural areas In this region, it is more abundant in forest fragments near the mountains than in those further away, in pine and oak woodlands than in sclerophyllous forests, and in forests with open water than in those lacking this resource The paper also analyzes whether habitat quality and geographic location of forests with respect to roe deer source areas are the two basic causes of its distribution, as predicted by some models of the species distribution in fragmented landscapes The results corroborate this hypothesis revealing that roe deer abundance is linked negatively to sclerophyllous forest cover and distance from mountains We conclude that this type of farmland seems to be sub-optimal for roe deer in comparison with forested, moist mountains

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The roe deer *Capreolus capreolus* reaches in the Iberian Peninsula the southern extreme of its western Palearctic distribution (Corbet 1978) Its range decreases towards the south, where its distribution is restricted to moist mountainous areas of the southern half of Iberian Peninsula (see Braza et al 1989, Aragón et al 1995) As with other Palearctic forest vertebrates in this area (see Tellería and Santos 1994), this distribution pattern of the roe deer appears to be due to its nonadaptation to the Mediterranean xericity (Sáez-Royuela and Tellería 1991, Aragon et al 1995) Despite these restrictions, the Iberian roe deer population has grown in central and northern Spain in the last decade, accompanying an expansion from mountains into peripheral agricultural areas where it was hitherto unknown (Tellería and Sáez-Royuela 1984, Braza et al 1989, Aragón et al 1995). Now it occupies forest fragments of plateaus at the foot of mountains, in an otherwise deforested landscape used for crops Several studies in central Europe have demonstrated the adaptability of the roe deer to these agricultural landscapes where, thanks to its ability to exploit the forest ecotone and open areas, it can reach higher densities than in the forests themselves (Kaluzinski 1974, Pielowski 1984, Cibien et al 1989, Aulak and Babinska-Werka 1990a, Wahlstrom and Kjellander 1995, Wahlström and Liberg 1995a) It is unknown, however, how roe deer adapts to these Mediterranean agricultural areas in central Spain

The roe deer colonization of forests at the foot of mountains has been interpreted as a spill-over by surplus individuals from the mountains (Tellería and Sáez-Royuela 1984) It thus appears to fit into a density-dependent process of landscape colonization (Wahlstrom and Kjellander 1995, Wahlström and Liberg 1995a) Under these circumstances, habitat selection and the species' dispersive ability should be the main determinants of its occupation patterns in a fragmented landscape (e g Wiens et al 1993, Ims 1995). We may thus predict that in this patchy landscape of

Accepted 7 October 1996

ISSN 0906-7590

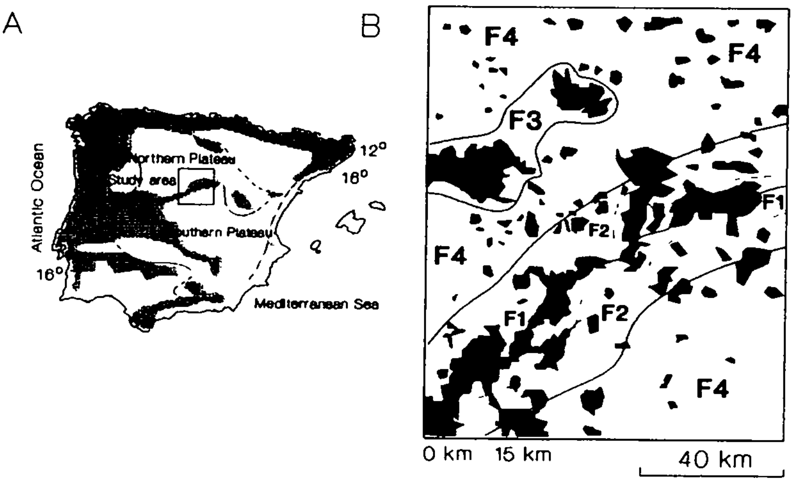

Fig 1 A) Study area in Iberian peninsula Mean annual temperature isotherms for 12°C and 16°C and areas with mean annual precipitation over 600 mm (shaded) are shown B) Forest distribution in the study area (shadings) Sierra de Guadarrama crests are also shown (continuous line), along with 1200 m contour (dotted line) The following lines mark 15 km from the crest (km 0) Forest typification is shown according to distances and sizes (see text)

central Spain, roe deer abundance is restricted by its adaptation to the different forests of the zone and the distance from source areas

Material and methods

Study area

The 12 000 km^2 study area includes the Sierra de Guadarrama, with several peaks above 2000 m, and the surrounding plateaus (Fig 1A) The northern plateau (above 800 m) is colder and rainier than its southern counterpart (above 600 m), and precipitation increases with altitude The mountain landscape (above 1200 m) is composed of forests, shrublands and pastures, while the surrounding plateaus are predominantly covered by extensive crops of wheat *Triticum aestivum* Vill and barley *Hordeum vulgare* L., where the forests have a patchy distribution There is a succession of forests along this altitudinal gradient the more xeric, basal zones are occupied by sclerophyllous forests (*Quercus ilex* L and *Quercus faginea* Lam.), Pyrenean oak *Quercus pyrenaica* Willd is predominant above 1200 m, being replaced by natural pinewoods of *Pinus sylvestris* L beyond 1700 m There are also large pine plantations along the whole of the altitudinal gradient, with a predominance of *Pinus sylvestris* on the mountains and *Pinus pinaster* Ait on the plateaus The forests of the region can be classified, according to size and isolation from mountains, into four groups F1) Large forests interconnected by pastures and scrublands in mountain areas, F2) small forests (100–1000 ha) lying in cultivated zones from the base of mountains to a maximum of 15 km from the crests, F3) large forests (> 10 000 ha) on the plateaus, at least 15 km from the mountains and F4) small forests (100–1000 ha) at least 15 km from the mountains (Fig 1B)

Methods

During the summer of 1995 (August–September), roe deer distribution was studied in 72 1 × 1 km plots distributed at random throughout the forests in the study area Roe deer abundance was typified by censusing fecal groups along a 2 km long × 2 m wide transect zigzagging from a corner to the opposite through each plot (Neff 1968, Mitchell et al 1985) We only counted recent fecal groups to attenuate the effects of some eventual differences in the decaying rates of pellets in different habitats and/or sectors (Neff 1968) The abundance of the species (ABUNDANCE) was expressed in number of fecal groups per km. Each plot was also typified by a series of geographic and habitat variables that could potentially determine the species distribution Some were aimed at typifying the location of the censused forest with respect to the mountains (DIST1 and DIST2) or some other source of secondary colo-

Table 1 Description of variables used to analyze the factors determining roe deer abundance in the study plots

Variable	Description
TREECOV	Tree cover (%) (height >2 m)
SHRCOV	Shrub cover (%) (height 50–200 cm)
PASCOV	Pasture cover (%)
FERNCOV	*Pteridium aquilinum* cover (%)
SCLCOV	*Quercus ilex* and *Q faginea* cover (%)
OAKCOV	*Quercus pyrenaica* cover (%)
PINCOV	*Pinus sylvestris* and *P pinaster* cover (%)
THORNCOV	Thorny shrubs (*Rosa, Rubus*) cover (%)
LEGCOV	Legume (*Leguminosae*) cover (%)
CISCOV	*Cistacea* cover (%)
HEIGHT	Tree height (m)
TREESPP	Number of tree species
SHRUBSPP	Number of shrub species
DIST1	Distance from mountain crest in intervals (<5, 5–15, >15 km)
DIST2	Distance from mountain crest (km)
DIST3	Distance from any >10 000 ha forest
WAT	Presence/absence of open water in plot

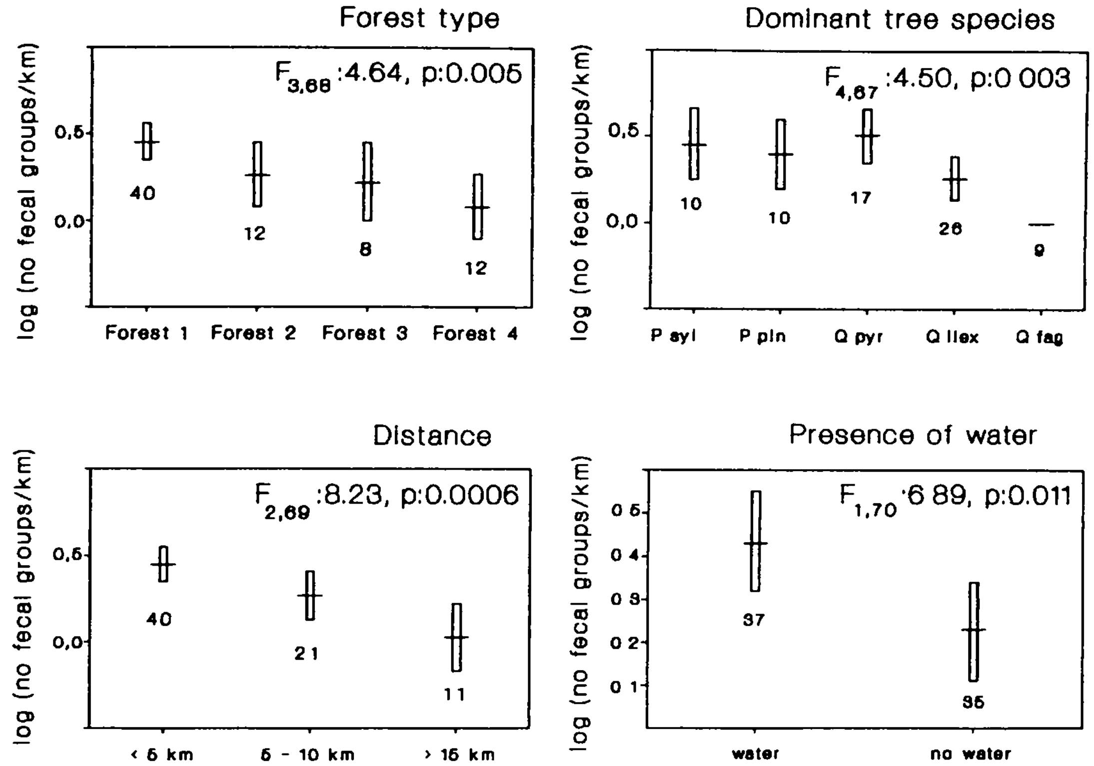

Fig 2 Distribution of roe deer abundance (mean and 95% interval in the four types of forests shown in Fig 1B, see text for details), according to predominant tree species (P syl *Pinus sylvestris*, P pin *Pinus pinaster*, Q pyr *Quercus pyrenaica*, Q ilex *Quercus ilex*, Q fag *Quercus faginea*), distance from mountain crest and presence/absence of water The result of an ANOVA for each case is also shown

nization such as large forests (F3) on the plateaus (DIST3, Table 1) The purpose of other variables was to typify the availability of shelter and food for the animal on the basis of the information available for the species (see Fandos et al 1987, Aulak and Babinska-Werka 1990b, Braza et al 1994, Cibien et al 1995) This was quantified in 25 m radius circles distributed every 100 m along the census itineraries We considered the physical structure of the environment (TREECOV, SHRCOV, PASCOV and HEIGHT), floristic diversity (TREESPP and SHRUBSPP) and the cover of tree and shrub species that were potentially usable as food (SCLCOV, PINCOV, OAKCOV, THORNCOV, LEGCOV, CISCOV and FERNCOV, see Table 1). We also included the presence or absence of open water (WAT) in the plot (permanent streams, rivers, pools or troughs) We analyzed the influence of the factors under consideration on roe deer abundance by simple regression, multiple stepwise regression (F to enter: 4) and analysis of covariance (Zar 1984). The variables were normalized by means of arcsine (covers) or logarithmic (the rest) transformations.

Results

The roe deer has an uneven abundance distribution in the four types of forest defined in the study area (Fig 2) Its abundance also differs significantly according to the predominant tree species, distance from mountain ranges and presence or absence of water (Fig 2) The distribution of its abundance is associated negatively with sclerophyllous forest cover (SCLCOV) and distance from the forests to the source areas (DIST2, DIST3), and positively with the forest development (TREECOV, HEIGHT) and cover by certain shrub types (LEGCOV, THORNCOV) It is not, however, associated with scrub, oak or pine cover, nor with the diversity of tree or shrub species (Table 2) The multiple stepwise regression analysis, which includes the availability of water as a dummy variable (Zar 1984), reveals in contrast that after eliminating the interactions between all of these variables, only schlerophyllous forest cover and distance from the source area are correlated significantly with roe deer abundance (ABUNDANCE = 0 497 – 0 307 SCLCOV – 0.168 DIST2, $F_{2,69} = 9\ 71$, $p = 0\ 0004$, $R^2 = 20\ 16$).

Table 2 Results of simple regression analysis between study variables and roe deer abundance (transformed data)

Variable	r	p
TREECOV	0 27	0 020
SHRCOV	−0 06	0 600
PASCOV	0 20	0 080
FERNCOV	0 07	0 520
SCCOVL	0 38	0 001
OAKCOV	0 13	0 280
PINCOV	0 20	0 090
THORNCOV	0 26	0 030
LEGCOV	0 23	0 050
CISCOV	−0 02	0 820
HEIGHT	0 30	0 010
TREESPP	−0 04	0 700
SHRUBSPP	0 11	0 350
DIST2	−0 38	0 001
DIST3	−0 31	0 006

In order to analyze the role of habitat quality in roe deer distribution without the restrictions imposed by isolation, we have repeated the multiple stepwise regression analysis on the 40 mountain plots (F1) The only decisive factor in roe deer presence is again schlerophyllous vegetation cover, which the animal seems to avoid (ABUNDANCE = 0 549–0 619 SCLCOV, $F_{1\ 38} = 9\ 13$, $p = 0\ 004$, $R^2 = 17\ 27$)

In order to ascertain whether roe deer colonization of isolated plateau forests is linked to isolation or habitat quality (given that many of the more distant forests are composed of schlerophyllous trees), we have performed a multiple stepwise regression analysis for the 32 plots located in plateau forests (F2, F3 and F4) None of the variables are fed into the regression model However, the effects of the different types of variables could offset each other, with a prevalence of habitat quality in the nearby habitats (F2) and the distance factor in those further away (F4) An analysis of covariance of roe deer abundance with WAT as classification factor and DIST2, DIST3 and SCLCOV as the covariates shows that none of the variables are associated with roe deer abundance in the nearby forests, while distance from a forest of over 10000 ha (DIST3) correlates with roe deer abundance in the distant forests (Table 3)

Table 3 Results of the analysis of covariance between roe deer abundance and habitat quality (SCLCOV), isolation (DIST2, DIST3) and water (WAT) in the island plots (F2, F4)

Source of variation	DF	Type III SS	F	p
A Near forest fragments (F2)				
WAT (factor)	1	0 06	0 36	0 57
DIST2 (covariate)	1	0 01	0.09	0 77
DIST3 (covariate)	1	0 02	0 12	0 73
SCLCOV (covariate)	1	0 02	0 13	0 73
Total	12			
B Remote forest fragments (F4)				
WAT (factor)	1	0 002	0.15	0 70
DIST2 (covariate)	1	0 06	3.62	0 10
DIST3 (covariate)	1	0 19	11 89	0 01
SCLCOV (covariate)	1	0 006	0 39	0 56
Total	12			

Discussion

The lower roe deer abundance in sclerophyllous mountain forests, where there is no isolation that may influence its distribution, confirms the prediction of its poor adaptation to these xeric Mediterranean forests Furthermore, its lower densities in the Mediterranean habitats of the Peninsula appears to confirm the ubiquity of this pattern (Delibes et al 1991, Sáenz de Buruaga et al 1991, Sáez-Royuela and Tellería 1991) While density is not necessarily an indicator of habitat quality (Van Horne 1983), there is some additional information with respect to its diet that appears to explain this pattern The Iberian roe deer tends to avoid the consumption of rough sclerophyllous vegetation and prefers trees and shrubs typical of moist sectors in Mediterranean forests (Fandos et al 1987, Braza et al 1994) This hypothetical misadaptation of roe deers to xeric sclerophyllous Mediterranean forests would thus partly explain its lower density in the study agricultural landscape in comparison with the mesic, forested mountains

The role of habitat quality in determining patterns of roe deer distribution in central Spain may be interpreted as a result of processes working at higher scales (e g Lawton 1993) Densities of roe deer in the Mediterranean forests of central and south Iberian peninsula tend to be lower than in mesic forests from northern Spain (a region in which Mediterranean drought does not occur) and central Europe (review by Sáez-Royuela and Tellería 1991), suggesting an overall decrease of the habitat suitability of these southern forests The small body size and decreased reproductive output of some populations from southern Iberia also seem to support this view (Braza et al 1994) This pattern of abundance distribution agrees with those observed for other forest vertebrates in Iberia, that show decreasing densities along a north-south, Atlantic/mesic-Mediterranean/xeric gradient (e g forest birds, Tellería and Santos 1993, 1994) An usual explanation of this distribution patterns of forest birds, that may be applied to roe deers, is that most forest species in the Mediterranean belong to the Palearctic realm, so that they tend to show increasing difficulties to adapt to the xeric conditions of this peripheral area of the Palearctic Region (Blondel 1990, Tellería and Santos 1994). This view is consistent with the models that predict higher abundances in the core areas of the species' ranges, where environmental conditions are optimum, and lower abundances in the peripheral areas with sub-optimum conditions (Hengeveld and Haeck 1982, Brown 1984)

Habitat quality, however, was not the only factor determining the abundance of the species in these fragmented landscapes of central Spain Distance from source areas also played a role in determining its regional distribution The results presented here are probably a "frozen image" of a dynamic process in which the plateau forests are continually being colonized by immigrant individuals from mountain areas or other fragments (e.g F3 in this study) In fact, there are some data on casualties (car collisions and drownings in agricultural canals) and records of wandering individuals in unsuitable sites of northern sectors of our study area (Sánchez pers comm) These wandering individuals are probably juveniles, because adults seem to be philopatric and show a relatively small radius of movement (Strandgaard 1972, Pielowski and Bresinski 1982, Fruzinski et al 1983, Wahlstrom and Liberg 1995b) The role of distance to sources as a determinant of the ability of roe deers to colonize forests suggests that their expansion has not been complete and hence that some suitable yet distant forests could still be colonized (e g Milne et al 1989)

Results in this paper support the view that the decreasing ability of roe deers to thrive in this border area is the result of both forest quality and distance to sources This suggests that unsuitable sclerophyllous forests, dominant in the most distant sectors from source areas, are probably acting as sinks (Pulliam 1988) for a part of the colonizing individuals, hampering the formation of stable populations

Acknowledgements – Olof Liberg, Jose Díaz and Tomas Santos considerably improved an early version of this manuscript This study was funded by the Dirección General de Investigación Científica y Tecnica de España (PB92-0238)

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