Roe deer habitat selection in Spain: constraints on the distribution of a species

E. Virgós and J.L. Tellería

Abstract: This study analyzes the role of summer habitat selection in determining the distribution of a population of roe deer (*Capreolus capreolus* L.) in central Spain, where surplus individuals have emigrated from mountains to the surrounding plateaus during the last decade. The species was more abundant in the mesic mountain forests (Scots pine (*Pinus sylvestris*), Pyrenean oak (*Quercus pyrenaica*)) than in the xeric, sclerophyllous holm oak (*Quercus ilex*) forests of surrounding plateaus. Roe deer prefer patches occupied by brambles (*Rubus* spp.) and rose bushes (*Rosa* spp.) and patches with higher cover on pastures and moors (*Erica* spp. and *Calluna* spp.). These vegetation types are linked to moist soils in the Mediterranean zone, indicating that roe deer prefer the moister, more productive patches. Roe deer actively selected productive patches covered by leguminous shrubs (*Sarothamnus*, *Retama*) and rejected poor patches covered by *Cistus ladanifer* and *Cistus laurifolius* (two shrubs that produce chemicals toxic to other plants). Low summer primary productivity of xeric, sclerophyllous forests can explain the low abundance of roe deer in these forests. This supports the view that habitat constraints limit numbers and distribution of this Palaearctic species at the southern edge of its range.

Résumé : Nous avons étudié les conséquences du choix d'un habitat d'été sur la répartition d'une population de Chevreuils du centre de l'Espagne, population augmentée par migration d'individus des montagnes aux plateaux environnants au cours de la dernière décennie. Les chevreuils sont plus abondants dans les forêts mésiques de montagne (*Pinus sylvestris* et *Quercus pyrenaica*) que dans les forêts xériques, sclérophylles de chênes de Holm (*Quercus ilex*) des plateaux environnants. Les chevreuils préfèrent les taillis de ronces (*Rubus* spp.), de rosiers (*Rosa* spp.) et les zones à végétation plus haute des pâturages et des landes (*Erica* spp. et *Calluna* spp.). Ces types de végétation sont reliés aux sols humides de la zone méditerranéenne, ce qui indique que les chevreuils préfèrent les zones plus humides, plus productives. Les chevreuils recherchent activement les bosquets productifs de légumineuses arbustives (*Sarothamnus*, *Retama*) et rejettent les zones plus pauvres recouvertes de *Cistus ladanifer* et *Cistus laurifolius* (deux arbrisseaux qui synthétisent des matières toxiques pour les autres plantes). La faible productivité primaire des forêts xériques sclérophylles explique la faible abondance des chevreuils dans ces forêts. Ces résultats supportent l'hypothèse selon laquelle les contraintes reliées à l'habitat déterminent l'abondance et la répartition de cette espèce paléarctique à la limite sud de sa zone d'occupation.

[Traduit par la Rédaction]

Introduction

The Iberian Peninsula is located at the southwestern edge of the roe deer (*Capreolus capreolus* L.) range (Corbet 1978). The species was restricted to mountains in this area, although during the last decade it has colonized the foot of mountains in central Spain. This was interpreted as emigration by surplus individuals from the mountains, where forest regeneration and hunting restrictions have led to recovery of the population (Tellería and Sáez-Royuela 1984; Braza et al. 1989; Sáez-Royuela and Tellería 1991; Aragón et al. 1995). Roe deer densities in colonized forests are lower than in mountains (Sáez-Royuela and Tellería 1991; Tellería and Virgós 1997). The densities of roe deer in central Spain were negatively related to distance from source populations in mountain zones and sclerophyllous oak forest cover (holm oak (*Quercus ilex*), Lusitanean oak (*Quercus faginea)*; Tellería and Virgós 1997). This pattern may be the result of two hypothetical processes (Tellería and Virgós 1997): (*i*) forests in the plateaus have low densities because they are not yet fully colonized by the increasing population of roe deer descending from mountains and (*ii*) these forests are suboptimal habitat for the species adapted to the mesic forests of central Europe.

This paper analyzes the contribution of cover and vegetation to the distribution of roe deer in central Spain. It has been suggested that the scarcity of many Palearctic forest vertebrates in the xeric forests of Mediterranean countries is the result of an old process of forest deterioration due to human disturbance (Blondel 1990). Iberian forests, for instance, have became increasingly shrubby and adapted to xeric conditions since the Holocene by replacing the formerly predominant deciduous mesic tree species (e.g., Pyrenean oak (*Quercus pyrenaica*)) with heliophytic tree species (e.g., holm oak, Costa et al. 1990; Peñalba 1994). It has been suggested that as most forest vertebrates in the Mediterranean belong to the "Palearctic" realm, they have diffi-

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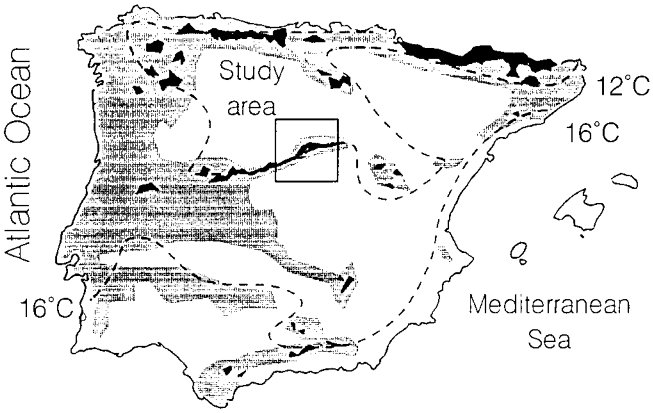
Fig. 1. Location of the study area in the Iberian Peninsula. Areas with mean annual precipitation over 600 mm (shaded) and mean annual temperature isotherms for 12 and 16°C are shown. Black areas show highlands over 1500 m.



culty in adapting to xeric forests, which sometimes may act as sink habitats for forest vertebrates (Blondel 1990; Dias 1996).

Population density may affect habitat selection (Fretwell and Lucas 1970; Rosenzweig 1991), so we attempted to select fully colonized xeric forests. To check the status of the colonization process, we selected two groups of holm oak forests: (*i*) forests at the foot of mountains, contiguous to the mesic woodlands and source populations, and (*ii*) isolated forests in the surrounding agricultural areas, several kilometres away from the source mountains. If roe deer colonization of those xeric forests still occurs, these isolated forests will have lower densities than their replicates in the mountains, whereas if already fully colonized, they will have similar abundances. We can then test the role of certain habitat features in determining the distribution of roe deer in xeric Mediterranean forests at the edge of the species' range.

Material and methods

The 12 000-km^2 study area includes the Sierra de Guadarrama (Sistema Central Mountains), with several mountains above 2000 m, and the surrounding plateaus (Fig. 1). The northern plateau is colder and rainier than its southern counterpart, and precipitation increases with altitude (Font 1983). The mountain landscape (above 1500 m) is composed of forests, shrubland, and pastures, whereas the surrounding plateaus are predominantly covered by extensive cereal crops, where forests have a patchy distribution. There is a change of forests along this altitudinal gradient: the more xeric, basal zones are occupied by sclerophyllous forests (holm oak), whereas the mesic Pyrenean oak forests predominate above 1200 m, being replaced by natural pinewoods (Scots pine (*Pinus sylvestris*)) above 1700 m.

We studied roe deer abundance in mesic (Scots pine, Pyrenean oak) and holm oak (mountain and isolated) forests during the summers of 1995 and 1996 (mid-July to mid-September). Summer food supply is a key aspect of roe deer population dynamics (Bobek 1977). This is likely to be more relevant in Mediterranean habitats, where summer is the most restrictive season for primary productivity (Blondel and Aronson 1995), thus affecting food availability and ultimately the biomass of ungulates (Coe et al. 1976; Oksanen et al. 1981). For species adapted to mesic habitats, such as the roe deer, summer habitat selection may be a good indicator of habitat restrictions in Mediterranean environments.

The isolated holm oak forests were located in a matrix of extensive cereal fields at a distance of 12.1 ± 1.3 km (mean ± SE; n = 28) from the mountains, whereas the remaining forest types were located on the mountains. Throughout this paper, *Pinus*, *Q. pyrenaica*, mountain holm oak, and isolated holm oak forests are referred to as pine, Pyrenean oak, holm oak 1, and holm oak 2, respectively. All the sampled forests were over 100 ha. Relative abundance of roe deer was evaluated by counting pellet groups (Neff 1968; Mitchell et al. 1985) along transects 2 km long × 2 m wide running through 72 randomly selected forests (pine, n = 14; Pyrenean oak, n = 13; holm oak 1, n = 8; holm oak 2, n = 28). The small sample size for holm oak 1 forests is a reflection of their scarcity in the mountains, where they are substituted by Pyrenean oaks forests just at the foot of the slopes. We counted only recent fecal groups, as assessed by the presence of a black and bright cuticle in pellets, to attenuate the effects of some eventual differences in decay rates of pellets in different habitats and (or) sectors (Neff 1968). Abundance was expressed as the number of pellet groups per kilometre. Each transect was also used to typify availability of shelter, the other basic habitat requirement of this species (Tufto et al. 1996). We evaluated certain physiognomic features and cover of the main tree and shrub species (Table 1), important for the species according to the information available on their requirements (e.g., Papageorgiou et al. 1981; Fandos et al. 1987; Maizeret 1988; Aulak and Babinska-Werka 1990; Braza et al. 1994; Cibien et al. 1995). The availability of these habitat features was quantified by visual estimation in 25 m radius circles distributed every 200 m along the transects (143, 140, 115, and 251 circles in pine, Pyrenean oak, holm oak 1, and holm oak 2 forests, respectively). We quantified roe deer intrahabitat usage by assessing the same variables in 25 m radius circles around each pellet group. To avoid the problem of eventual non-independence of data, only pellet groups separated by more than 250 m were used for analyses. Thus, we obtained a sample of 112 (pine, n = 58; Pyrenean oak, n = 54) and 36 (holm oak 1, n = 19; holm oak 2, n = 17) independent pellet groups for xeric and mesic forests, respectively.

We analyzed habitat selection by roe deer by comparing the available versus selected mean scores of the study variables by means of a two-way ANOVA with use/availability (to evaluate habitat selection) and forest type (to evaluate environmental variation) as classification factors. As the breadth of habitat use is an indicator of degree of specialization in resource exploitation by a species (James and Lockerd 1986), we also studied the breadth of their intrahabitat selection (within forest types) by comparing used versus available coefficients of variation of the log-transformed variables through Levene's test (Zar 1984; Manly 1994). If roe deer were poorly adapted to holm oak forests, they would be expected to make more restrictive, less flexible use of the environment in this habitat and therefore have lower variation coefficients than those obtained from pine and Pyrenean oak forests.

To avoid the effect of multiple comparisons in type I statistical error, Bonferroni sequential corrections were applied in these tests (Rice 1989). We attempted to normalize variables by arcsine (cover) or logarithmic (the rest) transformations (Zar 1984).

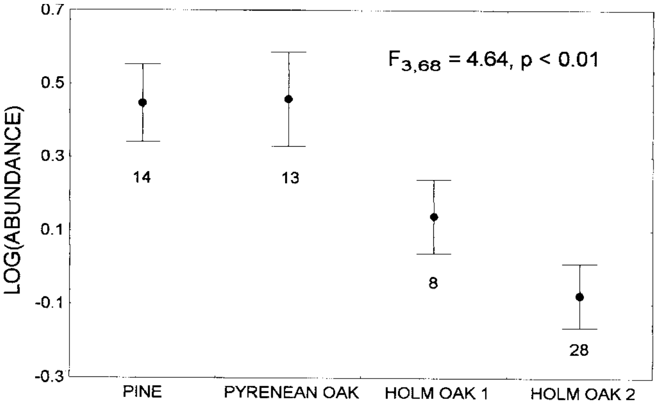
Results

The mesic forests tended to have higher abundance indices than the xeric forests (Fig. 2). However, Pyrenean oak and pine forests had similar abundances (Student's t test, $t_{(25)} = 0.07$, $p = 0.95$), as did the two types of holm oak forest ($t_{(34)} = 1.56$, $p = 0.13$). However, in the last test, the p value is close to a significant result and the sample size for

Table 1. Variables used to investigate habitat selection by roe deer on the two forest types.

Variable	Description
TREECOV	Tree cover (height >2 m) (%)
SHRCOV	Shrub cover (height 50–200 cm) (%)
PASCOV	Pasture cover (%)
SCLCOV	*Quercus ilex* plus *Quercus faginea* cover (%)
PYROAKCOV	*Quercus pyrenaica* cover (%)
PINECOV	*Pinus sylvestris* cover (%)
FERNCOV	*Pteridium aquilinum* cover (%)
THORNCOV	Thorny shrub (*Rosa*, *Rubus*, *Crataegus*, *Prunus*) cover (%)
LEGCOV	Leguminous shrub (*Retama*, *Sarothamnus*) cover (%)
CISCOV	Cistaceae shrub (*Cistus ladanifer*, *Cistus laurifolius*) cover (%)
MOORCOV	Ericaceae shrub (*Erica*, *Calluna*) cover (%)

Fig. 2. Roe deer abundance (number of pellets/km (mean ± SE)) in the different forest habitats of the study area. Sample sizes are given below the data points. Holm oak 1 is mountain holm oak forest; holm oak 2 is isolated holm oak forest.



holm oak 1 forests is relatively low. In this case, the probability of type II statistical error is not negligible and we needed to check the power of the test. The result of power analysis (power 67%) indicated that we may consider this result statistically adequate.

Low roe deer abundance in these forests was attributed not to slow colonization but to habitat restrictions. Both forest groups were pooled into two groups (henceforth mesic and xeric forests) to study roe deer habitat selection.

The study forests differed in physiognomy and floristic composition (Table 2, Fig. 3). The mesic forests had a higher cover of pines, Pyrenean oaks, ferns, thorny shrubs (Rosaceae), and Leguminosae shrubs, whereas the xeric forests had a higher cover of holm oaks and shrubs. Roe deer tended to make a positive selection of higher tree cover (marginal difference), pastures, thorny shrubs, and Leguminosae shrubs and tended to avoid (marginally) Cistaceae shrubs (Table 2, Fig. 3). On the other hand, legume and pasture cover indicates a significant interaction (habitat × use/availability). This reveals a change in roe deer usage between the two forest types (these variables were selected only in the xeric forests). The pattern of habitat selection at the regional scale seems to be mainly affected by intrahabitat selection in the xeric forests, with less flexible use of habitat, as indicated by their low variation coefficients. The usage scores were significantly lower there than those available for most of the variables (pasture, thorny shrub, leguminous shrub, Cistaceae, and moor cover; Table 3). In the mesic habitats, however, the roe deer also had a more restrictive pattern for thorny shrub (high values) and Cistaceae cover (low values), in accordance with its microhabitat selection in xeric forests.

Discussion

Habitat selection by ungulates is strongly influenced by food availability and quality (Duncan 1983; Murden and Risenhoover 1993). The observed intra- and inter-habitat selection by roe deer was related to their food preferences, whereas cover variables (e.g., tree cover, shrub cover) were weakly related to their distribution. On the other hand, summer food supply is a key factor in determining the population size and performance of roe deer populations (Bobek 1977). Roe deer tend to have more restricted patterns of microhabitat selection in holm oak forests than in mesic forests. This pattern and the related low variation coefficients of the selected variables in sclerophyllous forests suggest that roe deer microdistribution in these forests is restricted to certain patches with high cover in pastures where several shrub species are common. Among the plant species related to roe deer microhabitat selection, moorland *Erica* species (primarily heather (*Calluna vulgaris*)), brambles (*Rubus* spp.), and rose bushes (*Rosa* spp.) are predominant items in their diet in Europe (Maizeret and Sung Gerea 1984; Maizeret 1988; Maizeret et al. 1989). Selection of pastures by roe deer in this study could also be related to the abundance of plant species that grow in pastures and frequently appear in their diet (e.g., *Trifolium* spp., *Poa bulbosa*, *Dactylis glomerata*, Kaluzinski 1982; Stüwe and Hendrichs 1984). These shrubs and pastures are related to deep soils, in small valleys or near rivers or springs, where edaphic water sources persist throughout the dry Mediterranean summer. As water is the main determinant of primary productivity in Mediterranean habitats (Blondel and Aronson 1995), the roe deer seems to utilize the more productive patches of these dry forests during the summer. This food tracking is also demonstrated by its relationships with two other types of shrub. The role of leguminous shrubs (e.g., *Sarothamnus*, *Retama*, *Adenocarpus*) in roe deer intrahabitat selection may be puzzling at first, since Maizaret and Sung Gerea (1984)

Table 2. Two-way ANOVA from habitat and availability/use classification factors for each studied variable.

Variable	$F_{[1,793]}$	p
TREECOV		
Habitat	14.22	<0.001
Use	2.74	0.098
Interaction	0.38	0.536
SHRCOV		
Habitat	8.36	<0.01
Use	1.28	0.258
Interaction	0.28	0.598
PASCOV		
Habitat	2.77	0.096
Use	18.57	<0.001
Interaction	5.98	<0.05
SCLCOV		
Habitat	541.8	<0.001
Use	0.81	0.369
Interaction	1.04	0.308
PYROAKCOV		
Habitat	56.54	<0.001
Use	1.04	0.308
Interaction	0.13	0.718
PINECOV	124.6	<0.001
Habitat	0.002	0.961
Use	0.05	0.827
Interaction		
FERNCOV		
Habitat	31.49	<0.001
Use	0.009	0.922
Interaction	0.019	0.889
THORNCOV		
Habitat	25.97	<0.001
Use	8.49	<0.01
Interaction	0.001	0.990
LEGCOV		
Habitat	15.30	<0.001
Use	41.65	<0.001
Interaction	33.92	<0.001
CISCOV		
Habitat	0.55	0.456
Use	3.81	0.051
Interaction	0.42	0.515
MOORCOV		
Habitat	0.15	0.699
Use	2.21	0.137
Interaction	2.41	0.199

Table 3. Results of Levene's tests to check differences in coefficients of variation for availability/use data in the two habitats considered.

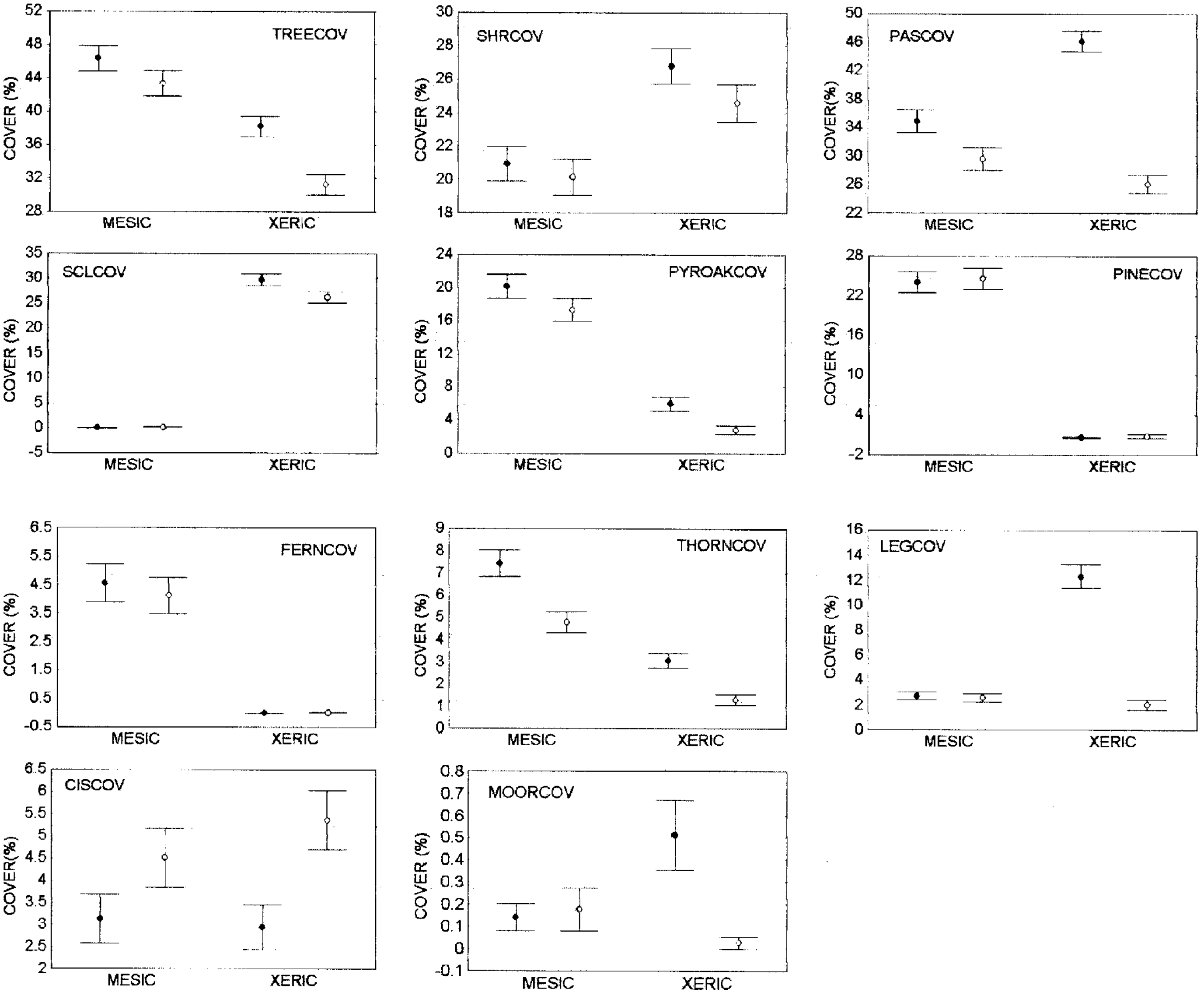
Variable	F	p
TREECOV		
Mesic	0.78	0.377
Xeric	0.005	0.940
SHRCOV		
Mesic	0.39	0.534
Xeric	7.67	<0.01
PASCOV		
Mesic	0.31	0..576
Xeric	7.94	<0.01
SCLCOV		
Mesic	1.64	0.201
Xeric	0.005	0.940
PYROAKCOV		
Mesic	2.98	0.085
Xeric	4.46	<0.05
PINECOV		
Mesic	0.71	0.399
Xeric	4.45	<0.05
FERNCOV		
Mesic	0.06	0.812
Xeric	0.43	0.511
THORNCOV		
Mesic	13.17	<0.001
Xeric	20.02	<0.001
LEGCOV		
Mesic	0.61	0.434
Xeric	70.63	<0.001
CISCOV		
Mesic	7.18	<0.01
Xeric	13.32	<0.001
MOORCOV		
Mesic	0.001	0.974
Xeric	18.90	<0.001

Note: F tests were performed with 1,393 and 1,400 df for mesic and xeric forests, respectively.

have pointed out the low digestibility of these species (Robbins et al. 1987). However, Costa (1992) suggested that habitats dominated by leguminous shrubs tend to improve the biomass of many other plants used as food by roe deer and other herbivores (Salisbury and Ross 1985; Pugnaire et al. 1996). In fact, Costa (1992) considers that this type of shrubland is one of the most suitable habitats for ungulates in northern Spain, a claim largely supported by cattle breeders. Similarly, roe deer tend to avoid patches with a heavy cover of *Cistus ladanifer* and *Cistus laurifolius*, since these shrubs tend to exclude other plants through the production of chemicals and colonize soils with poor productivity (Moreno 1983).

The highest densities of roe deer found in the Pyrenean oak and Scots pine forests coincide with the abundance patterns found in other forest vertebrates that show decreasing densities on a gradient from Atlantic/mesic to Mediterranean/xeric forests (Tellería and Santos 1993, 1994). The observed pattern of roe deer microhabitat selection indicates the low habitat suitability of the dominant sclerophyllous forests in xeric areas of the Mediterranean and supports the view that this forest vertebrate suffers habitat constraints at the limit of its range. This basically concurs with the hypothesis according to which species niches (sensu Hutchinson 1957) are determined by many variables that are spatially autocorrelated (Brown 1984, 1995). Increasing distance from the optimal, core areas for a species (e.g., mesic forest of central Europe for roe deer) would frequently entail a concomitant decrease in its densities becuse of increasingly unfavorable

Fig. 3. Means and standard errors for use (●) and availability (○) data from each variable studied (for codes see Table 1) in the two environments considered (mesic, which includes pine and Pyrenaean oak forests, and xeric, which includes the two types of holm oak forest).



ecological conditions (Lawton 1993; Brown 1995). The lack of ability of these populations to cope with environmental constraints at the borders may be interpreted as being a result of asymmetrical gene flows from large central populations to peripheral ones that inhibit local adaptation (Hoffmann and Blows 1994).

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References

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

Aulak, W., and Babinska-Werka, J. 1990. Preference of different habitats and age classes of forest by roe deer. Acta Theriol. **35**: 289–298.

Blondel, J. 1990. Biogeography and history of forest bird fauna in the Mediterranean zone. *In* Biogeography and ecology of forest bird communities. *Edited by* A. Keast. SPB Academic Publishing, The Hague, the Netherlands. pp. 95–107.

Blondel, J., and Aronson, J. 1995. Biodiversity and ecosystem function in the Mediterranean basin: human and no-human determinants. *In* Mediterranean-type ecosystems: the function of biodiversity. *Edited by* J.W. Davis and D.M. Richardson. Springer-Verlag, New York. pp. 43–120.

Bobek, B. 1977. Summer food as the factor limiting roe deer population size. Nature (Lond.), **268**: 47–49.

Braza, F., Varela, I., San José, C., and Cases, V. 1989. Distribution actuelle du chevreuil (*Capreolus capreolus*), du daim (*Dama

dama) et du cerf (*Cervus elaphus*) en Espagne. Z. Saeugetierkd. **54**: 393–396.

Braza, F., San José, C., Aragón, S., and Delibes, J.R. 1994. El corzo andaluz. Junta de Andalucía, Sevilla.

Brown, J.H. 1984. On the relationship between abundance and distribution of species. Am. Nat. **124**: 255–279.

Brown, J.H. 1995. Macroecology. University of Chicago Press, Chicago.

Cibien, C., Bideau, E., Boisaubert, B., Biran, H., and Angibault, J.M. 1995. Seasonal diet and habitat use in field roe deer (*Capreolus capreolus*) in the Picardie region. Gibier Faune Sauvage, **12**: 37–49.

Coe, M.J., Cumming, D.H.M., and Phillipson, J. 1976. Biomes and production of large African herbivores in relation to rainfall and primary production. Oecologia, **22**: 341–354.

Corbet, G.B. 1978. The mammals of the Paleartic region: a taxonomic review. British Museum (Natural History), London, and Cornell University Press, Ithaca, N.Y.

Costa, L. 1992. Una propuesta de gestión cinegética para el corzo en el norte de España. Ecologia (Madrid, Spain), **6**: 165–185.

Costa, M., García, M., Morla, V., and Sainz, H. 1990. La evolución de los bosques de la Península Ibérica: una interpretación basada en datos paleobiogeográficos. Ecologia (Madrid, Spain), **4**: 31–58.

Dias, P.C. 1996. Sources and sinks in population biology. Trends Ecol. Evol. **11**: 326–329.

Duncan, P. 1983. Determinants of the use of habitat by horses in a Mediterranean wetland. J. Anim. Ecol. **52**: 93–109.

Fandos, P., Martínez, T., and Palacios, F. 1987. Estudio sobre la alimentación del corzo (*Capreolus capreolus*) en España. Ecologia (Madrid, Spain), **1**: 161–186.

Font, I. 1983. Climatología de España y Portugal. Instituto Nacional de Meteorología, Madrid.

Fretwell, S.D., and Lucas, H.L., Jr. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheor. **19**: 16–36.

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

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. **22**: 415–427.

James, D.A., and Lockerd, M.J. 1986. Refinement of the Shugart–Patten–Dueser model for analyzing ecological niche patterns. *In* Wildlife 2000. Modelling habitat relationships of terrestrial vertebrates. *Edited by* J. Verner, M.L. Morrison, and C.J. Ralph. University of Wisconsin Press, Madison. pp. 51–56.

Kaluzinski, J. 1982. Composition of the food of roe deer living in fields and the effects of their feeding on plant production. Acta Theriol. **27**: 457–470.

Lawton, J.H. 1993. Range, population abundance and conservation. Trends Ecol. Evol. **8**: 409–413.

Maizeret, C. 1988. Stratégies alimentaires des chevreuils : les fondements écologiques d'une diversification du régime. Acta Oecol. Oecol. Appl. **9**: 191–211.

Maizeret, C., and Sung Gerea, D. 1984. Étude du régime alimentaire et recherche du déterminisme fonctionnel de la sélectivité chez le chevreuil (*Capreolus capreolus*) des landes de Gascogne. Gibier Faune Sauvage, **3**: 63–103.

Maizeret, C., Boutin, J.-M., Cibien, C., and Carlino, J.-P. 1989. Effects of population density on the diet of roe deer and the availability of their food in Chizé Forest. Acta Theriol. **34**: 235–246.

Manly, B.F.J. 1994. Multivariate statistical methods: a primer. 2nd ed. Chapman and Hall, London.

Mitchell, B., Rowe, J.J., Ratcliffe, P., and Hinge, M. 1985. Defecation frequency in roe deer (*Capreolus capreolus*) in relation to the accumulation rates of faecal deposits. J. Zool. (Lond.), **207**: 1–7.

Moreno, J.M. 1983. Ecología y fitosociología del ecotono de dos jarales de Cistion laurifolii de la S^{a} de Guadarrama (España). Lazaroa, **5**: 45–58.

Murden, S.B., and Risenhoover, K.L. 1993. Effects of habitat enrichment on patterns of diet selection. Ecol. Appl. **3**: 497–505.

Neff, D.J. 1968. The pellet group count technique for big game trend, census and distribution: a review. J. Wildl. Manage. **32**: 597–613.

Oksanen, L., Fretwell, S.D., Arruda, J., and Niemelä, P. 1981. Exploitation ecosystems in gradients of primary productivity. Am. Nat. **118**: 240–261.

Papageorgiou, N., Neophytou, C., Spais, A., and Vavalekas, C. 1981. Food preferences, and protein and energy requirements for maintenance of roe deer. J. Wildl. Manage. **45**: 728–733.

Peñalba, M.C. 1994. The history of the Holocene vegetation in northern Spain from pollen analysis. J. Ecol. **82**: 815–832.

Pugnaire, F.I., Haase, P., Puigdefábregas, J., Cueto, M., Clark, S.C., and Incoll, L.D. 1996. Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. Oikos, **76**: 455–464.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution, **43**: 223–225.

Robbins, C.T., Hanley, T.A., Hagerman, A.E., Hjeljord, O., Baker, D.L., Schwartz, C.C., and Mautz, W.W. 1987. Role of tannins in defending plants against rumiants: reduction in protein availability. Ecology, **68**: 98–107.

Rosenzweig, M.E. 1991. Habitat selection and population interactions: the search for mechanism. Am. Nat. **137**: 5–28.

Sáez-Royuela, C., and Tellería, J.L. 1991. Roe deer (*Capreolus capreolus*) distribution in Central Spain. Folia Zool. **40**: 37–45.

Salisbury, F.B., and Ross, C.W. 1985. Plant physiology. 3rd ed. Wardsworth Inc., Belmont, Calif.

Stüwe, M., and Hendrichs, H. 1984. Organization of roe deer (*Capreolus capreolus*) in an open field habitat. Z. Saeugetierkd. **49**: 359–367.

Tellería, J.L., and Sáez-Royuela, C. 1984. The large mammals of Central Spain: an introductory view. Mammal Rev. **14**: 51–56.

Tellería, J.L., and Santos, T. 1993. Distributional pattern of insectivorous passerines in the Iberian forests: does abundance decrease near the border? J. Biogeogr. **20**: 235–240.

Tellería, J.L., and Santos, T. 1994. Factors involved in the distribution of forest birds in the Iberian Peninsula. Bird Study, **41**: 161–169.

Tellería, J.L., and Virgós, E. 1997. Distribution of an increasing roe deer population in a fragmented Mediterranean landscape. Ecography, **20**: 247–252..

Tufto, J., Andersen, R., and 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.

Zar, J.H. 1984. Biostatiscal analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, N.J.