Habitat preferences of the bank vole *Myodes glareolus* in a Mediterranean mountain range

Ignasi TORRE and Antoni ARRIZABALAGA

Torre I. and Arrizabalaga A. 2008. Habitat preferences of the bank vole *Myodes glareolus* in a Mediterranean mountain range. Acta Theriologica 53: 241–250.

The bank vole *Myodes glareolus* Schreber, 1780 is a widely distributed rodent in Europe, being numerically dominant in small mammal communities living in temperate woodlands. However, it becomes scarce in southern Europe (Mediterranean area) where it reaches the southernmost limit of its distribution range. We studied the habitat preferences of bank voles in 9 plots in a transitional area between Mediterranean and Eurosiberian regions within a Mediterranean mountain. During the study period we captured 1919 small mammals of 9 species, including 287 bank voles (14.95%). Mean density ranged from zero individuals per plot (1.1 ha) at the boreo-subalpine scrubland to 10.27 ± 2.84 (SE) at a Mediterranean river woodland. Statistical path analysis was used to investigate relationships between mean bank vole density and climate and vegetation structure measured within plots. The variables selected by the structural equation model were those related to forest structure, like tree cover and height, dead vegetation, moss, and rock cover. Habitat moisture was also important (microclimatic conditions). Mean climate conditions (and elevation) did not have any significant effect on mean bank vole density, and no significant association with understorey vegetation (eg shrub and herbaceous cover) was observed. Our results pointed out that bank voles were habitat specialists in our study area, being more abundant and frequent in moist woodlands, and rare or absent in shrublands and grasslands.

Museu de Granollers-Ciències Naturals, Francesc Macià 51, 08402 Granollers, Spain, e-mail: i.torre@museugranollers.org

Introduction

Small mammal species select habitats mainly according to their requirements for food and safety (Mazurkiewicz 1994, and references therein), but many other factors, like the degree of habitat specialization and behaviour (territoriality and competition), also have an influence on the distribution of individuals (Wolff 1999). Generalist species are able to exploit a broader spectrum of habitats, whereas specialists are only able to persist in some habitats (Seamon and Adler 1996). Otherwise, demographic processes

and feedback structure (density-dependence; Montgomery 1989) affect habitat selection in territorial species, and higher occupancy of habitats of higher quality in terms of food and/or refuges can be expected. The viability of individuals and populations in suboptimal habitats will depend on species plasticity (life history traits, degree of specialization, etc.), and, in general, gradients of habitat quality are expected to be linked to gradients of population performance (Morris 1989, Halama and Dueser 1994).

The bank vole *Myodes glareolus* Schreber, 1780 is a widely distributed rodent in Europe, ranging from the Mediterranean to Scandinavia, and from Great Britain to the Black Sea (Sptizenberger 1999). Bank voles are considered as habitat generalists with a preference for woodlands with dense understorey cover (Gurnell 1985, Mazurkiewicz 1994). The preference for woodland and avoidance of open habitats throughout its range (eg set-asides, grasslands) led other authors to define the bank vole as a habitat specialist (Tattersall *et al*. 2002).

As a temperate forest species, the bank vole is common in small mammal communities of central Europe, being numerically dominant among woodland rodents (Mazurkiewicz 1994, and references therein). However, this species becomes scarce towards the southern limit of its distribution range where it can be found in montane forests (Sptizenberger 1999). In transitional areas between Mediterranean and Eurosiberian Regions, bank voles increased their abundance towards rainy, higher and northern localities (Moreno and Barbosa 1992, Torre *et al*. 1996, Kryštufek and Griffiths 1999). Despite being a species with mid-European requirements, bank voles are tolerant to Mediterranean conditions since they show significant penetrations into Mediterranean areas (Torre *et al*. 1996, Sans-Fuentes and Ventura 2000). Nonetheless, studies on distribution patterns of the bank vole at the habitat level are lacking in Mediterranean areas, and most studies were centered on preferences at larger spatial scales (eg biotic regions, Sans-Fuentes and Ventura 2000; geographical patterns; Moreno and Barbosa 1992, Torre *et al*. 1996) and inferences on habitat preferences could not be made.

The aim of this study is to increase the knowledge on the distribution patterns and habitat preferences of the bank vole in a transitional area between Mediterranean and Eurosiberian Regions, at the southernmost limit of its distribution range in Western Europe. According to habitat preferences and Mid-european requirements of the bank vole, we expected higher densities to be associated with woodland with dense ground cover, and increased densities in habitats under the influence of Eurosiberian climate and vegetation than in areas under Mediterranean climate and vegetation. Also, we investigated whether bank voles behaved as habitat specialists or generalists in this marginal population situated at the southernmost limits of its geographic range.

Study area

The study was carried out in the Montseny Natural Park and Reserve of the Biosphere (Barcelona, Catalonia, NE Spain; 41°46'N, 2°23'E, 29 960 ha, Fig. 1). The main orographic unit in the study area reaches moderate elevation (Turó de l'Home, 1714 m a.s.l.) and is partially isolated from the surrounding mountains, and near to the Mediterranean Sea. The topography and climate vary markedly with elevation and nearness to the sea producing a mild climate without strong thermal oscillations. Rainfall peaks in spring and fall, with moderate drought periods in summer (typical of the Mediterranean climate). Average annual rainfall rises from 700 mm, in the lowest Mediterranean localities, to 1200 mm at the top of the Montseny mountain. Mean annual temperatures range from 7 to 15°C. Almost all the surface of the area is covered by forests (80%) and other natural habitats (scrublands, grasslands, 15%). A small fraction of the area is devoted to agriculture (4%), and only 1% is covered by human settlements. This mountain has particular topographic and climatic characteristics that confer remarkable biogeographic interest (Terradas and Miralles 1986) with the presence of well-established Mid-European vegetational (Bolòs 1983) and animal communities (Terradas and Miralles 1986).

Material and methods

Small mammal sampling

Sampling was performed from February 1995 to July 1997 on nine plots during eleven trapping sessions of three days each. Every plot was sampled by a 7×7 trapping grid, with 49 Sherman traps (Sherman folding small animal
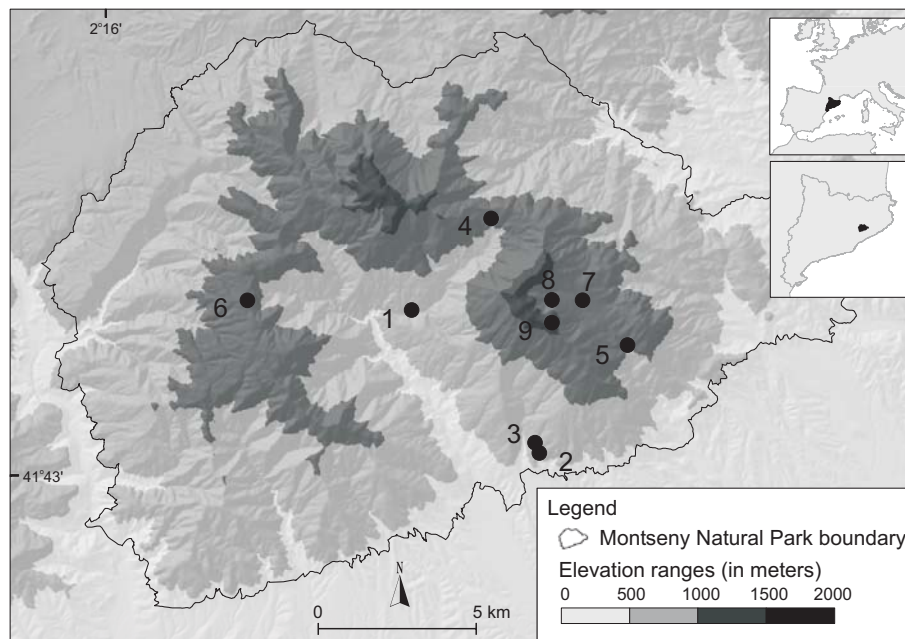
Fig. 1. Situation of the nine plots (numbers as in Table 1) within the study area (Montseny Natural Park, NE Spain).

trap; 23 × 7.5 × 9 cm; Sherman Co., USA) spaced 15 m apart (covering one ha), and open for three consecutive nights. Plots had an effective surface of 1.1 ha (Krebs 1999). The plant communities sampled were characteristic of the Biogeographic Regions found in the Montseny (Bolòs 1983): evergreen woodlands of *Quercus suber* and *Quercus ilex*, deciduous woodlands of *Alnus glutinosa*, *Fagus sylvatica*, *Quercus petraea*, and *Populus nigra*, boreo-subalpine woodlands of *Abies alba* and scrublands of *Juniperus communis nana* and *Calluna vulgaris-Erica scoparia*. The nine plots sampled were situated along an elevation gradient from 540 to 1550 m a.s.l. Grids were sampled on six occasions in 1995, in late winter (February–March), spring (April–May), summer (June–July and August–September), autumn (October–November), and winter (December); on four occasions in 1996, in winter (January), spring (April–May), summer (June–July), and autumn (November–December); and on two occasions in 1997, in spring (March) and summer (July) (eleven trapping sessions of three days each, collectively lasting 33 days). December 1995 and January 1996 were considered as the same trapping session. Every plot was operative for 1617 trapnights. All plots were situated within large habitat patches, and all habitats were interconnected by the extensive forest matrix. Minimum distance between plots was 400 m and maximum 10 600 m., and all plots were situated within an area of 4500 ha (Fig. 1).

Traps were baited and rebaited when necessary (when the bait was eaten) with a piece of apple and a mixture of tuna, flour and oil, and were set under the cover of shrubs or dense herbs to conceal them and to provide some thermal insulation. The small mammals caught were identified to species, uniquely marked by toe-clipping (Adler *et al*. 1999,

Gurnell and Flowerdew 1990), and released at the point of capture. We used counts (eg the number of different individuals trapped within the three days, Morris 1996, Anderson and Meikle 2006) as a biased index of population size in each study plot, assuming that the unseen proportion of the population is constant (Slade and Blair 2000), and that in some situations (not necessarily our situation), counts and estimates yielded similar results (Slade and Blair 2000). According to recommendations, we did not apply unbiased estimators of population size due to the low number of sampling occassions (Slade and Blair 2000).

The vegetation structure of each plot was recorded in the summer of 1996 by visually estimating height and cover in a 5 m-radius circle centered on alternate traps in the trapping grid, and then by averaging the values obtained from each plot (see Torre and Bosch 1999, for a similar approach). The variables measured were: the cover of rocks, trees, shrubs, herbaceous plants, mosses and leaf litter, all measured as a percentage of area covered (%), and the height of trees, shrubs, and herbaceous plants measured in meters.

In order to estimate microclimatic differences between plots, a moisture index was roughly estimated as a function of slope and the presence of permanent water streams. This was a categorical variable, including two dimensions: the exposure (north = 1, valley and south = 0) and the presence of permanent water streams (1 = yes; 0 = no). A plot with northern exposure and permanent water will have a 2 (moist), whereas a plot exposed to the south and with no water will have a zero (dry). We expected moisture to have an influence on habitat preferences by bank voles as has been confirmed in northern latitudes (Van Appeldoorn *et al*. 1992, Olsson *et al*. 2005).

Mean climatic data were obtained from the Catalan Climatic Atlas (Ninyerola *et al*. 2003), with a spatial resolution of 180 m. We used data on mean temperature, mean cumulative rainfall, mean evapotranspiration, mean humidity (Thornthwaite index) and mean water deficit, from series obtained during the last two decades (Ninyerola *et al*. 2003). Mean climate features of the sampling plots were obtained with GIS Miramon (http://www.creaf.uab.es/miramon), after combining of the geographic coordinates of plots with isocline maps of environmental variables.

Data analysis

Mean (arithmetic) density indices of bank voles were calculated after the eleven sampling sessions conducted on the nine plots. We consider these indices to be good measures of real densities since sampling was performed over three years that had important interannual variation in rainfall and productivity (Torre 2004). We relied on population density as the simplest indicator of habitat quality for bank voles, regarding the relationship between population density and resource availability predicted by theory (Wheatley *et al*. 2002, and references therein). Other parameters, like breeding performance, survival, and immigration, may be more adequate than density to test wildlife-habitat relationships (Van Horne 1983, Wheatley *et al*. 2002), but were not considered due to the low number of individuals trapped in many plots throughout the study period.

Spatial variation of mean bank vole density in the Montseny Mountain was assessed by Statistical path analysis, an extension of multiple regression which was developed to decompose correlations into different pieces for interpretation of effects (Everitt and Dunn 1991). Independent variables for analysis were vegetation structure and climate. To avoid multicollinearity of independent variables, we used Principal Components Analysis (PCA) to obtain orthogonal components that were interpreted as gradients of vegetation structure and climate. The Kaiser criterion was used to determine the number of principal components extracted (eigenvalues > 1).

We tested the significance of regression models by means of structural equation modeling software (SEM, Amos 5.0, Arbuckle 1983–2003). The appropriateness of models was assessed by means of the Goodness of fit index (GFI) which ranges from 0 (maximum lack of fit) to 1 (maximum fit), and the matrix permutation test (Hesterberg *et al*. 2005). In order to test the reliability of the parameter estimates of the SEM, we used bootstrapping techniques creating many resamples by repeatedly sampling (200 resamples, the default option in the program used) with replacement from the only random sample to obtain information about the sampling distribution (Hesterberg *et al*. 2005). Permutations tests and bootstrapping estimates were implemented in the Amos software (Arbuckle 1983–2003). Akaike Information Criterion (AIC) was used to select the most parsimonious model.

Temporal variation in bank vole density was analysed with ANOVA, using year (1995, 1996 and 1997) and plot (n = 9) as categorical factors. During 1996, the study area received twice as much rainfall as during 1995 and 1997, with being autumn the season with the highest cumulative rainfall (Torre 2004).

Prior to analysis, all variables were properly transformed to reach homoscedasticity and normality. Frequency variables were arcsin transformed, and continuous variables were log-transformed (Zar 1996).

Results

Climate and vegetation patterns of plots

Mean values for climatic and vegetation structure variables measured at the nine plots are shown in Table 1. A principal components analysis (PCA) was performed to summarize climate attributes of plots. This PCA accounted for 82% of variance in the original variables, and only a single principal component (PC) was extracted. This climate-PC1 was positively correlated to water deficit ($r = 0.95$, $p < 0.001$), temperature ($r = 0.95$, $p < 0.001$) and evapotranspiration ($r = 0.86$, $p = 0.003$), and negatively correlated to Thornthwaite's moisture index ($r = -0.97$, $p < 0.001$) and rainfall ($r = -0.91$, $p = 0.001$). This principal component was also negatively correlated with elevation ($r = -0.88$, $p < 0.002$) and latitude ($r = -0.80$, $p = 0.009$), but was uncorrelated with longitude ($r = -0.10$, $p = 0.77$).

A second PCA was performed to summarize vegetation structure profiles and moisture within plots (Table 2). This PCA accounted for 90% of variance in the original variables; the first component, vegetation-PC1, was positively correlated to moss cover ($r = 0.93$, $p < 0.001$), tree cover ($r = 0.74$, $p = 0.02$), moisture ($r = 0.72$, $p = 0.02$) and rock cover ($r = 0.62$, $p = 0.05$). The second component, vegetation-PC2, was positively correlated to tree height ($r = 0.95$, $p < 0.001$) and dead vegetation cover ($r = 0.89$, $p < 0.01$). The third component, vegetation-PC3, was positively correlated to herbaceous cover ($r = 0.93$, $p < 0.001$), herbaceous height ($r = 0.90$, $p < 0.01$), and shrub cover ($r = 0.65$, $p = 0.05$); and the fourth, vegetation-PC4, was negatively correlated to shrub height ($r = -0.98$, $p < 0.001$).

Table 1. Number of different bank voles captured, mean abundance (± SD), persistence (defined as the number of sampling sessions during which bank voles were captured on a plot divided by the total number of sampling sessions), and mean values for climatic and vegetation structure variables measured at the nine plots.

Variables/Plot	1	2	3	4	5	6	7	8	9
Dominant Tree/ Shrub species	Alnus glutinosa	Quercus suber	Quercus ilex	Populus nigra	Quercus petraea	Calluna vulgaris-Erica scoparia	Fagus sylvatica	Abies alba	Juniperus communis
Bank voles total captures	113	8	56	24	6	8	26	46	0
Bank voles mean (SD)	10.27 (9.42)	0.73 (1.79)	5.09 (3.65)	2.4 (4.09)	0.55 (1.81)	0.73 (2.41)	2.36 (3.38)	4.18 (4.58)	0
Persistence	0.91	0.27	0.91	0.50	0.09	0.09	0.64	0.82	0
Elevation (m)	540	550	600	1060	1070	1150	1150	1450	1550
Rainfall (mm)	975	825	825	1025	1025	875	1075	1075	1075
Temperature (°C)	10.5	13.5	13.5	9.5	11.5	9.5	9.5	8.5	7.5
Water deficit	50	150	150	50	50	50	0	0	0
Rock cover (%)	18.05	2	7.24	1	15.85	7.24	8.65	31.76	18.4
Tree cover (%)	86.19	49.89	51.03	40.2	35	10	70.5	50.83	0
Tree height (m)	10.35	6.43	10.17	12.5	8.27	3	12.65	20.5	0
Shrub cover (%)	23.33	25.04	45.9	25.5	14.26	45.9	12.49	12.39	59.89
Shrub height (m)	1.24	1.22	0.77	0.76	1.01	1.25	0.3	0.35	0.32
Herbaceous cover (%)	41.58	11.58	3.02	87.7	21.88	25	18.23	15.15	33.26
Herbaceous height (m)	0.37	0.29	0.07	0.92	0.14	0.2	0.095	0.038	0.084
Mosses cover (%)	11.68	2	5.78	2	4.53	2	2.45	5.79	1.4
Dead leaf cover (%)	78.66	45.6	73.14	69	53.4	25.3	69.52	40.39	10.62

Table 2. Results of the Principal Component Analysis with the vegetation structure variables estimated visually on the nine plots. Correlations marked with an asterisk are significant at $p < 0.05$.

Variables	PC1	PC2	PC3	PC4
Rock cover (%)	0.62*	–0.19	–0.38	0.58
Tree cover (%)	0.74*	0.46	0.11	–0.29
Tree height (m)	0.24	0.95*	–0.14	0.07
Shrub cover (%)	–0.12	–0.47	0.65*	0.10
Shrub height (m)	0.15	–0.04	0.02	–0.98*
Herbaceous cover (%)	0.06	0.02	0.93*	0.02
Herbaceous height (m)	–0.02	0.23	0.90*	–0.27
Mosses cover (%)	0.93*	0.25	–0.12	–0.10
Dead leaf cover (%)	0.26	0.89*	0.16	–0.11
Moisture	0.72*	0.57	0.24	0.14
Explained variance (%)	26.00	25.00	24.00	15.00

Number of bank voles captured and patterns of density

During the study periods we captured 1919 small mammals of 9 species, including 287 bank vole individuals (14.95%). Wood mice (*Apodemus* sp.) were dominant in all habitats studied, with 1356 individuals trapped (70.6%). Frequency of occurrence of bank voles strongly varied between habitats, from 0% at the boreo-subalpine scrubland (*Juniperus communis nana*) to 41% of the small mammals captured in the river woodland (*Alnus glutinosa*). Number of individuals trapped varied from zero, at the boreo-subalpine scrubland, to 113 at the river woodland (Table 1). Mean density ranged from 0 to 10.27 ± 9.42 (SD) individuals per plot (Table 1). Mean density of bank voles per plot was strongly correlated with persistence ($r = 0.95$, $p = 0.0005$, $n = 9$), defined as the number of sampling sessions in which bank voles were captured on a plot divided by the total number of sampling sessions ($n = 11$). So, the habitats with higher mean density were those in which the presence of the species was more regular throughout the study period.

ANOVA showed that bank vole density varied between years and plots ($F = 15.87$, df = 2, 72, $p < 0.0001$; $F = 11.57$, df = 8, 72, $p < 0.0001$, respectively), and *post-hoc* comparisons showed that density was higher in 1996 than in 1995 and 1997, whereas no differences were found between the latter two (Tukey HSD test: 1995–1996, $p =$ 0.0008; 1996–1997, $p = 0.019$; 1995–1997, $p =$ 0.97). Density was higher in the *Alnus glutinosa* wood than in the other 8 plots except the *Quercus ilex* wood. Mean persistence was slightly higher during 1996 ($\bar{x} = 0.63 \pm 0.49$) than in 1995 and 1997 ($\bar{x} = 0.41 \pm 0.49$, and $\bar{x} = 0.39 \pm 0.50$, respectively), but differences were not significant ($F = 11.57$, df = 1, 96, $p = 0.13$).

To analyze whether mean bank vole density was related to climate and vegetation structure of plots, a structural equation model (SEM) was built with all the independent variables (climate-PC1, vegetation-PC1 to PC4 of vegetation structure and moisture) and mean vole density as the dependent variable. SEM explained 89% of variance, showed high goodness of fit ($\chi^2 = 1.56$, df = 6, $p = 0.96$, *GFI* = 0.95), and marginal significance (permutation test, $p = 0.05$). The permutation test showed that only 25 out of 500 permutations of the observed data improved the model fit, and the 475 remaining resulted in a higher discrepancy function ($p = 25/500 = 0.05$). Alternatively, we tested the model considering only the significant paths. This model was more parsimonious (according to Akaike Information Criterion, AIC value were 31.56 and 28.34, respectively), explained 88% of variance, showed high goodness of fit ($\chi^2 = 1.32$, df = 6, $p = 0.97$, *GFI* = 0.94) and was significant ($p = 16/500 = 0.03$), so this latter model can be considered as more appropriate to describe bank vole abundance relationships with climate and vegetation
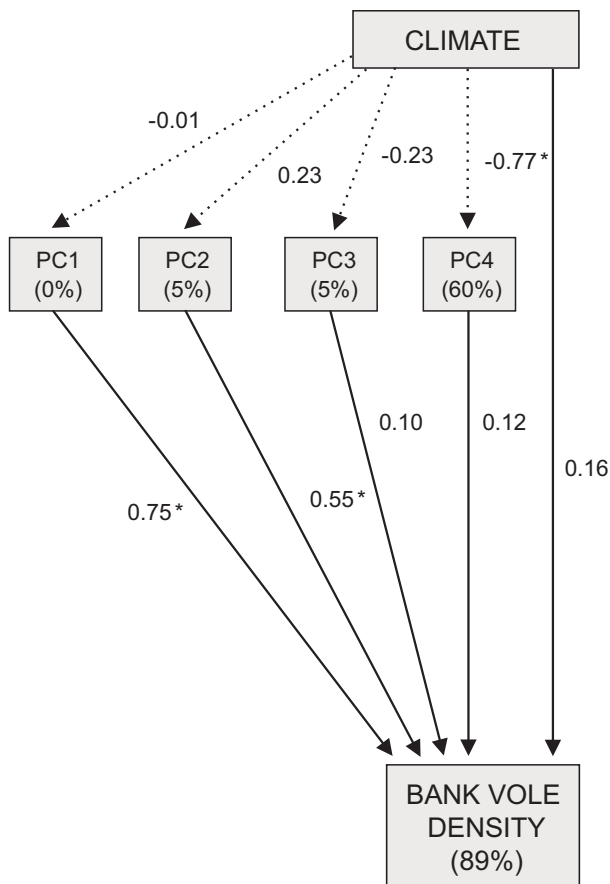
Fig. 2. Structural Equation Model (SEM) built to determine the effects of environmental variables (climate, vegetation structure and moisture, PC1 to PC4) on mean bank vole density. All the standardized regression coefficients and their statistical significance are shown (** $p < 0.01$), and the explained variance by predictors on dependent variables is also shown in the boxes.

structure. The model with all the regression paths and their significance, obtained by means of percentile confidence intervals after bootstrapping, is shown in Fig. 2. Three path coefficients were significant: vegetation-PC4 was negatively affected by climate-PC1 (*beta* = –0.77, $p < 0.001$), and bank vole density was positively affected by vegetation-PC1 (*beta* = 0.75, $p < 0.001$) and vegetation-PC2 (*beta* = 0.55, $p < 0.001$). Climate-PC1 did not affect significantly vegetation structure and moisture of plots, except in the case of shrub height, that decreased with elevation. Climate-PC1 did not show any significant effect on mean bank vole density. However, vegetation structure and moisture of plots signifi-

cantly affected mean bank vole density. Bank vole density was mainly affected by vegetation-PC1 (gradient of tree, rock and moss cover, and moisture) and by vegetation-PC2 (gradient of dead vegetation cover and tree height). Mean bank vole density did not show significant associations with understorey vegetation, summarized by vegetation-PC3 (herb layer and shrub cover) and vegetation-PC4 (shrub height).

Discussion

Our results pointed out a significant relationship between mean bank vole density and vegetation structure measured on 9 plots representing different habitats situated on an elevation gradient within a Mediterranean mountain range. The variables selected by a structural equation model were those related to forest structure, like tree cover and height, dead vegetation cover, but also some variables related to habitat moisture, like moss cover, plot exposure, and the presence of streams, seemed to be important. As a general pattern, higher mean vole densities were observed in woodlands near to streams and exposed to the north, and lower mean vole densities were observed in open dry habitats with southern exposures and with no streams. Highest densities were recorded in the Mediterranean river woodland (*Alnus glutinosa*), and lowest densities were recorded in the boreo-subalpine juniper shrubland (the only habitat that was avoided throughout the study period). The spatial and temporal patterns of distribution and abundance of bank voles in the studied area were consistent with a habitat specialist strategy, being more abundant and frequent in moist woodlands, and rare or absent in shrublands and grasslands. The preference for woodland and avoidance of open habitats throughout its range (eg set-asides, grasslands) led other authors to define the bank vole as a habitat specialist (Tattersall *et al*. 2002), despite bank voles being traditionally considered as habitat generalists (Gurnell 1985, Mazurkiewicz 1994).

Bank voles inhabit all kind of forests (Gurnell 1985, Mazurkiewicz 1994), but also can be found

in open habitats like scrublands (Canova and Fasola 1991), grasslands (Wijnhoven *et al.* 2005), and agricultural landscapes (woodlots, Van Appeldoorn *et al.* 1992, Fitzgibbon 1997, Tattersall *et al.* 2002; hedgerows, Kotzageorgis and Mason 1997). The factors that mainly influence the abundance of the species are those related to the presence of a well developed understorey vegetation or ground cover (Gurnell 1985, Mazurkiewicz 1994). This preference for ground cover seems to be general and independent to the habitats sampled. In this sense, studies on habitat preferences in woodlots surrounded by agricultural land showed bank voles to prefer grounds covered by *Rubus* sp. and herbaceous plants (Van Appeldoorn *et al.* 1992, Fitzgibbon 1997), and similar patterns were found in river floodplains (Wijnhoven *et al.* 2005). In the same way, studies on hedgerows showed preference for ground cover in many seasons (Kotzageorgis and Mason 1997). In forest habitats, bank voles also showed preference for patches with dense ground cover like understorey and herbaceous vegetation (Fernandez *et al.* 1994, Mazurkiewicz 1994). As Mazurkiewicz (1994) pointed out, these patches within forest habitats supported high vole densities because of higher breeding performance (high number of sexually active individuals) and related demographic processes (higher survival and emigration, lower immigration). As a conclusion, forest patches with dense ground cover represent high quality habitats for bank voles, providing antipredatory refuges as well as food supply (Mazurkiewicz 1994, Fitzgibbon 1997).

However, our results illustrated that mean bank vole density do not show significant relationships with gradients of understorey vegetation (herbaceous and shrub cover, and shrub height) in the habitats studied. The lack of such an association can be explained because the habitats with higher understorey vegetation were open habitats (*Calluna* and *Juniperus* shrublands) which were avoided by bank voles, and the forest habitats were generally poor in understorey vegetation. Despite limited intepretation of the role of single variables due to the use of principal components, we can conclude that understorey vegetation does not play a central

role in habitat selection by bank voles in the studied area.

Vole density was directly related to the structural characteristics of woodlands summarized by the vegetation-PC1 and vegetation-PC2, increasing density from open to closed habitats. Preferred woodlands were also covered by rocks in form of scree, and this microhabitat may provide refuge in the absence of ground cover. Otherwise, moisture was correlated with vegetation-PC1, so it was difficult to establish whether bank voles selected forest habitats because of their well known preference for these habitats (Gurnell 1985), or moisture also played a role in the preferred habitats. Microclimatic conditions seemed to play a role in habitat preferences by bank voles, since soil humidity has been suggested to be important for bank voles in forest habitats (Van Appeldoorn *et al.* 1992, and references therein), even in northern latitudes (Olsson *et al.* 2005). The study area represents the southern limit of the distribution of the bank vole in Western Europe (Spitzenberger 1999) and bearing in mind bank voles have mid-European or Eurosiberian requirements (Gosálbez and López-Fuster 1985, Sans--Fuentes and Ventura 2000), preference might well be associated with moisture in Mediterranean environments. Bank voles displayed significant penetrations into Mediterranean environments in the study area (Torre *et al.* 1996), but we expected that these penetrations might occur through moist habitats like riverbeds and favorably exposed woodlands (northern slopes). Other authors suggested moisture as a factor influencing the distribution of the bank vole in northern Spain (Castién and Mendiola 1985, Gosálbez 1987) and southern France (Saint-Girons 1984).

Climate had no significant influence on bank vole density along the elevation gradient sampled, and this finding was contrary to expectations. We expected higher mean bank vole densities in Eurosiberian or Boreo-subalpine woodlands than in Mediterranean woodlands. In transitional areas between Mediterranean and Eurosiberian Regions, bank voles increased their abundance towards higher, rainy and northern localities (Moreno and Barbosa 1992,

Torre *et al*. 1996, Kryštufek and Griffiths 1999), since the lower limit of mean annual precipitation has been established between 600 and 800 mm in the areas inhabited by the bank vole in northern Spain (González and Román 1988, Gosàlbez 1987, Sans-Fuentes and Ventura 2000). Indirect approaches to the study of bank vole distribution in the Montseny and surrounding area pointed out an increase in frequency towards humid Mediterranean lowlands (Torre *et al*. 1996). However, all these studies were performed at larger spatial scales (using larger sampling units) and inferences about habitat preferences of bank voles could not be inferred. Nonetheless, bank vole distribution seems to be limited by the availability of forest habitats and can be independent from elevation (and hence the climate), as has been pointed by Saint-Girons (1973). However, other authors suggested that bank vole density decreased with elevation in large mountain ranges (Delibes de Castro 1985).

Otherwise, mean density varied between years maybe as a consequence of interannual variation in cumulative rainfall that was twice as high during 1996 than during the other two years (Torre 2004). So, during the abnormally wet year bank voles were more abundant in all the study plots, and also we observed an increase in persistence during this year (0.63 vs 0.41 and 0.39), but in this latter case differences were non-significant.

The role of interespecific competition between bank voles and wood mice (*Apodemus sylvaticus* – *A. flavicollis*, which were numerically dominant throughout habitats) was not analyzed in the present study because of the difficulty of correct identification of the two congeneric species of *Apodemus*. There is evidence that bank voles and wood mice coexist in many habitats, but niche overlap is minimized by microhabitat, food and time partitioning (Gurnell 1985, Canova 1993). We detected a slight negative and non-significant correlation between mean densities of both taxa, suggesting that densities were independent of each other. However, Fasola and Canova (2000) showed asymmetrical competition between both species, so distribution of bank voles may be affected by the presence of wood mice. Interespecific competi-

tion cannot be ruled out as a source of variation in habitat preference of bank voles in our study area, and more specific tests need to be performed in order to search for interspecific interactions between species (Morris 1996).

References

Adler G. H., Mangan S. A. and Suntsov V. 1999. Richness, abundance, and habitat relations of rodents in the Lang Bian mountains of southern Viet Nam. Journal of Mammalogy 80: 891–898.

Anderson C. S. and Meikle D. B. 2006. Annual changes in structural complexity of understory vegetation and relative abundance of *Peromyscus leucopus* in fragmented habitats. Acta Theriologica 51: 43–51.

Arbuckle J. L. 1983–2003. AMOS 5.0, Student Edition. Small Waters Corporation, Chicago, USA.

Bolós O. de 1983. La vegetació del Montseny. Diputació de Barcelona, Barcelona: 1–170.

Canova L. 1993. Resource partitioning between the bank vole *Clethrionomys glareolus* and the wood mouse *Apodemus sylvaticus* in woodland habitats. Bollettino di Zoologia 60: 193–198.

Canova L. and Fasola M. 1991. Communities of small mammals in 6 biotopes of northern Italy. Acta Theriologica 36: 73–86.

Castién E. and Mendiola I. 1985. Atlas de los Mamíferos Continentales de Álava, Vizcaya y Guipúzcoa. [In: Atlas de los Vertebrados Continentales de Álava, Vizcaya y Guipúzcoa. J. Alvarez, A. Bea, J. M. Faus, E. Castién and I. Mendiola, eds]. Estudios Gráficos Zure, S.A., Bilbao: 271–325.

Delibes de Castro J. 1985. Distribution and abundance of small mammals in a gradient of altitude. Acta Zoologica Fennica 173: 53–56.

Everitt B. S. and Dunn G. 1991. Applied multivariate data analysis. Edward Arnold, London: 1–316.

Fasola M. and Canova L. 2000. Asymmetrical competition between the bank vole and the wood mouse, a removal experiment. Acta Theriologica 45: 353–365.

Fernandez F. A. S., Evans P. R. and Dunstone N. 1994. Local variation in rodent communities of Sitka spruce plantations – the interplay of successional stage and site-specific habitat parameters. Ecography 17: 305–313.

Fitzgibbon C. D. 1997. Small mammals in farm woodlands: The effects of habitat, isolation and surrounding land--use patterns. Journal of Applied Ecology 34: 530–539.

González J. and Román J. 1988. Atlas de los micromamíferos de Burgos. Talleres Gráficos Diario de Burgos, Burgos: 1–153.

Gosàlbez J. 1987. Insectívors i Rosegadors de Catalunya. Ketres Editora S.A., Barcelona: 1–241.

Gosàlbez J. and López-Fuster M. J. 1985. The natural communities of small mammals (insectivores and rodents) of Catalonia (Spain). Miscelània Zoològica 9: 375–387.

Gurnell J. 1985. Woodland rodent communities. [In: The ecology of woodland rodents, bank voles and wood mice. J. R. Flowerdew, J. Gurnell and J. H. W. Gipps, eds]. Symposia of the Zoological Society of London 55: 377–402.

Gurnell J. and Flowerdew J. R. 1990. Live trapping small mammals. A practical guide. Occassional Publications of the Mammal Society of London 3: 1–39.

Halama K. H. and Dueser R. D. 1994. Of mice and habitats: tests for density-dependent habitat selection. Oikos 69: 107–114.

Hesterberg T., Moore D. S., Monaghan S., Clipson A. and Epstein. R. 2005. Bootstrap Methods and Permutation Tests. 2nd edition. W. H. Freeman, New York: 1–82.

Kotzageorgis G. C. and Mason C. F. 1997. Small mammal populations in relation to hedgerow structure in arable landscape. Journal of Zoology, London 242: 425–434.

Krebs C. J. 1999. Ecological methodology. Addison Wesley, New York: 1–620.

Kryštufek B. and Griffiths H. I. 1999. Mediterranean *v.* Continental small mammal communities and the environmental degradation of the Dinaric Alps. Journal of Biogeography 26: 167–177.

Mazurkiewicz M. 1994. Factors influencing the distribution of the bank vole in forest habitats. Acta Theriologica 39: 113–126.

Montgomery W. I. 1989. Population regulation in the wood mouse, *Apodemus sylvaticus*. I. Density dependence in spatial distribution and reproduction. Journal of Animal Ecology 58: 477–494.

Moreno E. and Barbosa A. 1992. Distribution patterns of small mammal fauna along gradients of latitude and altitude in Northern Spain. Zeitschrift für Säugetierkunde 57: 169–175.

Morris D. W. 1989. Habitat-dependent estimates of competitive interaction. Oikos 55: 111–120.

Morris D. W. 1996. Coexistence of specialist and generalist rodents via habitat selection. Ecology 77: 2352–2364.

Ninyerola M., Pons X. and Roure J. M. 2003. Atlas Climàtic Digital de Catalunya. Universitat Autònoma de Barcelona and Generalitat de Catalunya.

Olsson G. E., White N., Hjalten J. and Ahlm C. 2005. Habitat factors associated with bank voles (*Clethrionomys glareolus*) and concomitant hantavirus in northern Sweden. Vector-borne and zoonotic diseases 5: 315–323.

Saint-Girons M. C. 1973. Les mammifères de France et du Benelux. (Faune marine exceptée). Doin, Paris: 1–484.

Saint-Girons M. C. 1984. Le Campagnol roussâtre *Clethrionomys glareolus*. [In: Atlas des Mammifères sauvages de France]. Societé Française pour l'Étude et la Protection des Mammifères, Paris: 160–161.

Sans-Fuentes M. A. and Ventura J. 2000. Distribution patterns of the small mammals (Insectivora and Rodentia) in a transitional zone between the Eurosiberian and the Mediterranean regions. Journal of Biogeography 27: 755–764.

Seamon J. O. and Adler G. H. 1996. Population performance of generalist and specialist rodents along habitat gradients. Canadian Journal of Zoology 74: 1130–1139.

Slade N. A. and Blair S. M. 2000. An empirical test of using counts of individuals captured as indices of population size. Journal of Mammalogy 81: 1035–1045.

Sptizenberger F. 1999. *Clethrionomys glareolus* (Schreber, 1780). [In: The atlas of European mammals. A. J. Mitchell-Jones, G. Amori, W. Bogdanowicz, B. Kryštufek, P. J. H. Reijnders, F. Spitzenberger, M. Stubbe, J. B. M. Thissen, V. Vohralík and J. Zima, eds]. T & AD Poyser, London: 212–213.

Tattersall F. H., Macdonald D. W., Hart B. J., Johnson P., Manley W. and Feber R. 2002. Is habitat linearity important for small mammal communities on farmland? Journal of Applied Ecology 39: 643–652.

Terradas J. and Miralles J. 1986. El patrimoni biològic del Montseny. Catàlegs de flora i fauna 1. Diputació de Barcelona, Barcelona: 1–155.

Torre I. 2004. Distribution, population dynamics and habitat selection of small mammals in Mediterranean environments: the role of climate, vegetation structure, and predation risk. PhD thesis, University of Barcelona, Barcelona: 1–177.

Torre I. and Bosch M. 1999. Effects of sex and breeding status on habitat selection by feral House mice (*Mus musculus*) in a small Mediterranean island. Zeitschrift für Säugetierkunde 64: 176–186.

Torre I., Tella J. L and Arrizabalaga A. 1996. Environmental and geographic factors affecting the distribution of small mammals in an isolated Mediterranean mountain. Zeitschrieft für Säugetierkunde 61: 365–375.

Van Apeldoorn R. C., Oostenbrink W. T., Vanwinden A. and Vanderzee F. F. 1992. Effects of habitat fragmentation on the bank vole, *Clethrionomys glareolus*, in an agricultural landscape. Oikos 65: 265–274.

Van Horne B. 1983. Density as a misleading indicator of habitat quality. The Journal of Wildlife Management 47: 893–901.

Wheatley M., Larsen K. W. and Boutin S. 2002. Does density reflect habitat quality for North American Red squirrels during a spruce-cone failure? Journal of Mammalogy 83: 716–727.

Wijnhoven S., Van Der Velde G., Leuven R. S. E. W. and Smits A. J. M. 2005. Flooding Ecology of voles, mice and shrews: the importance of geomorphological and vegetational heterogeneity in river floodplains. Acta Theriologica 50: 453–472.

Wolff J. O. 1999. Behavioral Model Systems. [In: Landscape ecology of small mammals, G. W. Barrett and J. D. Peles, eds]. Springer, New York: 11–40.

Zar J. H. 1996. Biostatistical analysis. Prentice Hall, Englewood Cliffs, New Jersey: 1–662.