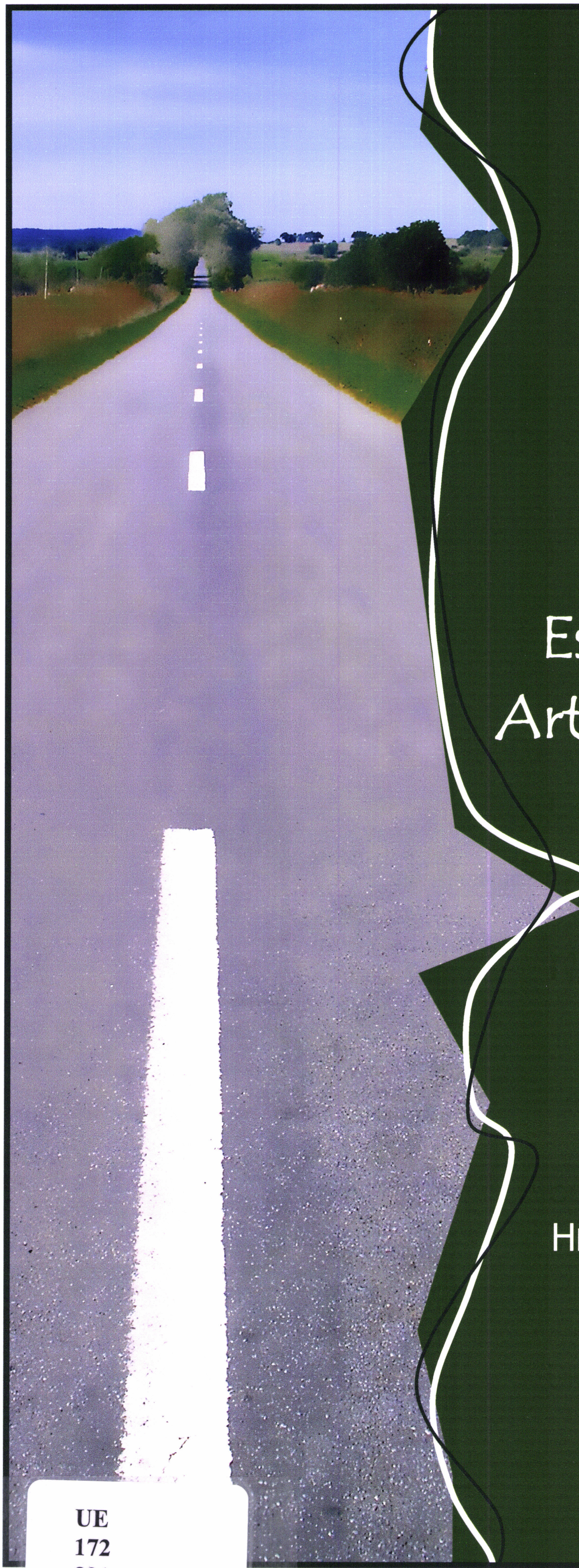

Universidade de Évora

Mestrado em
Biologia da Conservação

O Papel das Estruturas Lineares, Artificiais e Naturais, como Locais de Refúgio de Micromamíferos

Dissertação realizada por:
Helena Isabel Sabino Marques

Orientação:
Prof. Dr. António Mira

Évora, 2010

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Living on the verge: are roads a more suitable refuge for small mammals than streams?

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Helena Marques[a] e António Mira[a]

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PALAVRAS-CHAVE

Habitats Lineares
Micromamíferos
Bermas de estrada
Ribeiras
Mus spretus
Crocidura russula

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RESUMO

Avaliámos a importância das bermas das estradas como áreas de refúgio para pequenos mamíferos, em paisagens Mediterrânicas intensivamente pastoreadas, e comparámos esta possível função das estradas como refúgio com o papel fundamental das galerias ripícolas como reservatórios de diversidade biológica. Para esse efeito, foram realizadas capturas de micromamíferos em dois segmentos de estrada e em duas ribeiras da região de Évora. Foram capturados 457 indivíduos de cinco espécies diferentes. *Mus spretus* foi a espécie mais capturada, seguida de *Crocidura russula* e *Apodemus sylvaticus*. *M. spretus* apresentou uma maior abundância nas bermas de estrada do que na vegetação ripicola, enquanto que a abundância de *C. russula* e *A. sylvaticus* era semelhante para ambos os habitats. O número de capturas das três espécies foi bastante superior dentro dos habitats lineares do que na matriz circundante. Os indivíduos de *M. spretus* eram maiores nas ribeiras, mas significativamente menores fora dos habitats lineares, e os indivíduos de *C. russula* apresentavam uma melhor condição corporal nas bermas das estradas. Tanto as estradas como as ribeiras exerceram um forte efeito de barreira aos movimentos dos micromamíferos. Concluímos então que as bermas das estradas actuam como habitat de refúgio em áreas sub-óptimas das paisagens Mediterrânicas.

Living on the verge: are roads a more suitable refuge for small mammals than streams?

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KEYWORDS

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ABSTRACT

We assessed the importance of road verges as refuge areas for small mammals, in highly intensified grazed pastures on a Mediterranean landscape, and compared road function as refuge with the fundamental role of riparian galleries as reservoirs of biological diversity. For this purpose, a small mammal trapping study was undertaken on road verges and on small stream sides. We sampled two road segments and two streams in the vicinity of Évora, Portugal. We captured a total of 457 individuals of five different species. *Mus spretus* was the most common species captured, followed by *Crocidura russula* and *Apodemus sylvaticus*. *M. spretus* was more abundant on road verges than on riparian strips, whilst the abundance of *C. russula* and *A. sylvaticus* were similar in the two habitats. Captures of the three species were much higher inside both linear habitats than on the surrounding matrix. *M. spretus* were bigger on stream sites but significantly smaller outside the linear habitats and *C. russula* had better body conditions on roads. Both roads and streams exerted a strong barrier effect to small mammals' movements. We conclude that roadside verges act as refuge habitat in sub-optimal Mediterranean landscapes.

1. Introduction

It is widely accepted that retaining natural remnant corridors of habitat is a useful and practical conservation measure, which can attenuate the effects of habitat loss and fragmentation on wildlife (Downes *et al.* 1997, Beier and Noss 1998, Bennett 2003). By providing additional habitat for species living in modified environments, linear structures make a direct contribution to the conservation of biodiversity. They may substantially increase the total amount of suitable habitat and, in some cases, comprise a substantial amount of the remaining habitat available to wildlife, supporting resident individuals or populations of animals, and playing a key role in maintaining the diversity of wildlife and continuity of ecological processes in heavily altered environments (Bennett 1990, 2003, Downes *et al.* 1997, Perault and Lomolino 2000, Gelling *et al.* 2007).

Riparian areas constitute one of the most widespread, diverse and dynamic natural remnant corridors, and are known as some of the most productive and diverse habitats available to wildlife, providing important habitat for many aquatic and terrestrial species (Naiman and Décamps 1997, Gomez and Anthony 1998, Cockle and Richardson 2003). They play a significant and often essential role in the maintenance of wildlife communities in the adjacent upland habitats (Gomez and Anthony 1998, Bennett 2003). Riparian strips are generally cooler, wetter, more structurally complex, and more productive than upland areas (Naiman and Décamps 1997, Bennett 2003, Cockle and Richardson 2003). Their diverse composition and structure of vegetation and variability in soil moisture may create important habitat for the survival and reproduction of many species by providing food and other essential resources, like shelter (Naiman and Décamps 1997, Gomez and Anthony 1998, Bennett 2003). In the case of small mammals, riparian systems are usually described as important habitat, and may be critical to the conservation of these species (Gomez and Anthony 1998, Maisonneuve and Rioux 2001, Waters *et al.* 2001, Cockle and Richardson 2003).

Ecologists have recently acknowledged that road systems are one of the largest and most extensive functioning systems of linear habitats on Earth (Forman and Alexander 1998, Bennett 2003). The vast network structure of road systems, their pervasive spread throughout many different environments, and the large area that they occupy are indicative of a significant ecological effect (Bennett 2003). There is much concern about the detrimental effects of road systems, particularly their role as ecological barriers, as a source of mortality for wildlife, and as a source of disturbance to adjacent habitats and the wider landscape (see reviews by Forman and Alexander 1998, Spellerberg 1998, Trombulak and Frissel 2000, Forman *et al.* 2003, Coffin 2007). Small mammals are often killed by traffic and may be reluctant to cross roads, even when the road is narrow and covered only by gravel (Oxley *et al.* 1974, Swihart and Slade 1984, Brock and Kelt 2004). However, the extent of road systems and their level of structural connectivity suggest that there may be advantages for species that are able to use the associated roadside habitats (Bennett 2003). Road verges do provide habitat for some animals, particularly insects and small mammals (Oxley *et al.* 1974, Bellamy *et al.* 2000, Forman *et al.* 2003, Coffin 2007) and some mammal species have been found to use roads as movement corridors (Forman and Alexander 1998, Brock and Kelt 2004, Coffin 2007). Moreover, in landscapes where almost all native vegetation has been removed for cultivation or pasture, roadside vegetation strips may be especially valuable as reservoirs of biological diversity (Forman and Alexander 1998, Coffin 2007).

Therefore, we wanted to assess the importance of road verges as refuge areas for small mammals, in highly intensified grazed pastures on a Mediterranean landscape, where little information exists on this subject. The grazing-induced changes in vegetation and in soil compaction produce strong effects on small mammal abundance and species richness (Eccard *et al.* 2000, Torre *et al.* 2002, 2007), so the subsistence of linear habitats in structurally simple grazed areas should be of high significance. Also, we intended to compare road function as refuge with the fundamental role of riparian galleries as reservoirs of biological diversity.

Small mammals have a major role in ecosystems. They are the primary prey for many carnivorous mammals, snakes and birds, and consume invertebrates, plants and their seeds, affecting plant species composition and soil fertility through selective herbivory and seed dispersal (Cockle and Richardson 2003, Michel *et al.* 2007, Torre *et al.* 2007, Sullivan and Sullivan 2009). The study of small mammals offer many advantages, since they are usually abundant, widespread and readily sampled by trapping techniques. Besides, these species usually respond to disturbances in a perceptible and measurable way, and their short generation times allow for quick detection of environmental changes (Coffman *et al.* 2001, Butet *et al.* 2006, Bissonette and Rosa 2009).

The main aim of our study was to evaluate, for small mammals:

1) The role of road verges as refuge in suboptimal landscapes, i.e. when the matrix is dominated by high intensity grazing by cattle;

2) Compare the importance of roads verges as refuges with the one from a natural linear habitat, riparian areas;

3) Compare the permeability of roads and small streams to movements of small mammals.

For this purpose, a trapping study was undertaken to survey the diversity and abundance of small mammals and to quantify small mammal movement both on road verges and small stream side. Specifically, our objectives were (i) to identify the habitat characteristics that favour the occurrence of small mammals, (ii) to assess and compare the effect of habitat on several population parameters, including sex ratio, age, body condition of the individuals, and population turnover rates, and (iii) to characterize the movements of the most abundant species and quantify the number of road and river crossings. We assumed that populations in inferior quality habitats would have skewed sex ratios, younger individuals, poorer body condition and a lower proportion of recaptured animals (lower residence time).

2. Methods

This study was conducted in the vicinity of Évora (38°34'N, 7°54'W), Central Alentejo region, southern Portugal. The region is included in the Mesomediterranean thermotype of the Mediterranean pluviseasonal-oceanic bioclimate (Rivas-Martínez and Arregui 1999), with dry and hot summers and cold and wet winters. During the study year (2007), monthly

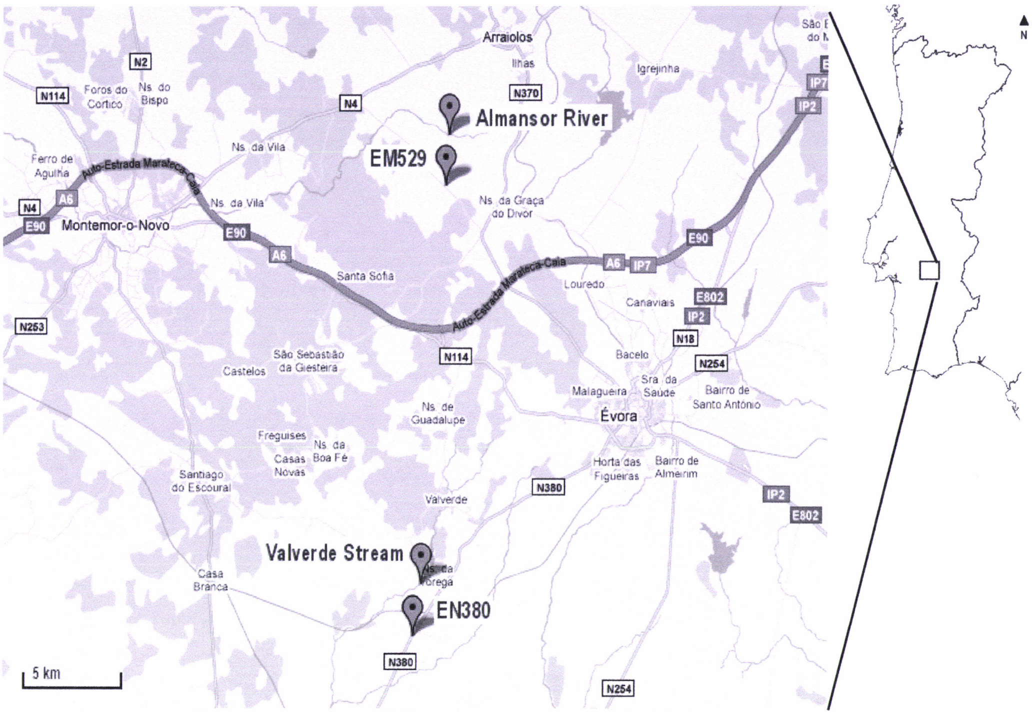

Figure 1. Location of the 4 sampling sites.

average precipitation ranged from 2.4 mm in July to 97.3 mm in February (SNIRH 2007). Specifically, the monthly precipitation during the field work data collection, in October 2007, was 48.5mm, less than the average monthly precipitation of 75.0mm (SNIRH 2007). Topography is mainly plain, with altitude ranging from 100 to 300 m. Landscapes are highly fragmented, with typical Mediterranean agro-pastoral woodlands of cork oak (*Quercus suber*) and holm oak (*Quercus ilex*), locally known as *montado*, and open areas of pastures, extensive cultures of cereals in a fallow cereal rotation basis, and irrigated annual crops.

Four study sites were chosen, two pairs of a road segment and a riparian vegetation area, to compare small mammal communities between these two types of linear habitats (Figure 1). Field data were collected in the last two weeks of October 2007, after the season's first rains and each pair of sites was sampled simultaneously. The first pair of sites was a section of national road EN380 (38°28'N, 8°02'W), and a portion of Valverde Stream (38°29'N, 8°02'W), which were sampled in the first week of data collection. These two sites were distanced from each other by approximately 2,2km to control the effect of geographical variation. The second pair of sites was located 20km to north and incorporated a section of the municipal road EM529 (38°39'N, 8°01'W), and a section of the Almansor River (38°40'N, 8°01'W). This pair of sites was sampled on the second week of field work, being the distance between these two locations also 2,2km. These four locations were chosen due to their similarities and linear structures width, allowing experimental design specifications to be respected (see further on). EN380 and EM529 are two-lane asphalt roads, with no paved verges and are 7 and 6m wide, respectively. Road verge vegetation was mostly grass, with small portions with shrubs and/or trees. Valverde Stream and Almansor River are medium width riparian lines, with herbaceous, shrub and arboreal layers constituting structured galleries of dense vegetation cover. Both stream sections were dry during data collection, allowing the crossing of small mammals between the two margins. All four study sites were within a matrix of open grassland, and were recently grazed by cattle.

2.1. *Field Methods*

Animals were captured using medium size Sherman live traps (8x9x23 cm), baited with a mixture of oat-flakes, sardines and vegetable oil, and raw cotton was provided for bedding. At each study site 90 traps were placed in three trapping lines sited parallel to the road or stream (Figure 2). Two of these lines (A and B) were positioned on either side of the linear habitat, in road verges or riparian vegetation, and the third (C) was placed further away from the linear habitat and within the pasture matrix on one side of the road or stream. All three lines were 12m apart from each other and consisted of 30 traps each, also placed at 12m intervals. In order to keep the same distance between the line traps on the two river margins, both lines A and B in the Almansor River

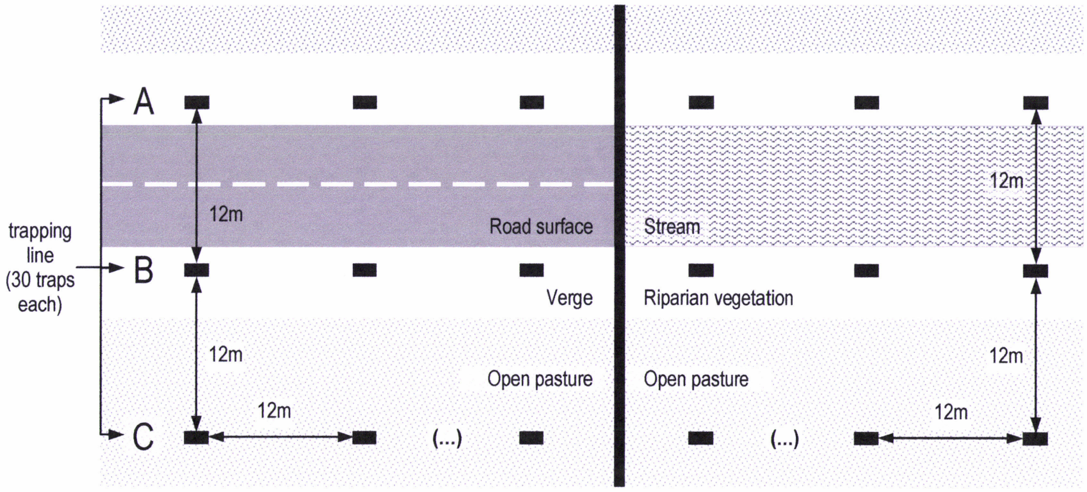

Figure 2. Schematic of Sherman live-traps positions along linear habitats in road and stream sites.

were sited at the exterior border of the riparian gallery, while in Valverde Stream trapping line A had to be positioned inside the riparian gallery.

Each trapping session consisted of four consecutive nights (360 trap-nights in each site, total trapping effort of 1440 trap-nights), during which traps were checked every morning at sunrise. Upon capture, all animals were identified, measured, sexed via examination of ano-genital distance (this was not possible for *Crocidura russula*, due to lack of external sexual features), inspected to determine reproductive condition, and weighed using hand-held Pesola® spring scales. Each captured individual was marked with a specific fur clip identifying trapping line and day of capture or recapture, and released at capture point immediately after data collection.

Microhabitat parameters describing vegetation structure were measured in 0.5m radius circles centred at each trap location. Substrate type was identified (bare ground, leaf litter or rocks), mean height of grass, shrub and tree were calculated (through the measurement of each stratum at two points, one at entrance of each trap, and another chosen randomly within the 0.5m radius circle), and its cover density were estimated (in 5 classes, see Table 1).

2.2. *Data Analysis*

Abundance in different habitats

Numbers of captured animals were used as a measure for comparing population size between linear habitat types (stream vs. road) and trapping lines (A vs. B. vs. C). Contingency tables were used for the comparison of species composition, and the Log-likelihood ratio, or *G*-test was applied (Zar 1996). Differences in abundance of small mammals in streams and roads and on the three trapping lines were analysed with chi-square goodness-of-fit test, and a 2 x 3 contingency table (stream vs. road x A vs. B vs. C) was used to check if the proportion of animals in each of the trapping lines was similar for the two habitats (Zar 1996).

Small mammal response to habitat characteristics

Generalized Linear Model (GLM) was used to estimate the effects of macro (linear habitat and trapping line) and microhabitat variables (describing vegetation structure, see Table 1) on the abundance of most common species (*Mus spretus* and *Crocidura russula*) (Zuur *et al.* 2007). Each individual trap was established as the sampling unit, and the response variables were defined as the number of individuals captured at a given trap for *Mus spretus* (using a Poisson regression with *log* link), and due to the lower number of captures, as the presence/absence of captures of *Crocidura russula* at a given trap (using a binomial regression with *logit* link).

Prior to statistical analysis, explanatory continuous variables were log-transformed (log (x+1)) to approach normality and to reduce the influence of extreme values (Zuur *et al.* 2007). Spearman rank correlations were computed between all pairs of explanatory variables, to investigate for the presence of collinearity. From each pair of highly correlated variables ($r > 0.7$), only the one showing stronger association with the response variable was retained for further analysis (Zar 1996, Tabachnick and Fidell 2001).

For each response variable, a preliminary screening of habitat variables was undertaken using univariate analysis to identify significant main effects

Table 1. Description and summary statistics of macro and micro habitat variables obtained for each trap location. *See Figure **2**

Variables set	Variables	Code	Categories	Type	Mean ± SD	Range
Response variables	Nº of *Mus spretus* captured	M. spretus	Number of captures per trap	Ordinal	-	0-4
	Presence of *Crocidura russula*	C. russula	Captured Not captured	Binary	-	0/1
Macro habitat	Linear habitat	Habitat	**1** - Stream **2** - Road	Nominal	-	-
	Trapping line	Line	**1** – A* **2** – B **3** – C	Nominal	-	-
Micro habitat	Grass – mean height (cm)	Grass.height	-	Continuous	27.7 ± 32.3	0 – 145
	Grass – cover density	Grass.cover	**1** - 0% **2** - 1 – 25% **3** - 26 – 50% **4** - 51 – 75% **5** - 76 – 100%	Ordinal	4.1 ± 1.2	1 – 5
	Shrub – mean height (cm)	Shrub.height	-	Continuos	32.8 ± 58.8	0 – 350
	Shrub – cover density	Shrub.cover	**1** - 0% **2** - 1 – 25% **3** - 26 – 50% **4** - 51 – 75% **5** - 76 – 100%	Ordinal	1.8 ± 1.1	1 – 5
	Tree – mean height (cm)	Tree.height	-	Continuos	160.6 ± 345.9	0 – 2100
	Tree – cover density	Tree.cover	**1** - 0% **2** - 1 – 25% **3** - 26 – 50% **4** - 51 – 75% **5** - 76 – 100%	Ordinal	1.8 ± 1.5	1 – 5
	Bare ground – cover density	Bare.cover	**1** - 0% **2** - 1 – 25% **3** - 26 – 50% **4** - 51 – 75% **5** - 76 – 100%	Ordinal	2.0 ± 0.9	1 – 5
	Leaf – cover density	Leaf.cover	**1** - 0% **2** - 1 – 25% **3** - 26 – 50% **4** - 51 – 75% **5** - 76 – 100%	Ordinal	1.7 ± 1.1	1 – 5
	Rock – cover density	Rock.cover	**1** - 0% **2** - 1 – 25% **3** - 26 – 50% **4** - 51 – 75% **5** - 76 – 100%	Ordinal	1.1 ± 0.4	1 - 4

in the abundance of small mammals. Only significant ($P < 0.05$) and nearly significant ($0.05 < P < 0.10$) variables were considered in multivariate model building. The nearly significant variables were also considered to reduce the incidence of Type II errors and avoid rejecting ecologically relevant effects at an early stage (e.g. Buhl 1996, Underwood 1997). Final multivariate model selection was produced with an automated forward and backward stepwise regression, using the Akaike Information Criteria (AIC) to select the best models (Zuur *et al.* 2007). For each final model, proportion of the explained deviance was used as a measure of the explained variance (Zuur *et al.* 2007).

Sex Ratio, size and body condition

For each of the species captured, chi-square goodness-of-fit test was used to assess biases from the 1:1 sex ratio, and contingency tables were used to verify if the ratio was the same for the two habitat types (2 x 2 tables: female vs. male x stream vs. road) and for the three trapping lines (2 x 3 tables: female vs. male x A vs. B vs. C).

Mean body length and mean body condition index (weight/body length) were compared between linear habitats and trapping lines using a two-way ANOVA with a Tukey HSD post hoc comparison (Zar 1996). Prior to this, data were log-transformed (log (x+1)) to approach normality and homocedasticity and to reduce the influence of extreme values (Zuur *et al.* 2007).

Population turnover

The number of recaptured individuals (individuals recaptured at least one time) relative to non-recaptured ones was compared for streams and roads and for trapping lines A, B and C, through the use of 2 x 2 (recaptured vs. non-recaptured x stream vs. road) and 2 x 3 (recaptured vs. non-recaptured x A vs. B vs. C) contingency tables.

Barrier effect

To test for a possible influence of both streams and roads on small mammal movements and if they represent a barrier effect, it was assumed that the movements in all directions would be equally likely to occur, since the distance between traps is the same within and between trap lines. Under this assumption, we compared the number of movements inside the same line with the number of movements between any two of the three lines. A 2 x 2 contingency table was used to check if this ratio was similar for streams and roads. Because the mark that was made on the captured individuals was not unique, and only identified the trapping line and day of capture, we defined as movement between traps when a recaptured animal was captured in a trap that had no registered captures in the previous mornings. However, this method potentially underestimates the animal movements inside the same trapping line.

Multivariate regression analysis were carried out in Brodgar 2.5.7 (contains an interface to the statistics package R version 2.5.0) (Highland statistics 2006), and all other calculations were performed with SPSS 15.0.0 (Norusis 1993). Critical significance level considered was 0.05, unless noted.

3. Results

During the trapping sessions a total of 457 individuals of five different species were captured, of which 30% (136 individuals) were recaptured at least once (105 were recaptured once, 28 twice and 3 were recaptured three times). Algerian mouse (*Mus spretus*, Lataste 1883) was the most common species captured (322 individuals, 71% of the total number of animals captured), followed by the Greater White-toothed Shrew (*Crocidura russula* (Herman 1780) - 105 individuals, 23% of the total captures) and the Wood mouse (*Apodemus sylvaticus* (Linnaeus 1758) - 24 individuals, 5% of the total captures). These three species were captured both in riparian areas and roads. On the other hand, Black rat (*Rattus rattus* (Linnaeus 1758) - 2 individuals) and Norway rat (*Rattus norvegicus* (Berkenhout 1769) -1 individual) were captured in very low numbers and only in streams, although 1 individual of *Rattus sp.*, that escaped, was captured on the road EN380.

The species composition was significantly different for streams and roads (G = 8.111, df = 3, P = 0.044), with *M. spretus* representing 74.3% of the total captures on roads and only 66.2% on streams, whereas *A. sylvaticus* was more abundant on streams (8.1% of the total captures) than on roads (3.1%). On road sites, species composition was similar for the three trapping lines (G = 10.950, df = 6, P = 0.090). Conversely, on stream sites species composition showed highly significant differences between trapping lines (G = 21.538, df = 6, P = 0.001) mainly because the proportion of both *M. spretus* and *C. russula* captures varied greatly between the three trapping lines (*M. spretus*: 67.6% in line A, 58.9% in line B and 100.0% in line C; *C. russula*: 19.7% in line A, 31.8% in line B and 0% in line C).

3.1. *Abundance in different habitats*

Small mammals were more abundant on road verges than on riparian strips (χ^2 = 7.617, df =1, P = 0.006), with 30% more individuals captured (Figure 3). An analogous pattern was detected for captures of *M. spretus* (χ^2 = 11.180, df = 1, P = 0.001), being 46% higher on road sides than along streams. The two other commonly captured species, *C. russula* and *A. sylvaticus,* did not differ in abundance between streams and roads (*C. russula*: χ^2 = 0.771, df = 1, P = 0.380; *A. sylvaticus*: χ^2 = 2.667, df=1, P = 0.102).

The number of small mammals captured in each of the trapping lines was significantly different (χ^2 = 117.694, df = 2, P < 0.001), as were captures of the three most common species (*M. spretus*: χ^2 = 63.435, df = 2, P < 0.001; *C. russula*: χ^2 = 62.229, df = 2, P < 0.001; *A. sylvaticus*: χ^2 = 6.750, df = 2, P = 0.034). The total number of captures in the trapping lines placed on either side of the linear habitats (trapping lines A and B) were, on average, 4.6 times higher than

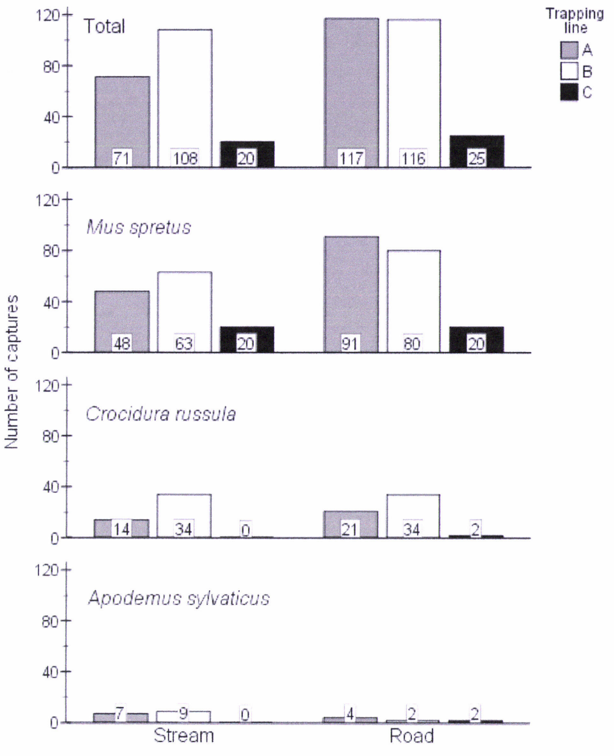

Figure 3. Number of total captures, captures of *Mus spretus*, *Crocidura russula* and *Apodemus sylvaticus* in the three different trapping lines (A – grey, B – white and C - black) at each linear habitat type (Stream, Road). Numbers inside bars represent individuals captured.

the number of animals captured on the adjacent matrix (trapping line C). In particular, captures in line A and B for *M. spretus*, *C. russula* and *A. sylvaticus* were respectively, 3.5, 25.8, and 5.5 times higher than in trapping line C. There was no significant interaction between linear habitat and trapping line, for the total number of small mammals and for the three species analysed (total: G = 4.575, df = 2, P = 0.102; *M. spretus*: G = 4.303, df = 2, P = 0.116; *C. russula*: G = 3.410, df = 2, P = 0.182; *A. sylvaticus*: G = 5.701, df = 2, P = 0.058).

3.2. *Small mammal response to habitat characteristics*

Microhabitat characteristics varied between linear habitats and between trapping lines (Table 2). Mean height of the herbaceous layer was higher on roads and lower on trapping line C, grass coverage was also higher on roads, and was higher on the surrounding matrix. Shrub and tree mean height and coverage were higher on streams and lower outside of the linear habitat. There was a higher proportion of bare ground coverage on trapping line C, and cover density of leafs was higher on streams and inside the linear habitat.

Out of the 360 traps, 239 captured small mammals (202 of them captured *M. spretus* and 82 of them *C. russula*). Some microhabitat features seemed to vary between sites with and without the presence of *M. spretus* and *C. russula* (Table 3). Sites used by *M. spretus* and *C. russula* had taller grass, a slightly higher shrub density cover and lower bare ground coverage than unused sites. For *C. russula*, the shrub layer also appeared to be taller. The same pattern was apparent when considering the total number of small mammals caught.

Some microhabitat variables were strongly correlated, and so they were not used in further analyses (Table A in Appendix). This was the case for shrub cover which showed high correlation (r = 0.89) with shrub mean height, and tree mean height, which was highly correlated with both tree cover (r = 0.93) and leaf cover (r = 0.82). Hence, out of these 5 variables, we only incorporated shrub cover and tree cover in the subsequent analysis.

The univariate analysis showed that the total number of small mammal captures had significant relations with seven explanatory variables (Table 4). Captures were higher in roads (P = 0.006) and much lower on line C (P = 0.001). A nearly-significant difference (P = 0.069) was found for the higher numbers of captures on line B. There was also a strong positive association between total captures and mean height of the herbaceous layer (P < 0.001). Grass, shrub and tree coverage had a positive effect on the abundance of small mammals, and bare ground density cover had a negative effect, even though there were only some of the categories of this variables that showed significant relations. After the variable selection procedure, the best model of abundance of small mammals included two variables, trapping line and density cover of grass, and explained 36.7% of the variation in this response variable.

The abundance of *M. spretus* showed significant univariate associations with six of the predictor variables: linear habitat, trapping line, mean height of grass, cover density of bare ground, cover density of shrub and cover density of grass (Table 4). Algerian mice were more abundant on road sites (P < 0.001), and trapping line C had a strong negative effect (P < 0.001). Further, captures of this species increased significantly with increasing grass height (P < 0.001). Coverage of bare ground was a negative correlate with the abundance of *M. spretus*, while cover density of shrub and herb were positively related with it. The multivariate model for the abundance of *M. spretus* included three variables: trapping line, linear habitat and grass coverage, and explained 22.3% of the variation in the number of individuals captured.

Captures of *C. russula*, analysed as a binomial variable, had significant univariate relations with five explanatory variables (Table 4). The probability of occurrence of *C. russula* increased with the mean height of the herbaceous layer ($P < 0.001$). Trapping line B had a positive association with *C. russula* ($P = 0.003$), while line C had a negative one ($P < 0.001$). Shrub and tree cover had a positive effect on the presence of this species, and bare ground density cover had a negative one, even though there were only some of the categories of this variables that showed significant relations. The best model explained 27.7% of the variation in the presence of *C. russula* and included three variables: trapping line, mean grass height and tree density cover.

3.3. *Sex ratio, size and body condition*

In both *M. spretus* and *A. sylvaticus*, there were no significant biases respecting the 1:1 sex ratio (*M. spretus*: $\chi^2 = 0.325$, df = 1, $P = 0.569$; *A. sylvaticus*: $\chi^2 = 1.087$, df = 1, $P = 0.297$), regardless of habitat (*M. spretus*: $G = 0.117$, df = 1, $P = 0.733$; *A. sylvaticus*: $G = 1.064$, df = 1, $P = 0.302$) or trapping line considered (*M. spretus*: $G = 1.201$, df = 2, $P = 0.549$; *A. sylvaticus*: $G = 3.414$, df = 2, $P = 0.181$).

The mean body length of *M. spretus* differed significantly by habitat type and trapping line: Algerian Mice were bigger on stream sites but significantly smaller in trapping line C than on A or B (see Table 5 for ANOVA results; Tukey HSD test: A-B: $P = 0.992$; A-C: $P = 0.006$; B-C: $P = 0.005$). There was no interaction between the two factors (linear habitat and trapping line). White-toothed Shrew offered a great variability in mean body-lengths, and the ANOVA results presented a significant difference between habitats, with slightly bigger individuals on roads, and no statistical differences between trapping lines, despite the lower value of body length in line C (Table 5). However, there was a highly significant interaction between these two factors, mainly due to the values discrepancy in line A between streams and roads. Wood Mice had similar body lengths between roads and streams, but the 2 individuals caught on line C were much smaller than the ones captured inside the linear habitats (Table 5). We did not perform further analysis for *A. sylvaticus* due to the low sample number.

For both *M. spretus* and *C. russula* the mean body condition index was not statistically different between trapping lines, although for *M. spretus* the lower value on line C is nearly significant (Table 5). This index, for *M. spretus*, was also similar between roads and streams, but for *C. russula*, was significantly superior

Table 2. Summary statistics (mean ± standard deviation) of microhabitat variables in trapping lines (A, B, C) at each linear habitat (Stream, Road).

	STREAM			ROAD		
	A	B	C	A	B	C
Grass.height (cm)	12.0 ± 14.7	14.9 ± 13.4	9.4 ± 6.9	73.2 ± 27.8	52.4 ± 32.1	4.4 ± 6.7
Grass.cover	3.2 ± 1.6	3.2 ± 1.0	4.6 ± 0.7	4.8 ± 0.4	4.6 ± 0.6	4.1 ± 1.0
Shrub.heigth (cm)	98.5 ± 77.7	78.3 ± 61.9	0.0 ± 0.0	5.6 ± 19.1	13.9 ± 31.8	0.6 ± 4.5
Shrub.cover	2.9 ± 0.7	3.2 ± 0.8	1.0 ± 0.0	1.3 ± 0.7	1.5 ± 0.9	1.0 ± 0.3
Tree.height (cm)	609.4 ± 386.4	311.8 ± 495.0	0.0 ± 0.0	0.0 ± 0.0	28.9 ± 98.5	13.3 ± 61.7
Tree.cover	4.1 ± 1.3	2.5 ± 1.7	1.0 ± 0.0	1.0 ± 0.0	1.2 ± 0.6	1.2 ± 0.8
Bare.cover	1.9 ± 0.9	2.0 ± 0.7	2.0 ± 0.8	1.8 ± 0.6	1.5 ± 0.6	2.7 ± 1.1
Leaf.cover	3.2 ± 1.1	2.3 ± 1.0	1.2 ± 0.4	1.0 ± 0.1	1.4 ± 0.6	1.1 ± 0.6
Rock.cover	1.2 ± 0.6	1.1 ± 0.3	1.1 ± 0.4	1.0 ± 0.1	1.1 ± 0.4	1.1 ± 0.4

Table 3. Summary statistics (mean ± standard deviation) of microhabitat variables in traps with and without captures of total small mammals, *Mus spretus* and *Crocidura russula*.

	Total		***Mus spretus***		***Crocidura russula***	
	PRESENCES	ABSENCES	PRESENCES	ABSENCES	PRESENCES	ABSENCES
Grass.height (cm)	36.4 ± 33.9	10.7 ± 19.7	36.0 ± 33.6	17.1 ± 27.1	45.3 ± 36.4	22.5 ± 29.0
Grass.cover	4.1 ± 1.1	3.9 ± 1.3	4.2 ± 1.1	3.9 ± 1.2	4.3 ± 0.9	4.0 ± 1.2
Shrub.height (cm)	39.2 ± 58.2	20.2 ± 58.0	35.9 ± 54.6	28.8 ± 63.6	45.7 ± 64.0	29.0 ± 56.7
Shrub.cover	2.0 ± 1.2	1.4 ± 0.8	2.0 ± 1.1	1.6 ± 1.0	2.2 ± 1.2	1.7 ± 1.1
Tree.height (cm)	161.4 ± 346.4	158.8 ± 346.3	164.4 ± 362.5	155.7 ± 324.6	152.6 ± 319.0	162.9 ± 354.0
Tree.cover	1.8 ± 1.4	1.8 ± 1.5	1.8 ± 1.5	1.8 ± 1.5	1.9 ± 1.4	1.8 ± 1.5
Bare.cover	1.8 ± 0.8	2.3 ± 1.0	1.8 ± 0.8	2.2 ± 1.0	1.6 ± 0.6	2.1 ± 0.9
Leaf.cover	1.7 ± 1.0	1.7 ± 1.2	1.7 ± 1.0	1.7 ± 1.2	1.7 ± 0.8	1.7 ± 1.1
Rock.cover	1.1 ± 0.5	1.1 ± 0.2	1.1 ± 0.5	1.1 ± 0.3	1.1 ± 0.4	1.1 ± 0.4

Table 4. Summary of relationships between the response variables (abundance of small mammals and *Mus spretus*, and presence of *Crocidura russula*) and habitat variables as assessed from poisson regression (total small mammal abundance, *M. spretus* abundance) and binomial regression (*C. russula*). Significance levels and directions of association, negative (-) or positive (+), are given for habitat variables showing significant ($P < 0.05$) or nearly significant ($0.5 < P < 0.10$) univariate relationships with at least one of the categories of the response variables. The interpretation of the regression coefficient for categorical variables is based on the first category (Indicator). Variables in bold are those also incorporating the best multivariate models. The amount of explained variation is given for each of the best models. See Table 1 for definition of variables.

	Total	*M. spretus*	*C. russula*
PROPORTION OF EXPLAINED VARIANCE	0.367	0.223	0.277
Habitat			
Stream	Indicator	Indicator	
Road	0.006 (+)	**< 0.001 (+)**	
Line			
A	**Indicator**	**Indicator**	**Indicator**
B	**0.069 (+)**	**0.766 (+)**	**0.003 (+)**
C	**< 0.001 (-)**	**< 0.001 (-)**	**< 0.001 (-)**
Grass.height	< 0.001 (+)	< 0.001 (+)	**< 0.001 (+)**
Grass.cover			
0%	**Indicator**	**Indicator**	
1 – 25%	**0.042 (+)**	**0.100 (+)**	
26 – 50%	**0.084 (+)**	**0.293 (+)**	
51 – 75%	**0.024 (+)**	**0.096 (+)**	
76 – 100%	**0.013 (+)**	**0.042 (+)**	
Shrub.cover			
0%	Indicator	Indicator	Indicator
1 – 25%	0.089 (+)	0.856 (+)	0.009 (+)
26 – 50%	< 0.001 (+)	0.010 (+)	0.001 (+)
51 – 75%	0.003 (+)	0.323 (+)	0.026 (+)
76 – 100%	0.535 (+)	0.763 (+)	0.237 (+)
Tree.cover			
0%	Indicator		**Indicator**
1 – 25%	0.006 (+)		**0.033 (+)**
26 – 50%	0.033 (+)		**< 0.001 (+)**
51 – 75%	0.745 (+)		**0.241 (+)**
76 – 100%	0.175 (-)		**0.553 (-)**
Bare.cover			
0%	Indicator	Indicator	Indicator
1 – 25%	0.681 (-)	0.445 (-)	0.459 (-)
26 – 50%	0.003 (-)	0.030 (-)	< 0.001 (-)
51 – 75%	< 0.001 (-)	0.002 (-)	0.030 (-)
76 – 100%	0.288 (-)	0.464 (-)	0.982 (-)

in individuals captured on roads (Table 5). There was no interaction between linear habitat and trapping line, for both species. The mean body length of *A. sylvaticus* was highly inconsistent.

3.4. *Population turnover*

During the 8 nights of sampling, 323 individuals were captured only once and never recaptured again (145 on streams, 178 on roads), and 135 animals were recaptured at least on one occasion (54 on streams, 81 on roads) (Figure 4). The ratio of lost animals (i.e., those that were marked but not recaptured) did not changed significantly between roads and streams, for the total captures and for each of the species analysed (all comparisons $P > 0.1$). However, for *M. spretus*, the proportion of recaptured individuals appears to be lower on line C, even though these differences were not statistically significant for any of the species (all comparisons $P > 0.07$).

3.5. *Barrier effect*

On the 4 sampled sites, we've identified 70 movements of small mammals among traps (47 were of *M. spretus*, 22 of *C. russula*, one of *A. sylvaticus*) (Table 6).Individuals preferred to move within the same trapping line (n = 65; 92.9% of detected movements) than to move among different lines (n = 5; 7.1% of detected movements). This pattern was observed for the total of the detected movements and the species' movements analysed separately. However, there were differences between the movement patterns found in each habitat. The ratio of movements between different lines was similar between streams and roads for *C. russula* ($G = 0.314$, df = 1, $P = 0.575$). For the total number of small mammals the difference in the ratios was nearly significant ($G = 3.353$, df = 1, $P = 0.067$), and for *M. spretus* this difference was statistically significant ($G = 5.089$, df = 1, $P = 0.024$), with more movements between trapping lines next to streams.

Of the five movements between different trapping lines, two were crossings of stream, one was a crossing of road, and two were movements between riparian habitat and the surrounding matrix. The low number of detected movements between trapping lines prevented further analyses of the permeability of different habitats and structures.

4. Discussion

In our study, the three most captured species, Algerian mouse (*Mus spretus*), white-toothed shrew (*Crocidura russula*) and wood mouse (*Apodemus sylvaticus*), are among the most abundant Mediterranean small mammals, and have been

Table 5. Body length and body condition index for *Mus spretus*, *Crocidura russula* and *Apodemus sylvaticus* (mean ± standard deviation, n in parenthesis), in each trapping line (A, B, C) and linear habitat. Analysis of variance results (F) are presented for differences between linear habitat, trapping lines, and for the interaction between linear habitat type and trapping line. [ns] Non significant; [a]$P < 0.1$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Linear Habitat	Stream			Road			ANOVA (F)		
Trapping Line	A	B	C	A	B	C	Linear Habitat	Trapping Line	Linear Habitat X Trapping Line
Body Length (cm)									
Mus spretus	7.69 ± 0.59 (46)	7.64 ± 0.59 (63)	7.24 ± 0.62 (20)	7.45 ± 0.78 (91)	7.45 ± 0.67 (80)	7.06 ± 0.66 (20)	5.476 *	6.255 **	0.051 ns
Crocidura russula	6.41 ± 0.81 (14)	7.00 ± 0.49 (34)	-	7.20 ± 0.47 (21)	6.86 ± 0.81 (34)	6.05 ± 0.92 (2)	4.199 *	2.130 ns	9.995 **
Apodemus sylvaticus	9.11 ± 1.03 (7)	8.94 ± 0.75 (8)	-	8.25 ± 1.24 (4)	9.45 ± 0.35 (2)	7.10 ± 1.56 (2)	-	-	-
Body Condition Index (g/cm)									
Mus spretus	1.69 ± 0.36 (46)	1.57 ± 0.21 (63)	1.46 ± 0.22 (20)	1.55 ± 0.29 (91)	1.65 ± 0.39 (80)	1.51 ± 0.32 (20)	0.036 ns	2.388 a	2.562 a
Crocidura russula	0.93 ± 0.14 (14)	0.97 ± 0.22 (34)	-	1.10 ± 0.24 (21)	1.16 ± 0.27 (34)	0.91 ± 0.02 (2)	12.498 ***	1.159 ns	0.076 ns
Apodemus sylvaticus	2.60 ± 0.48 (7)	2.53 ± 0.34 (8)	-	1.74 ± 0.63 (4)	3.50 ± 0.43 (2)	2.47 ± 1.50 (2)	-	-	-

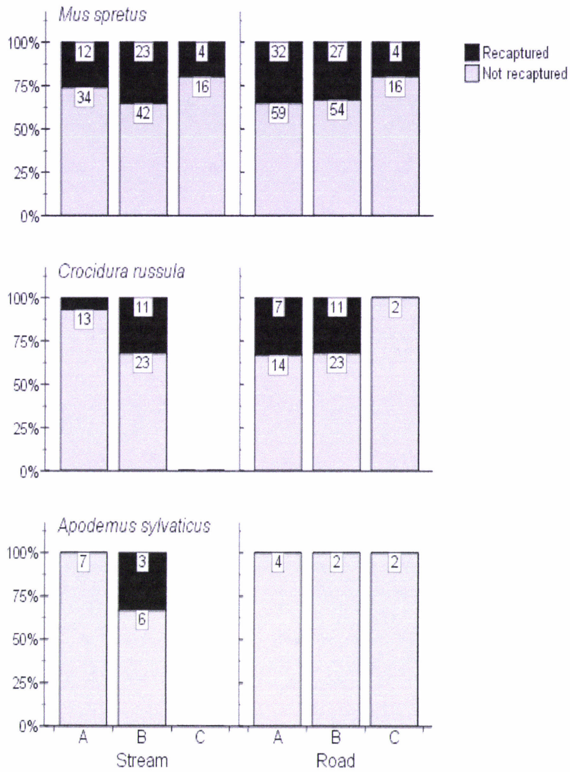

Figure 4. Turnover rate of *Mus spretus*, *Crocidura russula* and *Apodemus sylvaticus* compared on streams and roads for the three trapping lines (A, B, C). Numbers inside bars represent individuals captured.

recurrently captured in the region (De Alba *et al.* 2001, Pita *et al.* 2003, Ramalho 2007, Silva 2008, Munõz *et al.* 2009). However, there were major differences in the number of captures of each species; the Algerian mouse captures being three times the number of the second most captured species, *C. russula*. This distinct pattern probably reflects both the seasonal patterns of population abundance and the habitat preferences of the studied species.

Our study took place in late October, at the beginning of the wet season, when the abundance of *M. spretus* is at its annual peak, after the spring and summer reproductive period (Pita *et al.* 2003, Palomo *et al.* 2009). Conversely, wood mouse and white-toothed shrew populations were at their lowest level since their peak reproductive period only occurs afterwards, in the winter months (De Alba *et al.* 2001, Torre *et al.* 2002, Pita *et al.* 2003).

The higher number of captures of *Mus spretus* can also be a consequence of the main habitat type in the matrix (grassland) surrounding the sampling sites, since Algerian mice prefer open fields with tall grass (De Alba *et al.* 2001, Khidas *et al.* 2002, Pita *et al.* 2003, Palomo *et al.* 2009), while *A. sylvaticus* often occurs in fields with high forest cover (De Alba *et al.* 2001, Khidas *et al.* 2002, Torre *et al.* 2002, Pita *et al.* 2003). *C. russula* shows a mixed pattern of habitat use: it is often associated with open landscapes and cultivated fields (Pita *et al.* 2003, Michel *et al.* 2007), but it appears to concentrate in forested patches during the winter season (De Alba *et al.* 2001).

4.1. *Linear habitats as refuges for small mammals*

Our results show that road side verges, in intensively grazed Mediterranean landscapes, act as important refuge habitat for small mammals, harbouring abundant populations on their narrow vegetation strips. Roadways thus constitute equally vital habitats for small mammals as do riparian vegetation strips, in landscapes where other suitable habitat (tall grass and/or shrub cover) is scarce.

The species composition, on roads, was similar on verges and on the surrounding matrix. Conversely, on streams, the only species captured outside the riparian gallery was *M. spretus*. This may be due to vegetation structure differences in these habitats. There were more similarities in the vegetation of the three trapping lines on roads than on streams. The herbaceous layer was dominant on roads, both in the verge strips and in the surrounding matrix. On streams the vegetation of the adjacent landscape was mainly grassland, but the riparian vegetation gallery had a much more complex stratification, that included grass, shrubs and trees.

Several studies have established the importance of linear habitats as refuges for small mammals in agricultural landscapes. For example, the use of hedgerows by these species is well known (Ouin *et al.* 2000, Tattersall *et al.* 2002, Butet *et al.* 2006, Gelling *et al.* 2007, Michel *et al.* 2007). Higher abundances of small mammals are also found on riparian strips than on the less favourable surrounding matrix (Gomez and Anthony 1998, Perault and Lomolino 2000, Maisonneuve and Rioux 2001, Waters *et al.* 2001, Chapman and Ribic 2002, Cokle and Richardson 2003), and recently the importance of roadside verges as also been recognized as habitats of higher abundance of small mammals (Adams 1984, Bennett 1990, Mauritzen *et al.* 1999, Meunier *et al.* 1999, Bellamy *et al.* 2000, Bolger *et al.* 2001, Forman *et al.* 2003, Brock and Kelt 2004, Bissonette and Rosa 2009, Fahrig and Rytwinski2009). Our results support these findings. The total captures of small mammals were much

Table 6. Number of movements between traps for the total number of captures and for each species, at streams and roads. Numbers in parenthesis are number of movements crossing the linear structure.

	Linear Habitat	Inside the Same Trapping Line	Between Trapping Lines
Total	Stream	25	4 (2)
	Road	40	1 (1)
M. spretus	Stream	18	3 (1)
	Road	26	0
C. russula	Stream	6	1 (1)
	Road	14	1 (1)
A. sylvaticus	Stream	1	0
	Road	0	0

higher on both roadsides and riparian strips than on the surrounding grazed matrix. Moreover, the same pattern was found for each of the three species. Therefore, based on the regularity of this pattern, we may ask how further away from the linear habitat we can detect differences in small mammal abundances. In a recent study in a road in the Évora region, southern Portugal, Ramalho (2007) found major differences in captures of small mammals between road verges and the surrounding matrix, where the trapping lines aiming to sample the small mammals in the matrix were placed 100m apart from the roadside. In our study, however, we found very uneven small mammal abundances at very short distances - 12m - from the linear habitat, on both road verges and riparian vegetation strips.

Our GLM analysis of the habitat characteristics favoured by each species indicates that the abundances of *Mus spretus* and presence of *Crocidura russula* are higher in the linear habitats. In addition, both *M. spretus* and *C. russula* have a preference to occupy sites with taller grass, higher shrubs coverage and less bare ground. *M. spretus* also selects sites with higher grass cover and *C. russula* sites with more tree cover. In the surrounding grazed matrix, some of these vegetation features seem to disfavour the presence of these two species, since the grass is shorter and the coverage of shrubs and trees is lower, and there the occurrence of bare ground is more common.

Individuals of all three species, captured at the surrounding grazed matrix presented, on average, a smaller body size, although the only two shrews caught in this trapping line prevented the detection of significant differences. Similarly, the body condition of Algerian mice and white-toothed shrew was also slightly lower in the matrix.

Habitat patches of high quality are usually occupied by dominant, territorial individuals, with better body condition (Fretwell and Lucas 1970, Shioya *et al.* 1992), while sub-adults are characterized by a low position in the social system and are normally not provided with established home-ranges and therefore have to move more often in unknown terrain, of below average quality (Fretwell and Lucas 1970, Hanski *et al.* 1991). Dispersers are usually individuals of relatively low competitive ability (mostly by age and body condition) that are excluded by dominant animals (Lawrence 1987, Hansky *et al.* 1991, Bowler and Benton 2005). This social structure is common to the three studied species because they all present a territorial behaviour at some point of their life cycle (*M. spretus* - Hurst *et al.* 1996, Gray and Hurst 1997; *A. sylvaticus* - Torre *et al.* 2002; *C. russula* - Favre *et al.* 1997).

Our data thus suggests that individuals captured at the surrounding grazed matrix are subadult, probably subordinates, which were probably chased away from the higher quality habitats of streams and roads by dominant ones (Collins and Barret 1997). The higher abundance of captured individuals of Algerian mouse in the matrix is probably related to the timing of our field work, in mid fall, that coincides with the end of the breeding season in this species (Pita *et al.* 2003, Palomo *et al.* 2009), thus increasing the proportion of young and dispersing individuals of the population. However, due to the small distance that separated the trapping lines, we cannot tell if the animals captured on this external trapping line were making dispersing movements, or if they are simply occupying less favourable portions of the large dominant animal territory (Cook *et al.* 2004). The low number of *C. russula* and *A. sylvaticus* captured in the surrounding matrix is probably due to the fact that both shrews and wood mouse were at their lowest population level, before the breeding season, when the population is mainly composed of adult animals (Torre *et al.* 2002, Pita *et al.* 2003).

We found no differences in the sex ratio of *M. spretus* and *A. sylvaticus* between the lines located inside and outside the linear habitats, which we could expect since dispersion in these species is male biased (Bowler and Benton 2005). For *M. spretus*, the recapture rate was slightly lower outside the linear habitats (although not statistically significant), which suggests that in this area we may have more transient individuals (Brock and Kelt 2004).

Summarising, *(i)* the higher abundances of small mammals inside roadside verges and riparian strips; *(ii)* the microhabitat characteristics that favour the occurrence of small mammals; *(iii)* the higher proportion of juveniles and their lower body condition in the surrounding matrix, and *(iv)* the tendency of animals to present a lower residence time in the matrix; point towards a higher suitability for small mammals of both linear habitats studied, when compared to the surrounding grazed matrix. In fact, grazing can have several detrimental effects for small mammals. Abundance and diversity of small mammals are usually affected strongly by grazing either due to decreased food availability or quality, decreased suitability of soil for building burrow systems due to trampling and/or due to increased predation risk in the structurally simpler grazed areas (Torre *et al.* 2007). Both riparian galleries and roadside verges are usually not grazed thus maintaining narrow strips of favourable habitat within the landscape that act as refuges.

4.2. *Comparison of the habitat quality of the two linear habitats, roads and streams*

We found a greater predominance of Algerian mice on road sites, and higher numbers of wood mice on streams. The vegetation on roads was composed mainly of grass, with scatter shrubs and trees, while on streams we had higher structured vegetation. Our results are in concordance with the habitat preferences of this two species. As mentioned above, *M. spretus* prefers open grassland sites, and *A. sylvaticus* selects shrubby habitats for nesting and foraging.

Algerian mouse was more abundant on roadsides than on stream side vegetation, but white-toothed shrew and wood mouse had similar abundances in both linear habitats. This suggests that roadsides and riparian strips present similar habitat quality for *C. russula* and *A. sylvaticus*, whereas road verges have better habitat quality for *M. spretus*. However, the placement of one trapping line (due to the constrain of maintaining similar distances among each trap) in the interior of the riparian gallery in one of the streams sampled, rather than on the exterior border, lowered the total number of small mammals captured on riparian high predation risk has been a common observation (Ylönen *et al.* 1992, Oksanen and Lundberg 1995, Norrdahl and Korpimäki 1998, Barreto and MacDonald 1999, Mohr *et al.* 2003, Yunger 2004, Díaz *et al.* 2005). Furthermore, if the amount of high quality food is limited, reduced foraging activity may lead to lower body growth rates, delayed maturation, deteriorated body strips, especially *M. spretus* and *C. russula*. This may be one of the reasons that caused a significant difference on the abundances of small mammals between the two linear habitats. However, if this is the case, the result also shows that small microenvironmental differences inside the narrow linear habitats may translate in significant changes in small mammal community composition.

The abundance of the Algerian mouse seems to be augmented on roadside verges with higher cover of grasses. In our four sampled sites, road habitats presented higher herbaceous cover than did stream vegetation. The raised soil of roadsides may also present better conditions for the excavation of burrows, which can enhance the availability of refuges and the habitat quality (Brock and Kelt 2004), thus increasing the abundance of *M. spretus*. *C. russula*, alternatively, seems to prefer a combination of taller grass with higher tree cover. On roadsides, grass was taller than on stream sides, but there was less coverage of trees, so both linear habitats had advantageous characteristics to shrews, which may explain the similar abundances on roads and streams.

The density of small mammal predator's present at each habitat may also be one of the most important ecological factors discriminating between roads and streams. In the Iberian Peninsula, most predators are associated with habitats containing well developed woody vegetation (Torre and Díaz 2004, Díaz *et al.* 2005, Neves 2009, Pita *et al.* 2009). In fact, mammalian predators in this region clearly prefer riparian habitats (Santos-Reis *et al.* 2004, Matos *et al.* 2009, Neves 2009). Additionally, several studies mention the detrimental effects of roads on the distribution of carnivores, with most animals avoiding them (Forman *et al.* 2003, Fahrig and Rytwinski 2009, Galantinho and Mira 2009, Neves 2009). Therefore, it is likely that riparian habitats have higher densities of predators than road verges, albeit recent records on the use of roads as feeding grounds by some predators (Silva 2008, Gomes *et al.* 2009,).

A reduction in foraging activity as a response to condition, and lower immunocompetence (Norrdahl and Korpimäki 2000, Norrdahl *et al.* 2004).

The explanations stated above may apply to our *C. Russula* results, where we found significantly better body conditions on animals captured on roadsides. Due to the expected higher density of predators on streams, individuals living in this habitat may adapt their behaviour and spend less time foraging, thus reducing their body condition and consequently their growth rate (shrews on roads were also bigger). This agrees with several studies that found a negative interaction between predation pressure and body weigth of small mammals (Yoccoz and Mesnager 1998, Karels *et al.* 2000, Norrdahl and Korpimäki 2002, Norrdahl *et al.* 2004). Shrews that inhabit riparian areas may also be subject to a higher degree of chronic stress related to the higher predation risk, which can affect their stress hormone levels and diminish their overall body condition (Boonstra *et al.* 1998, Karels *et al.* 2000).

Differences in prey availability may also contribute for the better body condition of shrews captured on roadsides. The high nitrogen content of roadside vegetation along a busy motorway in the United Kingdom was believed to be responsible for the rate of increase and the outbreaks of insect populations on road sites (Forman *et al.* 2003). This possible higher abundance of insects (Bennet 2003) on road verges translates in more food availability for the insectivorous *C. russula*. Nonetheless, riparian vegetation strips are also expected to have higher densities of insects and other invertebrates (O'Connell *et al.* 1993) than the landscape matrix. Further studies are necessary to clarify the differences in small mammal body conditions between both habitats.

The results found for body size and condition in *Mus spretus* may show the influence of other biological and ecological mechanisms: Algerian mice were bigger on streams, but showed no differences in body condition between the two habitats (roads and streams), despite of being more abundant on roads. This probably reflects a higher survival of young small sized individuals in the absence of predators. Norrdahl *et al.* (2004) found that predator reduction had a clear positive effect on the abundance of *Microtus rossiaemeridionalis*, as well as a decrease on the mean body size and age ratio. They concluded that the strong positive response in vole abundances to predator reduction was due to a higher survival of young individuals. In our study, the higher abundance of Algerian Mice and the lower mean body size on roads are consistent with this conclusion. Further, Jędrzejewska and Jędrzejewski (1990), in a seminatural enclosure, found that adult bank voles were less vulnerable than young ones to weasel predation, which reflects the development of escape abilities as voles' age. Sub-adults of common voles (*Microtus arvalis*) and wood mice were also preferentially captured by diurnal avian predators, which is caused by their higher exposure to predators as a consequence of their lack of established territories and erratic movements (Halle 1988).

On the other hand, Bowers and Dooley (1993) refer that density is probably a poor indicator of patch quality, for *Microtus pennsylvanicus* and *Peromyscus leucopus*. Their analysis of population–level attributes show that larger patches of unmowed vegetation have individuals with longer patch residence times than smaller patches, and a size/age make-up that is biased towards adults rather than juveniles. Anderson (1989 *in* Bowers and Dooley 1993) predicted that habitat patches of high quality may be occupied by dominant, territorial individuals that maintain relatively stable, but low density populations (Fretwell and Lucas 1970). By contrast, nonterritorial subdominants may actually occur at higher densities in lower quality habitats (van Horne 1983, Morris 1991, Bowers and Dooley 1993). If this is the case, our results may indicate that, for *Mus spretus*, streams are a higher quality habitat than roads. However, other studies illustrate that small mammals show relaxed territoriality and a decrease in agonistic behaviours as food conditions improve (Montgomery and Dowie 1993, Collins and Barret 1997, Corp *et al.* 1997, Díaz *et al.* 1999, Torre *et al.* 2002), thus diminishing their home ranges and increasing their densities.

The similarities in sex ratios and recapture rates, in road verges and riparian strips, suggest that none of these habitats are preferentially used as dispersal corridors. A lower rate of recaptured animals on roads could reflect a greater number of transient individuals using roads to move to new territories, has as been verified for Stephens' kangaroo rat (*Dipodomys stephensi*) in California (Brock and Kelt 2004).

In conclusion, it is difficult to establish a common pattern for referring to habitat suitability for each of the three species of small mammals studied when comparing road verges and riparian galleries. In fact, several complementary and contrasting effects of the biological and ecological processes are in place and their relative importance must be the aim of further and more specific studies. The higher abundance of Algerian mice on road verges, and the more favourable microhabitat characteristics occurring therein, suggests that roadsides may be a better quality habitat for this species, but the lower body size of the individuals inhabiting roads suggests otherwise. The white-toothed shrew is equally abundant on roads and streams, but the higher body condition presented by animals on roads may indicate that roadside verges are a better habitat for this species.

4.3. *Linear habitats as barriers to movement of small mammals*

Our trapping results suggest that the apparent barrier effect to small mammals' movements of the studied roads is as strong as the barrier effect observed in small streams. This is a surprising result because at the time of sampling, our two streams were dry at almost their entire extension, so the barrier due to the presence of water doesn't occur, and we expected a higher degree of crossings of small mammals through the riparian galleries than across the roads.

Some studies have demonstrated that roads may act as barriers to small mammal movements. It seems that small mammals mainly avoid the road surface itself, rather than noise or traffic intensity (Rico *et al.* 2007, McGregor *et al.* 2008). Roads are effectively partial barriers or filter barriers that block some but not all movements across them (Oxley *et al.* 1974, Swihart and Slade 1984, Rondinini and Doncaster 2002, Forman *et al.* 2003, McGregor *et al.* 2008). However, this partial road barrier effect may result in genetic differences. Gerlach and Musolf (2000) found a significant genetic subdivision of bank vole (*Clethorionomys glareolus*) populations separated by a highway, but not within populations separated by a country road or railway. Nevertheless, the role of roads as barriers has seldom been compared to that of natural barriers. In a translocation study, McDonald and St. Clair (2004) compared the animal movement of three species of murid rodents across a highway and different natural barriers, and found that individuals were 20% less successful crossing the highway than natural (forested) barriers and 10% less successful crossing natural barriers than continuous habitat, but exhibited marked variation among species.

In conclusion, the low number of crossings of small mammals through the sampled narrow roads and small streams suggests that both may show barrier effect two small mammal movements, contributing to a segregation of subpopulations on each side of these linear structures. However only further studies, including population genetics analyses, may prove this predict population structure caused by these landscape linear features.

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Appendix

Table A. Spearman rank correlation coefficients of the explanatory variables. Numbers in bold show the high correlation (r>0.7) between variables.

	Habitat	Line	Grass.height	Grass.cover	Shrubs.height	Shrubs.cover	Trees.height	Trees.cover	Bare.cover	Leaf.cover
Line	0.00									
Grass.height	0.40	-0.39								
Grass.cover	0.37	0.11	0.54							
Shrubs.height	-0.50	-0.40	-0.15	-0.47						
Shrubs.cover	-0.50	-0.39	-0.12	-0.48	**0.89**					
Trees.height	-0.46	-0.40	-0.30	-0.50	0.53	0.50				
Trees.cover	-0.47	-0.40	-0.36	-0.50	0.53	0.50	**0.93**			
Bare.cover	0.03	-0.00	-0.39	-0.48	-0.08	-0.09	-0.12	-0.13		
Leaf.cover	-0.51	-0.36	-0.36	-0.59	0.49	0.46	**0.82**	**0.83**	-0.12	
Rocks.cover	-0.09	0.26	-0.09	-0.23	0.08	0.08	0.13	0.12	0.10	0.12