


Road effects on demographic traits of small mammal populations

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Abstract Recent studies have highlighted the positive effects of road verges on the abundance of small mammals. However, most of these studies occurred in intensively grazed or cultivated areas, where verges were the last remnants of suitable habitats, which could mask the true effects of roads on population traits. We analysed the effects of roads on small mammal populations living in a well-preserved Mediterranean forest. We used the wood mouse (*Apodemus sylvaticus*) as a model of forest-dwelling small mammals that probably are among the species most affected by road clearings. Our study compared populations in similar habitat areas with and without road influence. We assessed abundance, survival and temporary emigration using extended Pollock's robust design capture-recapture models. Moreover, we analysed population turnover, sex ratio, age structure and body condition. We found that wood mouse abundance and body condition were lower at the road bisected area, whereas the remaining population traits were similar. This suggests that the reduced habitat availability and quality due to the physical presence of the road and verge vegetation clearing are the main drivers of

demographic differences in wood mouse populations between areas. Nevertheless, our results also suggest that in high-quality habitats surrounding national roads, wood mouse populations present similar dynamics to others living in undisturbed areas, despite the decrease in abundance and body condition. Overall, the often-reported increased small mammal abundance in road surroundings should not be generalized independently of habitat quality or to other population traits.

Keywords *Apodemus sylvaticus* · Capture-recapture · Extended robust design models · Population estimation · Roadless area · Road effects

Introduction

Roads are essential to modern human societies. These infrastructures exist throughout most landscapes, and their extension, complexity and use are set to rise around the world due to growing economic and social demands (Forman et al.

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2003). Numerous studies have addressed the impacts of roads on wildlife and pointed out their deleterious effects on many species (Forman et al. 2003; Fahrig and Rytwinski 2009; Benítez-López et al. 2010).

Documented negative road effects common to several small mammal species or communities include road kills (Carvalho and Mira 2011), enhanced metal concentrations in tissues and negative consequences on stress indices (Marcheselli et al. 2010), barriers or filters to movement (Macpherson et al. 2011), home range rearrangements (McGregor et al. 2008) and changes in community structure (species richness and diversity) (Goosem 2000). Nevertheless, several studies have highlighted positive or neutral effects of roads on small mammal abundance (e.g. Fahrig and Rytwinski 2009; Ascensão et al. 2012; Bissonette and Rosa 2009). This is because most species have small home ranges, high reproductive rates and abundance and avoid crossing roads regardless of traffic volume (Fahrig and Rytwinski 2009). Therefore, small mammals may use road verges as habitats and dispersal routes (Bennett 1990; Bellamy et al. 2000), undergoing only low levels of road kills (Ruiz-Capillas et al. 2015).

In non-natural habitats, such as intensively grazed or cultivated areas, roads seem either to enhance abundance (Sabino-Marques and Mira 2011) or to level population outbreaks (Redon et al. 2010), whereas in less modified landscapes, the abundance of some species is lower near roads (Goosem 2000). Therefore, the effects of roads on small mammal populations may depend on the quality of the surrounding habitats.

However, the effects of roads on small mammal populations are still poorly understood in well-preserved habitats. Most studies on small mammals rely on relative abundance to infer habitat suitability and population responses to roads (Fahrig and Rytwinski 2009). Nonetheless, abundance is insufficient to truly reveal the effects of roads on wildlife populations (van Horne 1983). Moreover, the most common measures of abundance (number of individuals per sampling effort and minimum number known alive) tend to be negatively biased because they ignore detection probabilities (Efford 1992).

Our main goal was to assess the effects of roads on the demography of small mammals in a well-preserved habitat. We used the wood mouse (*Apodemus sylvaticus*) as a model of forest-dwelling small mammal species (Ascensão et al. 2016). Gaps in vegetation cover due to the presence and maintenance of roads would affect mostly forest-dwelling species (Ascensão et al. 2016). The wood mouse is common on road verges and surrounding woodland areas and is a key prey of many mammalian carnivores and birds of prey (Sarmiento 1996; Pezzo and Morimando 1995). We hypothesize that roads decrease the quality of a well-preserved habitat and will therefore negatively affect wood mouse populations, as suggested for other species (D'Amico et al. 2016; Torres et al.

2016). Previous studies have shown that the wood mouse is one of the most road-killed small mammals in Portugal (Carvalho and Mira 2011); hence, we expect lower abundance and survival near roads. Also, as paved lanes hinder movement (Ford and Fahrig 2008) and force individuals to disperse through verges (Bennett 1990), we predict higher population turnover near roads. Moreover, poorer body condition due to traffic-induced stress may occur, as suggested by other studies (Ware et al. 2015). We compared two populations living on a well-preserved Mediterranean woodland region, one of which was bisected by a medium-traffic-intensity national road. We used capture-mark-recapture data to assess several population traits besides abundance, such as survival, recruitment and turnover. The lack of studies such as ours that account for imperfect detection is likely due to the amount of effort needed to collect enough data to estimate these parameters. Our work allows us to isolate the pure effect of roads on several population parameters rather than to assess their combined effect with that of habitat disturbance.

Methods

Study area

Our study was conducted in Alentejo, southern Portugal. The climate is Mediterranean with hot, dry summers and mild winters. During the study period, the monthly mean temperature was 17.6 °C (ranging from 11.0 °C in April to 22.8 °C in August) and the monthly mean precipitation was 16.3 mm (ranging from 0.4 mm in August to 42.4 mm in October) (CGE 2011).

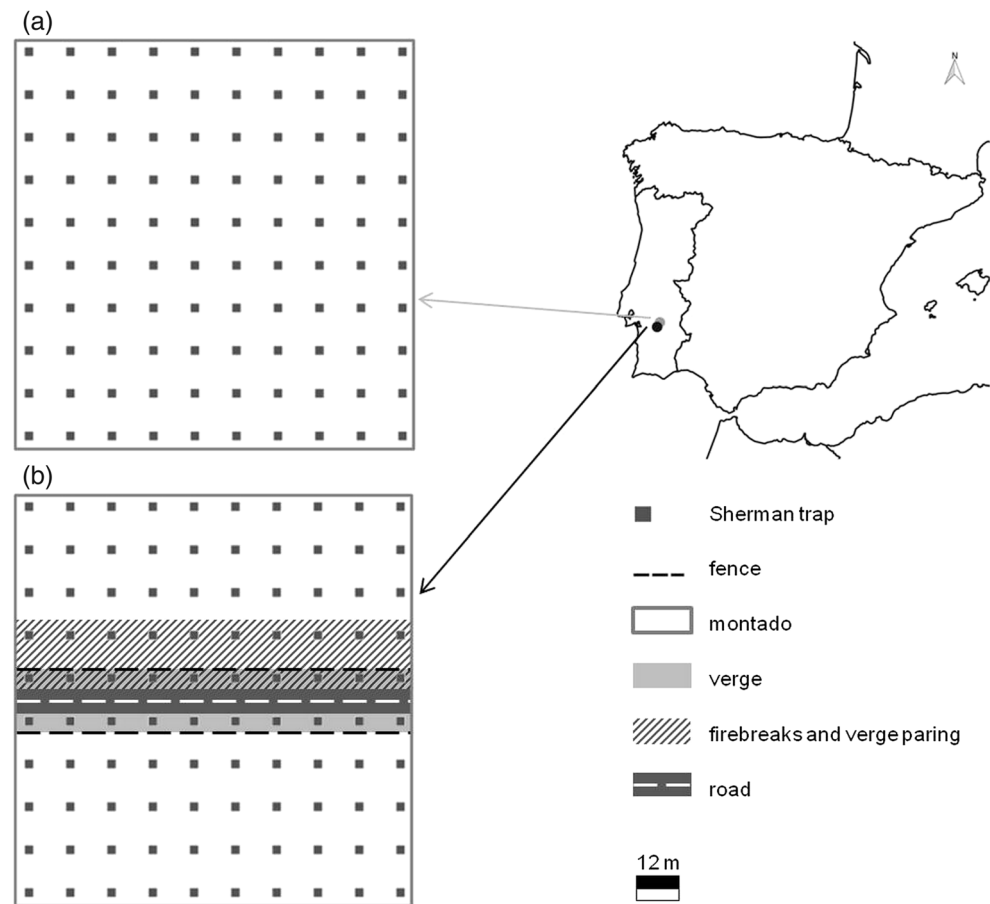
The landscape is dominated by *montado*, a traditional Mediterranean savannah-like forest of stands of cork (*Quercus suber*) and holm (*Quercus rotundifolia*) oaks trees with herbaceous and shrub strata (Pinto-Correia and Mascarenhas 1999). Several national roads cross the region, and firebreaks (~15 m wide) are opened along both verges every year to decrease the fire risk associated with traffic.

Study design

We carefully selected trapping sites, accounting simultaneously for high similarity between areas and optimal habitat for the species.

The study was conducted on two plots of 1.2 ha each, 16 km apart (Fig. 1). The roadless area (38° 31' N, 8° 01' W) was more than 1 km away from any national paved road at the University of Évora field station. The road area (38° 24' N, 8° 06' W) was bisected by the national road EN257, a two-lane paved road with an average traffic volume of approximately 5000 vehicles per day (~600 vehicles per night) (EP 2005).

Fig. 1 Schematic location of Sherman traps on the roadless (a) and road (b) areas. Diagonal lines show the grid section affected by verge paring and firebreaks during 2009



The areas were very similar in vegetation structure and composition, soil type, slope and, a priori, also in predator pressure. The main difference between areas was the presence/absence of road verges and paved lanes. The study sites were sampled simultaneously every 4 weeks from March to October 2009 (eight trapping sessions) using a square grid of 10×10 traps spaced at 12-m intervals. This period includes the most relevant events in the wood mouse annual cycle in the Mediterranean region: the peak of reproduction (March and April); the harsh dry season when reproduction almost ceases (June and July); and the resumption of reproduction after the first autumn rains (September and October) (Rosário and Mathias 2004).

Data collection

Wood mice were live trapped at each site and trapping session with Sherman medium-sized live traps ($8 \times 9 \times 23$ cm). Traps remained opened on the field for four consecutive nights and were checked every day at sunrise, summing 6400 trap-nights (3200 trap-nights per area). One trap was placed on every node of each square grid (Fig. 1). At the road area, the two central trap lines were placed at each road verge. Road verges

were flanked by wired fences (~ 10 m from the asphalt) permeable to both small mammals and their predators. A mixture of sardines, oil and oat flakes was used as bait and hydrophobic cotton was provided for nesting.

Trapped individuals were sexed, aged, measured, weighted to the nearest 0.5 g (micro-line spring scale Pesola AG, Baar, Switzerland) and released at the place of capture. Males with scrotal testes and females with either perforated vagina, vaginal plug, visible or enlarged nipples or those that were pregnant were considered reproductively active (Gurnell and Flowerdew 2006).

Each individual was assigned to an age class based on its weight, body length and breeding condition using measurement references for the Iberian Peninsula (Jubete 2002). Upon first capture, animals were individually marked with passive integrated transponders tags (PIT, TXP148511B, $8.5 \text{ mm} \times 2.12 \text{ mm}$, 134.2 kHz ISO, 0.067 g, Biomark, Boise, USA).

At every field session, we collected information on vegetation traits in a 1-m square around each trap to control for changes across time and similarities between areas. We assessed cover (%) and height (cm) for herbaceous and shrub strata and also cover (%) for bare ground, litter, rocks and tree

strata. We categorized measurements in 25% classes for cover and in 10-cm classes for height of herbaceous and shrub strata (Ascensão et al. 2012).

Data analysis

Capture-recapture data were analysed using extended Pollock's robust design models (Kendall et al. 1997). The eight trapping sessions (months) were defined as primary periods, and the four consecutive trapping nights as the secondary periods within each primary period, totalling 32 trapping occasions. Among primary periods, the population is considered open, allowing for immigration, emigration, births and deaths, and among secondary periods, the population is considered closed to gains and losses (Kendall et al. 1997). Extended Pollock's robust design models estimate abundance (N) and capture probabilities (p) within primary periods and survival probability (ϕ), temporary emigration (Y'') and temporary immigration ($1-Y'$) among primary periods (Kendall et al. 1995; Kendall et al. 1997). All parameters are estimated jointly using a full likelihood approach (Kendall et al. 1995; Kendall et al. 1997). This approach allows for parameter estimation considering them constant or time varying (Kendall et al. 1995).

Analyses were performed using closed captures parameterization for robust design models in the program MARK (White and Burnham 1999). Several candidate models were proposed to find evidence of time variation in each of the population parameters and to test for temporary emigration at each study site. We estimated population parameters with the corresponding 95% confidence intervals. Estimates with coefficients of variation greater than 50% and/or confidence intervals including zero were considered unacceptable for further analysis (Brandstätter 1999; White et al. 1982). In the capture-recapture context, coefficients of variation should be less than 20% for reliable scientific studies and up to 50% for management or monitoring studies (White et al. 1982). Parameter estimates were obtained assuming in both areas even flow movement (the probability of leaving the area and re-entering is the same: $Y'' = 1 - Y'$) and this type of movement was tested against the no movement model ($Y'' = 0$; $Y' = 1$) (Sanders and Trost 2013). Even flow models were plausible because habitat type was similar across and outside of the trapping grids. Analyses were conducted for each area separately to account for the possibility of different parameter estimates and movement models. Dead individuals were excluded from the analysis (Pollock et al. 1990).

Population turnover was accounted for in each area and primary period as the ratio of the sum of recruits and losses to the number of residents (Bertolino et al. 2001). Body condition was evaluated by the scaled mass index (SMI) to

account for the scaling relationship between body mass and a linear body measurement as growth occurs (Peig and Green 2010). For comparison purposes, we only used male body condition to exclude the effect of pregnancies on scaling (Díaz and Alonso 2003). Age structure (juveniles and adults), sex ratio (males/females), turnover, residents, losses and recruits were compared between the two areas using the Wilcoxon rank-sum test (W) with continuity correction (Sokal and Rohlf 1997). The overall sex ratio was tested for deviations from the balanced sex ratio (1:1) in each area with a chi-square test (Sokal and Rohlf 1997).

SMI was estimated using the package `lmodel2` (Legendre 2011) for R software, version 2.13.0 (R Core Team 2011). The effect of roads on body condition was modelled with linear mixed-effects models (`nlme` package; Pinheiro et al. 2015) considering area (roadless/road) as the fixed effect and individual identity (PIT tag) as the random effect. Also, in the road area, we analysed the effect of microhabitat (eight variables mentioned above), row (to account simultaneously for distance to the road and firebreaks) and session with linear mixed models, considering individual identity as the random effect. We log transformed body condition to approach normality. Temporal patterns in body condition were checked using the autocorrelation function (`nlme` package; Pinheiro et al. 2015). The Akaike's Information Criterion was used for selection of robust design models (corrected for small sample sizes, AICc) and linear mixed-effects models (AIC; Burnham and Anderson 2002). We considered models within two AIC units of the best model to have substantial support, except those with non-informative parameters (Burnham and Anderson 2002; Arnold 2010). Effect sizes were considered as the magnitude of the differences found between areas and were significant if their confidence intervals did not overlap zero (Cooch and White 2013).

Estimates for all parameters (except age structure and sex ratio) are presented with their corresponding 95% confidence intervals. We report the dominant classes (mode) for each microhabitat variable.

Results

Abundance, capture probability, survival and temporary emigration

We recorded 494 captures of 119 different wood mice (66 in the roadless area and 53 in the road area) in 6400 trap-nights. Trap mortality was extremely low; we found only three dead individuals (one in the road area and two in the roadless area) and excluded them from the data set.

From the 24 robust design candidate models fitted (Online Resource), only four had reliable estimates for all parameters for each study area (Tables 1, 2 and 3). All models with

Table 1 Extended Pollock’s robust design model selection for the road and roadless areas

Area	Model	AICc	ΔAICc	w_i	No. Par.	Deviance
Road	Even flow; all parameters constant $\phi(\cdot); Y''(\cdot) = 1 - Y'(\cdot); p(\cdot); N(\cdot)$	393.58	0.00	0.77	4	446.98
	No movement; all parameters constant $\phi(\cdot); Y'' = 0 Y' = 1; p(\cdot); N(\cdot)$	396.57	2.99	0.17	3	452.04
	Even flow; time-varying abundance $\phi(\cdot); Y''(\cdot) = 1 - Y'(\cdot); p(\cdot); N(t)$	399.82	6.24	0.03	10	440.31
	No movement; time-varying abundance $\phi(\cdot); Y'' = 0 Y' = 1; p(\cdot); N(t)$	401.14	7.56	0.02	9	443.83
Roadless	Even flow; all parameters constant $\phi(\cdot); Y''(\cdot) = 1 - Y'(\cdot); p(\cdot); N(\cdot)$	412.45	0.00	0.58	4	610.68
	Even flow; time-varying abundance $\phi(\cdot); Y''(\cdot) = 1 - Y'(\cdot); p(\cdot); N(t)$	413.34	0.89	0.37	9	601.05
	No movement; time-varying abundance $\phi(\cdot); Y'' = 0 Y' = 1; p(\cdot); N(t)$	418.58	6.13	0.03	8	608.42
	No movement; all parameters constant $\phi(\cdot); Y'' = 0 Y' = 1; p(\cdot); N(\cdot)$	419.92	7.46	0.01	3	620.20

Notation: survival (ϕ), temporary emigration (Y''), temporary immigration ($1 - Y'$), recapture rate (p), type of movement (even flow $Y'' = 1 - Y'$ and no movement $Y'' = 0, Y' = 1$), abundance (N), constant parameter (\cdot), time-dependent parameter (t), difference in AIC value ($\Delta AICc$), Akaike weights (w_i), number of parameters (No. Par.)

parameters varying among sessions resulted in estimates with poor precision (coefficient of variation >50% or confidence intervals including zero), except for time-varying abundance models.

Thus, the four models considered for further analysis comprised even flow movement and no movement models, both applied with either all parameters held constant or with time-varying abundance. In the roadless area, the second best model adds time-varying abundance and has delta AIC of 0.88. Since the change in deviance was not enough to compensate for the increase in parameters, we considered time-varying abundance as uninformative and inferred only from the top model. The best plausible models emphasized the presence of temporary emigration in both areas. The more parsimonious models assume the same probability for individuals temporarily leaving and re-entering the area (even flow movement), and all parameters constant along the eight primary sessions. In each area, the top model had coefficients of variation below 10% for all estimates except for temporary emigration, which was, nevertheless, below 31% (Tables 2 and 3). Probabilities of capture were 0.43 (95%CI, 0.38–0.48) in the road area and 0.46 (95%CI, 0.41–0.50) for the roadless area. Temporary emigration was 0.24 (95%CI, 0.13–0.42) in the road area and 0.21 (95%CI, 0.11–0.36) for the roadless area. Probability of survival was 0.69 in both areas (95%CI, 0.59–0.78 for the road area; 95%CI, 0.60–0.77 for the roadless area). Abundance estimates were significantly lower in the road

area (20.79; 95%CI, 20.23–22.67) than in the roadless area (32.69; 95%CI, 32.19–34.45) (effect size = 11.9; 95%CI, 10.46–13.34). More specifically, estimates of abundance were significantly lower in the road area from March to July (Fig. 2).

Turnover, age structure, sex ratio and body condition

Population turnover and proportion of residents were slightly higher at the roadless area (1.59; 95%CI, 0.65–2.53 and 0.46; 95%CI, 0.32–0.60, respectively) than at the road area (1.20; 95%CI, 0.59–1.81 and 0.42; 95%CI, 0.24–0.60, respectively). The reverse situation occurred for the proportion of recruits (0.12; 95%CI, 0.02–0.22 at the roadless area; 0.17; 95%CI, 0.05–0.29 at the road). However, none of these differences were statistically significant (Table 4). In both areas, on average, the joint number of losses and recruits outweighed the number of residents (turnover >1).

The number of juveniles was low at both sites: three juveniles out of 20 individuals in March in the road area, two juveniles out of 32 in March and one out of 40 in April in the roadless area.

The sex ratio was similar between areas along the eight sessions ($W = 31.5; p = 0.7$) and the global values were not significantly different from the balanced sex ratio: 34 (52%) females and 32 (48%) males in the roadless area ($\chi^2 = 0.0606, df = 1, p = 0.81$); 29 (57%) females and 22 (43%) males in the road area ($\chi^2 = 0.9608, df = 1, p = 0.33$).

Table 2 Extended Pollock's robust design model results for the road area

Model	Par	Est	SE	LCI	UCI	cv
Even flow; all constant $\phi(\cdot); Y''(\cdot) = 1 - Y'(\cdot); p(\cdot); N(\cdot)$	ϕ	0.694	0.048	0.594	0.779	0.069
	Y''	0.244	0.075	0.127	0.417	0.307
	Y'	0.756	0.075	0.583	0.873	0.099
	p	0.430	0.027	0.377	0.484	0.064
	N	20.786	0.542	20.232	22.670	0.026
No movement; all constant $\phi(\cdot); Y'' = 0; Y' = 1; p(\cdot); N(\cdot)$		0.607	0.044	0.518	0.689	0.073
	p	0.400	0.024	0.354	0.449	0.061
	N	21.156	0.612	20.436	23.065	0.029
Even flow; time-varying abundance $\phi(\cdot); Y''(\cdot) = 1 - Y'(\cdot); p(\cdot); N(t)$	ϕ	0.694	0.048	0.592	0.780	0.070
	Y''	0.225	0.080	0.106	0.417	0.355
	Y'	0.775	0.080	0.583	0.894	0.103
	p	0.409	0.028	0.355	0.466	0.070
	N	22.256	1.883	20.542	29.384	0.085
	N	31.369	2.272	29.015	39.185	0.072
	N	24.534	1.985	22.653	31.830	0.081
	N	19.976	1.779	18.437	26.943	0.089
	N	15.417	1.555	14.248	22.093	0.101
	N	8.569	1.167	8.046	15.050	0.136
	N	5.134	0.929	5.003	11.406	0.181
	N	1.000	1.98E-04	1.000	1.000	0.000
	No movement; time-varying abundance $\phi(\cdot); Y'' = 0; Y' = 1; p(\cdot); N(t)$	ϕ	0.610	0.044	0.521	0.692
p		0.383	0.025	0.336	0.432	0.065
N		22.880	2.096	20.802	30.336	0.092
N		32.241	2.523	29.442	40.476	0.078
N		25.220	2.208	22.954	32.871	0.088
N		20.539	1.980	18.658	27.804	0.096
N		15.856	1.732	14.393	22.757	0.109
N		8.824	1.299	8.092	15.363	0.147
N	5.298	1.031	5.013	11.873	0.195	
N	1.000	1.85E-04	1.000	1.000	0.000	

Notation: parameter (Par), estimates (Est), standard errors (SE), confidence intervals (LCI, lower limit and UCI, upper limit), coefficient of variation (cv), survival (ϕ), temporary emigration (Y''), temporary immigration ($1 - Y'$), recapture rate (p), type of movement (even flow $Y'' = 1 - Y'$ and no movement $Y'' = 0, Y' = 1$), abundance (N), constant parameter (\cdot), time-dependent parameter (t). No movement models imply fixed temporary movements and hence variation coefficients are not computed

Body condition was significantly lower in the road area (22.44 g; 95%CI, 21.63–23.25) than in the roadless area (24.16 g; 95%CI, 23.44–24.87) ($p = 0.0019$) (effect size = 1.72; 95%CI, 0.64–2.80). In the road area, we did not find a considerable effect of row or cover of shrubs and trees on body condition (Table 5). Models including each of these three variables were within 2 AIC units from the top model, but did not improve the likelihood considerably. According to the top model, body condition was lower from April to August than in March and decreased with litter cover above 50% and herbaceous and shrub height from 10 to 20 cm. Also, body condition increased with herbaceous cover from 20 to 50% and herbaceous and shrub height above 20 cm (Table 6).

Microhabitat structure

Both areas presented the same dominant classes for cover and height for all of the variables measured. The most frequent cover classes were 0–25% for herbaceous, trees, rocks and bare ground; 25–75% for shrubs; and 75–100% for litter. Herbaceous and shrub height were below 20 and 60 cm in more than 70 and 75% of traps (out of a total of 100 traps per area), respectively.

During our study, firebreaks were only opened on one side of the road (May 2009). The grid lines affected by the firebreaks (20 traps; Fig. 1) had lower shrub cover and higher herbaceous strata than the corresponding lines of the roadless area, where no firebreaks occurred. Also, the dominant class

Table 3 Extended Pollock’s robust design model results for the roadless area

Model	Par	Est	SE	LCI	UCI	cv
Even flow; all constant $\phi(\cdot); Y''(\cdot) = 1 - Y'(\cdot); p(\cdot); N(\cdot)$	ϕ	0.691	0.042	0.603	0.768	0.061
	Y''	0.211	0.063	0.114	0.358	0.296
	Y'	0.789	0.063	0.642	0.886	0.079
	p	0.456	0.023	0.411	0.502	0.051
	N	32.685	0.497	32.192	34.450	0.015
Even flow; time-varying abundance $\phi(\cdot); Y''(\cdot) = 1 - Y'(\cdot); p(\cdot); N(t)$	ϕ	0.691	0.043	0.601	0.768	0.062
	Y''	0.195	0.065	0.097	0.351	0.332
	Y'	0.805	0.065	0.649	0.903	0.080
	p	0.434	0.024	0.387	0.481	0.055
	N	35.161	2.143	32.947	42.552	0.061
	N	44.082	2.426	41.389	51.997	0.055
	N	27.354	1.874	25.596	34.295	0.069
	N	24.008	1.751	22.460	30.766	0.073
	N	20.660	1.620	19.334	27.249	0.078
	N	6.131	0.913	6.003	12.296	0.149
	N	4.000	0.001	4.000	4.001	0.000
	N	1.000	0.000	1.000	1.000	0.000
	no movement; time-varying abundance $\phi(\cdot); Y'' = 0 Y' = 1; p(\cdot); N(t)$	ϕ	0.613	0.039	0.535	0.685
p		0.409	0.022	0.367	0.452	0.053
N		35.941	2.374	33.324	43.729	0.066
N		45.056	2.686	41.903	53.433	0.060
N		27.964	2.077	25.859	35.231	0.074
N		24.545	1.940	22.675	31.592	0.079
N		21.126	1.796	19.504	27.959	0.085
N		6.284	1.007	6.012	12.732	0.160
N		4.000	0.000	4.000	4.000	0.000
N		1.000	0.000	1.000	1.000	0.000
No movement; all constant $\phi(\cdot); Y'' = 0 Y' = 1; p(\cdot); N(\cdot)$	ϕ	0.610	0.039	0.533	0.683	0.063
	p	0.429	0.021	0.388	0.470	0.049
	N	33.011	0.561	32.366	34.789	0.017

Notation: parameter (Par), estimates (Est), standard errors (SE), confidence intervals (LCI, lower limit and UCI, upper limit), coefficient of variation (cv), survival (ϕ), temporary emigration (Y''), temporary immigration ($1 - Y'$), recapture rate (p), type of movement (even flow $Y'' = 1 - Y'$ and no movement $Y'' = 0, Y' = 1$), abundance (N), constant parameter (\cdot), time-dependent parameter (t). No movement models imply fixed temporary movements and hence variation coefficients are not computed

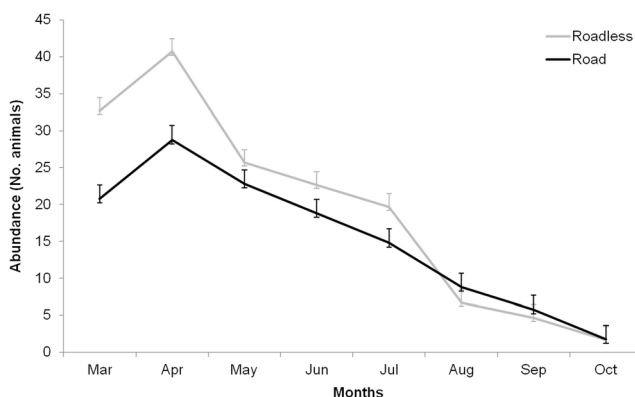


Fig. 2 Abundance estimated by extended Pollock’s robust design models at the road and roadless areas. Bars represent 95% confidence intervals

cover for the herbaceous strata was 0–25% before the fire-breaks and 25–50% afterwards, whereas in the roadless area, herbaceous strata remained in the lowest class (0–25%).

Discussion

We found that a wood mouse population living in an area surrounding a road has similar demographic parameters to another in a roadless area within a comparable habitat. Nevertheless, the road population has a lower abundance and males present on average a lower body condition. Both areas have similar habitat structure, except for the presence/absence of the road; therefore, we believe that this

Table 4 Population turnover and percentages of recruits, losses and residents for the road and roadless areas (means and 95%CI)

	Road	Roadless	Wilcoxon test
Turnover	1.20 (0.59, 1.81)	1.59 (0.65, 2.53)	$W = 21; p = 0.5286$
Recruits (%)	0.17 (0.05, 0.29)	0.12 (0.02, 0.22)	$W = 30.5; p = 0.2404$
Losses (%)	0.41 (0.25, 0.57)	0.42 (0.26, 0.58)	$W = 27.5; p = 0.3744$
Residents (%)	0.42 (0.24, 0.60)	0.46 (0.32, 0.60)	$W = 21; p = 0.3504$

Differences between areas were assessed with the Wilcoxon rank sum test statistics (W) and associated significance level (p)

infrastructure was the main factor responsible for our findings. These results show that the previously documented positive effects of roads on the abundance of small mammals (Fahrig and Rytwinski 2009; Ascensão et al. 2012) do not hold true under all circumstances. Thus, the effects of roads seem to depend on the quality of the surrounding habitat, or more precisely, on the quality of road verges within each habitat.

Road vicinity effects on small mammal population traits

In similar well-preserved habitats, the road area supported, on average, one third less individuals than the roadless area. Previous positive or neutral effects of roads on the abundance of small mammals highlight verges as refuges in poorer-quality habitat matrices, either intrinsically or due to grazing pressure or agricultural intensification (Fahrig and Rytwinski 2009; Ascensão et al. 2012; Ruiz-Capillas et al. 2013). Lower abundance was reported near roads only in a few circumstances and for species prone to using undisturbed habitats (Goosem 2000; Barrows et al. 2006). The significantly lower abundance at the road area was no longer evident at the end of summer and beginning of autumn when both populations reached their lowest abundances, as previously reported for the Mediterranean dry season (Rosário and Mathias 2004). Therefore, the road area can maintain the same minimal abundance but is unable to sustain the maximum numbers reached in the roadless area during favourable seasons. Essentially, this may reflect the lower habitat availability at the roadside. The road pavement itself reduces the available habitat by approximately 11% (1/9 inter-row distance). Moreover, at least

once a year, nearly one fifth (2/9 inter-row distance) of the sampled road area loses most of its shrub cover due to vegetation clearing on verges and firebreaks reopening along the road. These interventions are enforced by law to prevent fires (Decree-Law 156/2004, 30th June of the Portuguese Ministry of Agriculture, Rural Development and Fisheries) and are applied on verges of every national road in Portugal. Similarly, verges are managed in other countries with documented effects on animal communities (e.g. Meunier et al. 1999). Together, road and vegetation clearing reduce the area of available suitable habitat by approximately one third. Vegetation clearing occurred on only one occasion, but a lower shrub cover and a higher herbaceous cover at those cleared grid lines remained throughout the entire study period. Moreover, although at the occasion of firebreak opening, the global proportion of individuals lost was similar in both study areas (30%), 55% of the losses in the road area corresponded to individuals previously trapped at the lines directly affected by clearing (unpublished data). Lower vegetation cover and height reduce resource availability (shelter and food) and the carrying capacity of the area. Furthermore, vegetation clearing occurs just before the beginning of summer, which is the most critical period, with shortages of food and water, in Mediterranean environments (Rosário and Mathias 2004). The decrease in resource availability could also explain the poorer body condition in the road area during this season. In fact, body condition increased with taller vegetation and decreased from April to August. Distance from the road (row) may not affect body condition, because wood mice may use more than one row per session. The consistent lower values

Table 5 Selection of models explaining male body condition at the road area (98 observations of 22 males)

	(Intercept)	Cover				Height		Session	Row	df	logLik	AIC	Δ AIC	w_i
		Litter	Herbaceous	Shrub	Tree	Shrub	Herbaceous							
Model 1	3.40	+	+			+	+			28	108.71	-161.40	0.00	0.29
Model 2	3.51	+	+			+	+		+	37	117.55	-161.10	0.31	0.25
Model 3	3.37	+	+	+		+	+			31	111.51	-161.00	0.40	0.24
Model 4	3.36	+	+		+	+	+			31	111.44	-160.90	0.55	0.22

Notation: Akaike weights (w_i), difference in AIC value (Δ AIC), log-likelihood (logLik), degrees of freedom (df), variables accounted by each model (+). We only show models within 2 AIC units from the top model (Δ AIC < 2)

Table 6 Estimates, standard errors (SE) and 95% confidence intervals (LCI, lower limit and UCI, upper limit) for variables in the selected top model explaining male body condition at the road area (98 observations of 22 males)

	Estimate	SE	LCI	UCI
(Intercept)	3.394	0.056	3.281	3.507
Session				
April	-0.229	0.049	-0.327	-0.130
May	-0.226	0.052	-0.330	-0.122
June	-0.257	0.053	-0.362	-0.151
July	-0.278	0.054	-0.387	-0.170
August	-0.421	0.084	-0.589	-0.252
September	-0.110	0.066	-0.243	0.024
October	-0.074	0.172	-0.432	0.284
Litter cover (%)				
]25–50]	-0.052	0.055	-0.162	0.057
]50–75]	-0.128	0.045	-0.219	-0.036
]75–100]	-0.167	0.031	-0.230	-0.105
Herbaceous cover (%)				
]25–50]	0.138	0.031	0.076	0.201
]50–75]	0.008	0.041	-0.074	0.090
]75–100]	-0.047	0.048	-0.144	0.050
Herbaceous height (cm)				
]10–20]	-0.082	0.039	-0.160	-0.005
]20–30]	0.108	0.043	0.021	0.195
]30–40]	0.003	0.051	-0.099	0.105
]40–50]	0.158	0.061	0.035	0.280
]50–60]	-0.069	0.089	-0.248	0.110
]90–100]	0.256	0.096	0.063	0.450
Shrub height (cm)				
]10–20]	-0.078	0.034	-0.146	-0.010
]20–30]	0.192	0.043	0.106	0.278
]30–40]	0.042	0.039	-0.036	0.120
]40–50]	0.054	0.056	-0.058	0.166
]50–60]	-0.042	0.065	-0.173	0.088
]100–110]	0.337	0.094	0.148	0.526

Confidence intervals excluding zero are in italic

for body condition near the road, besides reflecting scarcity of resources (Alcántara and Díaz 1996), may also reveal physiological stress (Tête et al. 2013) induced by traffic (Ware et al. 2015). Other studies found that traffic tended to modify several physiological stress indices (cadmium and plumb kidney/liver ratios and kidney/body weight ratios; Marcheselli et al. 2010) and increase levels of stress hormones (faecal corticosterone metabolites; Navarro-Castilla et al. 2014) in the wood mouse. Additionally, the foraging efficiency of animals may decrease in periods of higher traffic volume (Lowry et al. 2013). Usually, males and females have similar body condition patterns (Rosário and Mathias 2004); thus, a poorer body

condition could translate into poorer breeding performance and, consequently, lower abundance in the road area. However, we have weak evidence (one juvenile in the roadless area vs zero juveniles at the road in April) that reproduction lasted longer in the roadless area. All juveniles (three in each area) were captured only once. Thus, the increase in abundance from reproduction may have resulted from the individuals born earlier in winter (Rosário and Mathias 2004).

Contrary to our predictions, the remaining parameters analysed were similar between road and roadless populations. Although reproduction, recruitment and turnover in wood mice are known to depend on abundance (Gurnell 1978; Montgomery 1989a, 1989b), these parameters represent proportions (e.g. percentage of residents) and rates (i.e. sex ratio) that are comparable as long as populations have similar structures, independently of their sizes.

Survival probabilities are also rates between the number of marked individuals presently found alive and the total number of previously marked individuals (Pollock et al. 1990). Even so, similar survival probabilities were unexpected because road kills should represent an additional source of mortality. However, during our study period, we never found any road-killed wood mice despite the fact that five individuals crossed the road (unpublished data). Therefore, road kills may not have a significant influence on population survival nor threaten the long-term persistence of an abundant and widespread small mammal, as suggested by Ruiz-Capillas et al. (2015). On the other hand, we found two road-killed wood mouse predators: *Martes foina* (Serafini and Lovari 1993) and *Buteo buteo* (occasional predator; Mañosa and Cordero 1992; Zuberogoitia et al. 2006). This may suggest that in the road area, lower mortality by predation could compensate for a higher mortality by road kills (predation release hypothesis; Fahrig and Rytwinski 2009). However, the effects of predation release near roads are still not proven (Planillo and Malo 2013; Downing et al. 2015), and we lack sufficient data to test it.

Temporary emigration results showed that residents entered and exited road and roadless areas at the same rate, meaning that animals' movements may not be significantly disturbed by traffic as suggested by Ford and Fahrig (2008) for other small mammal species. The similarities between the two areas in terms of temporary emigration, turnover and related traits suggested that the road surroundings were not acting as dispersal routes, as initially expected. Indeed, verges may be favoured dispersal corridors for small mammals only when roads cross habitats highly modified by humans (Getz et al. 1978), or in natural or semi-natural habitats, if they offer additional conditions, such as food or shelter (Brock and Kelt 2004).

Potential limitations and strengths

Precise estimations in capture-recapture studies demand large data sets, frequently preventing the desired replication due to

budget constraints (Bailey et al. 2004). Therefore, many capture-recapture studies use one or two areas (e.g. Rosário and Mathias 2004; Wang and Getz 2007; Borges and Marini 2010; Silva et al. 2011). Model complexity increases data demands, and extended Pollock's robust design is among the most complex models available for estimating population parameters (Cooch and White 2013). This method is particularly important in the presence of temporary emigration and the lack of perfect detectability (Kendall et al. 1997), as we found in our study.

Inferences in capture-recapture studies are often model-based (likelihood-based approach) rather than design-based (Burnham et al. 1987; Bailey et al. 2004; Borchers et al. 2002). Model-based inference is independent of how we choose sampling units and rather relies on model assumptions (e.g. unknown detection probability and other assumptions related to the parametric model structure) (Borchers et al. 2002).

We acknowledge that model-based inference is necessary because the detection probability is unknown, but it could eventually be combined with design-based methods to test model assumptions. However, this would require sampling as many areas as possible over the range of the survey region (Borchers et al. 2002). Nonetheless, our model-based estimates could be used to calibrate parameters in a similar habitat (Pollock et al. 2002; Bailey et al. 2004).

We used a high number of traps and temporal replication (in each area) to compare, for the first time, several traits of small mammal populations living in similar road and roadless areas. Our analysis did not show evidence of capture probabilities being affected by a possible behavioural response to trap bait. However, a possible violation of this assumption, due to a trap-happy scenario, would overestimate encounter probability and underestimate abundance (Pollock 1982). Although our temporal replication encompassed three seasons, it was conducted in a dry year. Different climatic conditions could affect our estimates. Rosário and Mathias (2004) found higher abundance and better body condition in a wood mouse population during a wetter year in the same roadless habitat and region. However, climate would affect both road and roadless areas and, consequently, our conclusions for comparison purposes would not be compromised.

Implications for road verge management

Our analysis suggested that common management actions to prevent fire risk associated with roads shape the population dynamics of a common and abundant small mammal, lowering the carrying capacity at a roadside area significantly. Part of this arises from the double intervention (verge vegetation clearing and firebreak opening) in contiguous areas at one side of the road. Probably, this management strategy will have an

even greater effect when implemented on both sides of the road as prescribed by law.

On roads crossing areas highly modified by human activity, verge management could hamper the populations of threatened small mammals by destroying their last refuges (e.g. *Microtus cabreræ*; Pita et al. 2006 and *Niviventer cameroni*; Musser and Ruedas 2008). On the other hand, in intensive agricultural areas, verge management would contribute to the control of small rodent outbreaks that compromise agriculture yield (e.g. *Microtus arvalis*; Redon et al. 2010).

To minimize fire risk and simultaneously maintain the availability of habitat for threatened small mammals, we suggest a maximum width of 10 m for the vegetation clearing strip (currently, this is the minimum width allowed by law). This maximum width should include verge paring and firebreaks. Most small mammal species depend on vegetation cover (Garratt et al. 2012) and would benefit from our recommendation without any additional cost. This would be important because the current habitat loss and fragmentation may compromise even abundant and widespread species. In fact, a former small mammal pest (*Cricetus cricetus*) is now extinct in parts of its distribution range (La Haye et al. 2014). Moreover, small mammals are key prey for many predators, including threatened species (Delibes-Mateos et al. 2011). Thus, any management action promoting small mammal abundance should help in the conservation of its predators (Delibes-Mateos et al. 2011).

Conclusions

In well-preserved habitats, a low-traffic road may negatively affect small mammals, even those with high reproductive ability like the wood mouse. We showed that abundance and body condition were lower in the road area, whereas survival and turnover were similar in both areas. We do not have evidence that road kills negatively affect survival or that verges positively affect turnover, as initially predicted. Thus, our results stress the need to test for more than one parameter before generalizing population trends.

Despite the study limitations, our conclusions could reasonably be extended to small mammal species that depend on vegetation cover and avoid crossing gaps such as those induced by roads (paved lanes and vegetation clearing on its surroundings) (Oxley et al. 1974, Macpherson et al. 2011).

Less available space to settle in due to road pavement and vegetation clearing associated with the presence of roads seems to drive the differences observed in wood mouse populations living in road and roadless areas. Additionally, physiological stress, presumably induced by traffic, might contribute to our findings (Ware et al. 2015), although we have not gathered data to test this.

Small mammals could be resilient to roads and verge management locally.

Nevertheless, populations might be affected if management further restricts resource availability across the road network, as roads are one of the most widespread infrastructures across all modern landscapes. Moreover, smaller populations with poorer body condition at the roadside may hardly recover after critical periods. Thus, road-dominated environments may hamper the persistence of other endangered small mammal species.

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Compliance with ethical standards This research involves animals.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All the procedures followed the guidelines approved by the Portuguese Institute for Nature and Forest Conservation (ICNF - Instituto de Conservação da Natureza e das Florestas) and the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011).

Conflict of interest The authors declare that they have no conflict of interest.

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