

Barrier effects of roads on movements of small mammals

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Abstract. Roads and highways represent one of the most important anthropogenic impacts on natural areas and contribute to habitat fragmentation, because they are linear features that can inhibit animal movement, thereby causing barrier effects by subdividing the populations adjacent to the roads. The study presented here aims to determine, to which extent roads act as a barrier, subdividing populations of three species of small forest mammals: bank vole, yellow-necked mouse and common shrew, and what is the relative importance of road width and traffic intensity on the barrier effect. The study was carried out at four 125 m long segments of roads, close to the city of České Budějovice. All segments crossed a forest. The capture-recapture method was applied to determine the crossing rates of animals. The traps were checked three times each day during four consecutive nights, in summer and in autumn. We found that: (1) roads strongly prevent crossing movements in all three studied species, (2) there are interspecific differences in road crossing rates, (3) species cross more often narrow than wide roads, (4) traffic intensity does not affect the crossing rates.

Key words: *Apodemus flavicollis*, *Clethrionomys glareolus*, habitat fragmentation, linear clearings, road barriers, road crossing rates, *Sorex araneus*

Introduction

Internal habitat fragmentation occurs when wildlife populations in their natural habitat are subdivided by linear clearings, like roads, railways or power lines (Schreiber & Graves 1977, Goosem 1997). As these occupy considerable and increasing areas of land, they perform one of the most obvious and extended anthropogenic impacts in the natural areas (Forman & Alexander 1998, Spellerberg 2002, Forman & Sperling 2002), contributing enormously to the total habitat fragmentation (Forman 2000, Saunders et al. 2002, Formann & Sperling 2002). Thus the reduction of population size of species living in habitats subdivided by linear clearings (Trombulak & Friswell 2000, Saunders et al. 2002), the appearance of edge effect (Murcia 1995, Fagan et al. 1999) and the restriction of animal movement across these linear clearings (Oxley et al. 1974, Mader 1984, Bąkowski & Kozakiewicz 1988, Gerlach & Musolf 2000, Goosem 2001) can have important negative consequences upon the species *via* division of populations into smaller isolated subpopulations (Frankham 1995, Keller & Waller 2002). Even if the linear clearings like roads may not represent a “barrier” for the animals, possible collisions with vehicles could be an important factor contributing to their mortality (Philcox et al. 1999, Clevenger et al. 2003) and sometimes the population could decrease or even become locally extinct (Fahrig et al. 1995, Huijser & Bergers 2000, Trombulak & Friswell 2000, Hels

& Buchwald 2001). Nonetheless, the reaction and even the quantity and quality of the effect can be strongly species-specific.

Several studies have been carried out to determine and understand the negative effect of roads and highways on different species in different habitats to provide solutions for roads that have already been built, and to give recommendations for the design of roads and highways under construction (Yanes et al. 1995, Clevenger & Waltho 2000, Hlaváč 2001, Dodd et al. 2004). This is very important, because systems of roads divide the landscape into many little patches, which increases their border and barrier effects (Goosem 1997, Forman 2000). Most of these studies have focused on medium size to large mammals; fewer studies were carried out with small mammals and even less with rodents. This is because of the belief that small mammals are usually not significantly affected by the presence of roads and highways, that populations living close them are large enough for long term survival and that small mammals have plenty of possibilities to cross the roads and highways through, e.g., underpass tubes (Dodd et al. 2004). Literature indicates that roads and highways either inhibit their crossing by rodents completely (Oxley et al. 1974, Kozakiewicz 1993, Gerlach & Musolf 2000), or act as partial barriers depending on the road width and particular behavioral responses of the species (Kozel & Fleharty 1979, Bąkowski & Kozakiewicz 1988, Richardson et al. 1997, Clark et al. 2001, Goosem 2001).

Here we test whether roads act as a barrier in terms of preventing their crossing by three species of small forest mammals: bank voles *Clethrionomys glareolus* (Schreber, 1780), yellow-necked mouse *Apodemus flavicollis* (Melchior, 1834) and common shrew *Sorex araneus* (Linnaeus, 1758). We then test, whether narrow roads (two lanes, road surface less than 10m wide) inhibit the frequency of road crossing of these three species to the same extent as wide roads (two lanes, road surface more than 10m wide). We also determine, how road crossing rates are influenced by traffic intensity and the species studied.

Material and Methods

Site description

The study was carried out at four 125 m long segments of roads crossing a forest landscape, close to the city of České Budějovice (48°58' N, 14°28' E) (Czech Republic). The sites were chosen to compare roads of different widths – two narrow roads: Borek 1, (4 m road surface, 7 m right-of-way) and Kaplice (7 m road surface, 10 m right-of-way) and two wide ones: Borek 2 (9 m road surface, 13 m right-of-way) and Hluboká (11 road surface, 19 m right-of-way). The right-of-way is the road surface plus the verges on either side – see Spellerberg (2000) for exact definitions. Borek 1 (49°02' N, 14°30' E) is a dirt road with no more than 5 vehicles per day; all three other roads are paved. The traffic intensity in Borek 2 (49°03' N, 14°30' E) is more than 5, but less than 50 vehicles per hour (vph); the traffic intensity in Kaplice (48°46' N, 14°27' E) and in Hluboká (49°07' N, 14°23' E) is more than 200 vph. At all sites, the forest parameters support occurrence of small forest mammals, although their composition is variable between sites.

The canopy of all the four sites is dominated by Norway spruce (*Picea abies*), Scotch pine (*Pinus silvestris*), common oak (*Quercus robur*), white birch (*Betula verrucosa*), Norway maple (*Acer platanoides*) and European alder (*Alnus glutinosa*). The prevailing species in the understory, the density of which increases towards forest edges, are red

raspberry (*Rubus idaeus*), common blackberry (*R. fruticosus*), dog rose (*Rosa canina*), common filbert (*Corylus avellana*), black elder (*Sambucus nigra*), the herb layer includes mainly tall oatgrass (*Arrhenatherum elatius*), quack grass (*Agropyron repens*), stinging nettle (*Urtica dioica*), thistle (*Carduus* sp.), white clover (*Trifolium repens*), streamside lupine (*Lupinus polyphyllus*), and coltsfoot (*Tussilago farfara*). Borek 1 is the only place with a closed canopy over the road surface; Kaplice and in some parts also Borek 2 are partially shaded by the canopy, while Hluboká is not shaded at all.

Experimental design

At each road segment, we have placed 100 live traps in four transect lines, two at each side, 5 m apart and parallel to the road, at each side of the road: one close to the road, at the boundary between the mown (road verge) and unmown vegetation, and the other one 5 m further inside the unmown vegetation or forest. Each line consisted of 25 live traps placed at 5 m intervals (Fig. 1). Traps were baited with a mixture of oats and sardines.

We have used the capture-mark-release (CMR) method (B e g o n 1989, A n o n y m o u s 1998). We have carried out the experiments during two sampling periods in the 2003 breeding season: in early summer (from the last week of June to the last week of July), and in late summer/early autumn (from the last week of August to the last week of September), with four consecutive nights at each site, and three revisions per each night: first one between 20:00 and 21:00 (sunset in summer), the second one two hours later, and the third one at 5:00 (at dawn).

The animals were marked by toe clipping, and their weight, sex, age-class (estimated in two categories: sub-adult and adult on the basis of their weight and external reproductive characteristics), reproductive status, side of the road, line number, number of the trap and the instants of the first and consecutive captures were recorded. Immediately after recording, all animals were released at the point of capture.

Statistical analysis

In theory, the frequency of road crossing by the animals can be affected by their abundance (animals may tend to avoid high densities by increased mobility when crowded), different

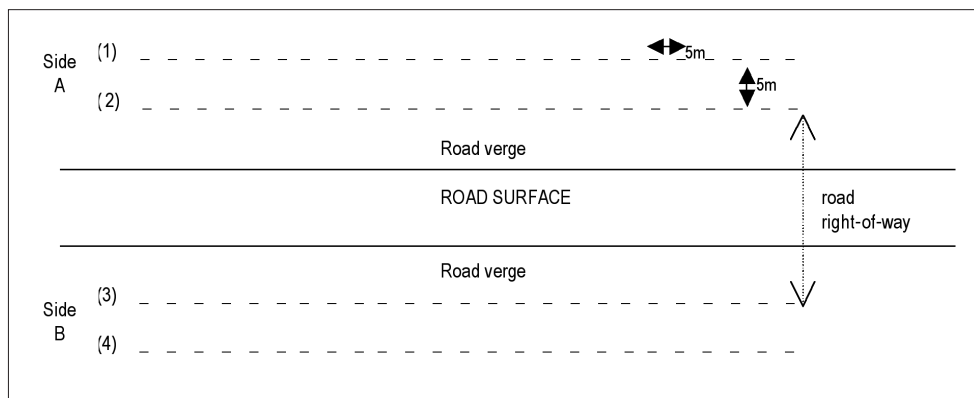


Fig. 1. Live traps positions along the road. The short lines represent traps and the numbers in the brackets are line numbers.

abundances between left and right side of the road (animals may tend to move from the higher to the less populated side of the road) and population sex ratio (females may be more territorial, while males may be more mobile in searching for females). Therefore, prior to the analyses of road crossing rates, we have examined the population structure and tested for difference in animal densities and for biases from 1:1 sex ratios in individual sites, sampling periods and sides of the road.

We have tested for differences in population size between the sites and individual sides within a site by means of analysis of variance (ANOVA), in which side was nested in site and season was considered as repeated measurement. The χ^2 goodness-of-fit analysis was used to test for biases from the 1:1 sex ratio.

We have tested for the barrier effect (i.e., whether the movements across the road are less frequent than movements in other directions within the forest) as follows. We assumed that if there were no barrier effect, the movements in all directions would be equally likely. Under this assumption, and in our system of four rows of traps, considering only “long distance” movements – those spanning considerably more than road width (we used 20 m for narrow roads, and 25 m for wide roads) – movements ending at the same side of the road should be equally frequent as those across the road. We estimated the former as the number of “long distance” movements, during which the animal stayed at one side of the road and the latter as the number of movements, which ended at the other side of the road. Thus we have used χ^2 goodness-of-fit analysis to test, whether the proportion of animals that stayed at the same side of the road after having moved for more than the critical distance (20 m for narrow and 25 m for wide roads), significantly deviates from the expected 50% of all “long distance” movements. Yates continuity correction was applied to data sets with small counts (Zar 1999).

The differences between wide and narrow roads and between individual species within one site in the percentages of animals that crossed the road were tested by χ^2 contingency analysis. Yates continuity correction was applied to data sets with small counts (Zar 1999).

The effect of traffic intensity was tested by comparing the percentages of animals that crossed the road between pairs of roads of the same width, in order to factor out road width as a possible confounding factor. This was done by testing the hypothesis “The percentage of animals that crossed the road with lower traffic intensity is higher than that for the road with larger traffic intensity”, for narrow and for wide roads separately, using one tailed Fisher exact test.

For these analyses, the data taken from summer and autumn samples were pooled. All the animals captured at least once after their marking and release were considered, unless they were found dead in the traps when first captured.

Results

Species captured

During the summer sample, from 1600 trap nights, we have got a total of 877 captures of 318 different individuals (19.9 animals per 100 traps), 44% of which (171 individuals) were recaptured at least once. In total, eight species were captured at the different sites: *Clethrionomys glareolus*, *Apodemus flavicollis*, *Sorex araneus*, *S. minutus*, *Microtus agrestis*, *Neomys fodiens*, *N. anomalus* and *Crocidura suaveolens*. However, only *C. glareolus* (*C.g.* thereafter), *A. flavicollis* (*A.f.*) and *S. araneus* (*S.a.*) were sufficiently abundant for statistical

analyses: each of these three species represented more than 25%, while each of the remaining species less than 1% of the total number of animals captured (Fig. 2).

In the autumn, nine species (*C.g.*, *A.f.*, *S.a.*, *S. minutus*, *N. anomalus*, *C. suaveolens*, *M. arvalis*, *A. sylvaticus* and *Mus musculus*) were captured in the total of 921 captures out of 1600 trap nights, which corresponds to 382 different animals (23.9 animals per 100 traps) and 212 individuals (55%) were recaptured. Although more species were found and a larger number of individuals was captured in the autumn, compared with the summer, the same pattern in species composition as in summer was found: *C.g.*, *A.f.* and *S.a.* represented more than 70% of all the captures (Fig. 2).

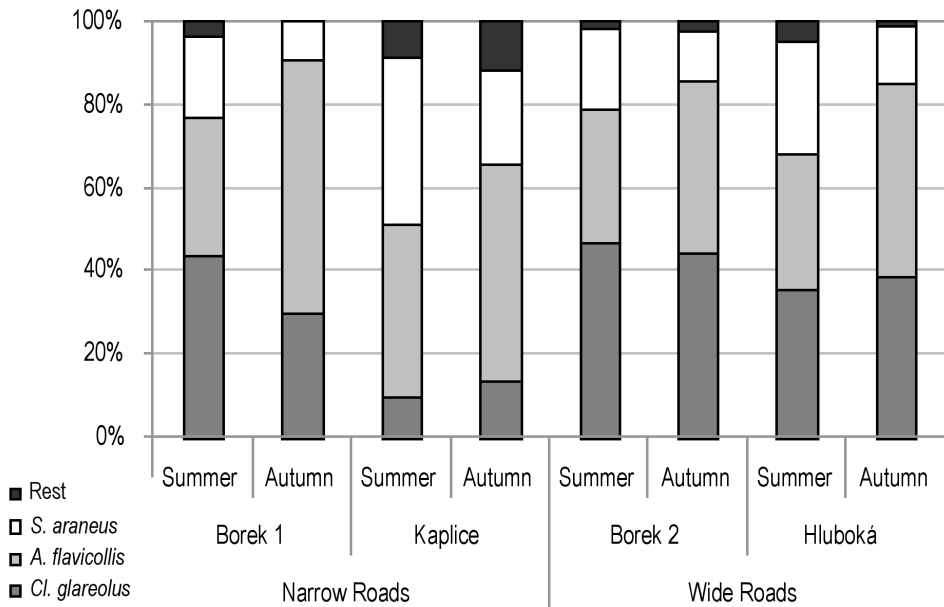


Fig. 2. Percentage of species captured (marked) at each site during the summer and autumn sampling periods.

Numbers of captured animals

C.g., *A.f.* and *S.a.* permanently inhabited the four sites under study, but the pooled frequency of captures of *S.a.* was lower than that of the two other species (Fig. 2, Tables 1 and 2). Note that sometimes the sums of numbers of captured animals in summer and autumn in Table 2 are higher than the corresponding number in Table 1. This is because some animals were captured both in summer and in autumn and therefore counted twice in Table 2, but only once in Table 1. Considering both seasons together (Table 1), 194 individuals of *C.g.*, were captured and marked, more than 60% of them repeatedly – up to 19 times, but most of them only twice. Out of 275 marked *A.f.* individuals, 59% were recaptured, mostly twice and at most 12 times. Out of 85 captured individuals of *S.a.*, only 39% were recaptured, mostly twice and at most 5 times. The average relative density (number of individuals captured per 100 trap nights) across all sites and both seasons in *C.g.* was 8.0 individuals. The relative density of *C.g.* in Kaplice was significantly lower than elsewhere (ANOVA, $F_{3,4} = 14.89$; $P = 0.01$): only 1.75 individuals. The average relative density of *A.f.* across all sites and both seasons was 7.12 individuals, with no significant differences between the sites (ANOVA, $F_{3,4} = 3.57$; $P = 0.13$).

No significant differences were found between the numbers of animals captured at each side of the road, independently of site for any of the three species (ANOVA, *C.g.* $F_{4,8} = 0.12$; $P = 0.97$; *A.f.* $F_{4,8} = 0.13$; $P = 0.97$; *S.a.* $F_{4,8} = 2.39$; $P = 0.14$).

In *C.g.*, and in *A.f.*, mostly no significant differences were found between the abundances of males and those of females, no matter which season, site or side of the road was considered. Significant biases from the 1:1 sex ratio were found only in *C.g.* in Hluboká in autumn (χ^2 goodness-of-fit test; side A: sex ratio 0.21, $P = 0.004$; side B: sex ratio 0.19, $P = 0.012$), in *A.f.* at one side of the road in Borek 1 in autumn (χ^2 goodness-of-fit test; sex ratio 0.68, $P = 0.039$) and in *A.f.* at one side of the road in Hluboká in summer (χ^2 goodness-of-fit test; sex ratio 0.81, $P = 0.012$). Bonferroni correction shows that they are most likely statistical artifacts, following from repeated tests. It was not possible to analyze the sex ratios for *S.a.*, because about 90% of captured animals were subadult individuals without external signs of sex.

Barrier effect

Individuals of the three species were able to move at larger distances than was the width of the widest roads (Table 1). We even registered movements of 6 individuals of *C.g.* and of 4 individuals of *A.f.* between Borek 1 and Borek 2 – sites that were more than 100 m apart from each other. Some individuals of both *C.g.* and *A.f.* – after having been captured and marked at one site – moved to the other site and stayed there. We did not register any return movements.

Table 1. Number of captured (marked) and recaptured animals at each site, their mean and longest movements. Data pooled over summer and autumn samples (2003) at each of the sites.

	Site (road right-of-way width in meters)	Total number of captures	Number of captured (marked) animals	Number of recaptured animals	Mean movement distance (SE) (m)†	Longest movement registered (m)†
<i>C. glareolus</i>	Narrow Roads	209	67	45	13.05 (1.06)	65
	Borek 1 (7)	166	53	37		
	Kaplice (10)	43	14	8		
	Wide Roads	483	127	82	14.49 (0.68)	75
	Borek 2 (13)	187	57	38		
	Hluboká (19)	296	70	44		
<i>A. flavicollis</i>	Narrow Roads	418	138	83	17.65 (1.01)	85
	Borek 1 (7)	202	86	45		
	Kaplice (10)	216	52	38		
	Wide Roads	408	137	111	16.62 (1.04)	85
	Borek 2 (13)	117	52	25		
	Hluboká (19)	291	85	59		
<i>S. araneus</i>	Narrow Roads	82	46	24	17.50 (2.46)	50
	Borek 1 (7)	26	18	6		
	Kaplice (10)	56	28	18		
	Wide Roads	93	39	28	19.28 (2.45)	90
	Borek 2 (13)	21	12	6		
	Hluboká (19)	72	27	22		

† Movements across the roads were not considered.

Table 2. Number of captured (marked) individuals of *C. glareolus*, *A. flavicollis* and *S. araneus* at individual sides of the road during summer and autumn samples.

		Narrow Roads				Wide Roads			
		Borek 1		Kaplice		Borek 2		Hluboká	
		Summer	Autumn	Summer	Autumn	Summer	Autumn	Summer	Autumn
<i>C. glareolus</i>	Side A	16	22	3	3	15	16	19	26
	Side B	9	17	4	4	16	25	25	16
<i>A. flavicollis</i>	Side A	9	45	15	13	3	18	24	26
	Side B	10	33	15	14	18	20	16	25
<i>S. araneus</i>	Side A	6	8	16	6	11	6	24	10
	Side B	5	4	13	6	2	5	9	5

The road crossing movements represented only 14 % of all long distance movements (longer than 20 m for narrow roads and longer than 25 m for wide roads) in narrow roads and 12 % in wide ones in *C.g.*, and 34% in narrow and 2% in wide roads in *A.f.* In *S.a.*, only one movement was registered in one of the wide roads (Table 3). The χ^2 test (Table 3) has shown that for both narrow and wide roads, the number of long-distance movements in each species was significantly lower than expected if the roads did not represent a barrier.

Narrow vs. wide roads

The number of individuals that crossed the different roads is shown in Table 4. Individuals of both *C.g.* and *A.f.* were able to cross both narrow and wide roads, but did it very infrequently, particularly in the case of wide roads. Out of all *C.g.* individuals, who were recaptured at least once, less than 12% crossed the road (Table 4). The proportion of *C.g.* individuals that crossed the road was lower for narrow compared with wide roads (Table 4), but not significantly so ($\chi^2 = 2.97$; $df = 3$; $P = 0.4$). The difference in proportions of individuals that crossed the

Table 3. Number of long distance (more than 20 m for narrow and more than 25 m for wide roads) road crossing (Cross) and not-crossing (No Cross) movements for each species and χ^2 test (No. of degrees of freedom = 2 in all cases), whether the ratio Cross : No Cross significantly differs from the expected proportion of 50%, performed separately for pairs of roads of the same widths and for each species.

Sp.	Road Width	No Cross	Cross	χ^2
<i>C. glareolus</i>	Narrow	28	4	18**
	Wide	47	6	31.72**
<i>A. flavicollis</i>	Narrow	76	26	24.51**
	Wide	50	1	47.08**
<i>S. araneus</i>	Narrow	10	0	---
	Wide	11	1	8.33*

* $P < 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

wide vs. narrow road was, however, significant for *A.f.* ($\chi^2 = 20.91$; $df = 3$; $P \ll 0.001$), in which 25% of the recaptured individuals crossed at least once the narrow roads, but less than 3% crossed the wide roads (Table 4). Only one *S.a.* individual crossed the road during the sampling (Table 4), which prevented any analysis.

The proportions of animals that crossed the road did not differ significantly between species for wide roads, but did so for the narrow roads (Table 4), which was caused by a large proportion of *A.f.* crossing the road in Kaplice ($\chi^2 = 11.16$; $df = 2$; $P = 0.004$, Table 4).

Table 4. Numbers of animals that crossed (Cross) and did not cross (No Cross) the road at each site (irrespective of the length of movement) and χ^2 contingency table test (No. of degrees of freedom = 2 in all cases), of differences in road crossing rates between the three species studied (last column) and between narrow and wide roads (last row).

	<i>C. glareolus</i>		<i>A. flavicollis</i>		<i>S. araneus</i>		Between species
	No Cross	Cross	No Cross	Cross	No Cross	Cross	χ^2
Narrow roads	40	5	62	21	24	0	10.02**
Borek 1	32	5	37	8	6	0	1.41
Kaplice	8	0	25	13	18	0	11.16**
Wide roads	76	6	81	3	27	1	1.36
Borek 2	34	4	25	0	6	0	3.46
Hluboká	42	2	56	3	21	1	0.08
Narrow vs. wide roads	χ^2	2.97		20.91***		1.39	
	df	3		3		3	

* $P < 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

Traffic intensity

For each of the three species studied, one tailed Fisher exact test (Table 5) has shown that there is no significant difference in the percentages of animals that crossed the road, if roads of same width are considered.

Table 5. One tailed Fisher exact test (significance level = 5%) of the hypothesis H_0 : “The percentage of animals that crossed the road with lower traffic intensity is higher than that for the road with larger traffic intensity”, performed for each of the three studied species, and for narrow and wide roads separately.

Low traffic vs. high traffic intensity in:		<i>C. glareolus</i>	<i>A. flavicollis</i>	<i>S. araneus</i>
Narrow roads	<i>P</i>	0.36	0.07	nc
Wide roads	<i>P</i>	0.27	0.34	0.79

nc = no cross movement was registered

Discussion

Numbers of captured animals

It is well known that the population size of small rodents varies within a year. The numbers of individuals increase from early spring until late summer or even until autumn, when they reach their peak (see N i e t h a m m e r & K r a p p 1978, 1982, 1990, M o n t g o m e r y 1979, 1980a, P e t r u s e w i c z 1983, P u c e k et al. 1993). Therefore we started our sampling in summer, to get sufficient numbers of individuals for our capture-recapture experiments.

In order to capture the maximum possible number and diversity of small mammals, with different daily activity rhythms, traps were open throughout the day and checked twice during the night, and once at dawn. Out of 9 species captured, only two rodent species (*C.g.* and *A.f.*) were captured in sufficient numbers for statistical analyses. One insectivorous species, *S.a.*, was captured at all sites, but its abundance was always low, and therefore it was not always considered in the analyses. *C.g.* has one daily activity peak before the dusk, a smaller one at midnight and another one early in the morning, while *A.f.* is most active between midnight and 2 a.m. (Wójcik & Wołk 1985). This is especially true when these two species live together and explains, why *C.g.* individuals were captured mainly during the first night trap checking, while *A.f.* was captured almost exclusively during the second trap revision.

The low species diversity and abundance, which was observed at all sites, and was not related with time of the year, may be attributed to the presence of the road – “road avoidance effect” (Forman & Alexander 1998).

Barrier effect, width of the road and traffic intensity

Many studies dealing with roads less than 30 m wide have reported that forest rodents cross narrow roads more often than wide ones (Oxley et al. 1974, Kozel & Fleharty 1979, Burnett 1992). This is supported by our results. Very wide roads – highways more than 100 m in width – seem to present an almost impenetrable barrier for them (Kozel & Fleharty 1979), even in the rare cases when traffic intensity is low there (Oxley et al. 1974). However, unless wide highways are considered, the width of the road *per se* may not be the principal reason for low road crossing rates of small mammals, because when inside the forest, the animals are able to move for distances larger than the width of the road (Oxley et al. 1974, Kozel & Fleharty 1979, Burnett 1992), as also shown here. Thus other aspects, like road surface, canopy openness or traffic intensity may – in theory – play a role.

It has been shown that dirt and gravel roads inhibit the crossing to a similar extent as paved roads (Oxley et al. 1974, Kozel & Fleharty 1979, Clark et al. 2001) and that even open non-road surfaces, like cleared powerline corridors covered by grassland, can restrict the movements of small forest mammals (Goosem 1997, Goosem & Marsh 1997). Our results support this conclusion: the road crossing rates in Borek 1, which is a dirt road, did not differ from those registered in the paved road of the same width, Kaplice.

Canopy closure over narrow roads can play an important role in the decision of the animals to cross the roads, mainly because it reduces the extreme microclimate conditions at the road surface and imitates the conditions inside the forest (Merriam et al. 1989, Goosem 2001). Thus it may be rather the presence of “open” space that reduces the frequency of crossing of wide roads and of the above-mentioned wide cleared powerline corridors. In our study, the narrow roads, but not the wide roads, were partially shaded by the canopy. Thus it may be the combination of shorter distance needed to cross the narrow roads plus the closed canopy above these roads or either one of these that have caused the higher road crossing rates of narrow roads.

The effect of traffic intensity by itself on crossing behavior of small mammals is difficult to disentangle from the effect of road width, because traffic intensity is usually closely and positively related with the width of the roads. Mader (1984) and Richardson et al. (1997) found that in roads of similar width, traffic had a negative effect on the displacement of the animals. In our study, even such medium traffic intensity as was observed in Kaplice and Hluboká (200 vehicles per hour at maximum) did not affect the rodent road crossing

rates. However, it has to be kept in mind that traffic intensity diminishes between midnight and the dawn, when these species, *A.f.* in particular, are active.

We did not find any animals killed by road casualties during the whole study. Thus we cannot make any conclusions about the effect of these roads on the mortality of the studied species. For this, a different experimental design would be needed.

There are interspecific differences in road crossing rates among small mammals, as the anatomy and physiology can make some species more “adapted” for crossing the roads than others (S w i h a r t & S l a d e 1984). For example, a 5 m wide gravel road did not act as a barrier for *A.f.*, but limited the movements of *C.g.* (B ą k o w s k i & K o z a k i e w i c z 1988). We have shown that roads up to 17 m wide represented a barrier for movement of *S.a.* The roads were crossed by both *A.f.* and *C.g.*, but the proportion of *C.g.* individuals that crossed the roads was much lower than that of *A.f.* It is unlikely that the lower mobility of *C.g.* (Z e j d a & P e l i k á n 1969, G e u s e et al. 1985, R a j s k a - J u r g i e l 1992) might alone account for this, because in many studies, including this one, long distance movements were registered in both species, vastly exceeding the width of the road examined (A n d r z e j e w s k i & B a b i Ń s k a - W e r k a 1986, S z a c k i & L i r o 1991).

The explanation for the interspecific differences in road crossing rates may be looked for in differences in life histories of these species. *C.g.* is a food generalist, inhabiting all types of forest (N i e t h a m m e r & K r a p p 1982, P u c e k 1983, B a n a c h 1987, B r y j a & Ř e h á k 1998), which passively avoids the risk of being eaten by predators (J ę d r z e j e w s k i & J ę d r z e j e w s k a 1990) by preferring places with dense overhead cover, large amount of dead wood and frequent fallen logs that provide it with hiding places (P u c e k 1983, M i k l ó s & Ž i a k 2002, S u n d e l l & Y l ö n e n 2004). *A.f.* is more specific in its habitat requirements (N i e t h a m m e r & K r a p p 1978, M o n t g o m e r y 1980b), but also much better adapted against predators: large ears, big eyes, and larger mobility render this species better abilities to actively escape from attack by predators (R a j s k a - J u r g i e l 1992, C a s t i e n & G o s a l b e z 1994). Thus *A.f.* is less vulnerable to predation, but more dependent on food. This means that *A.f.* may be more inclined to move and look for better feeding places, but because of its better antipredator defensive abilities it may perceive the narrow roads as less dangerous than *C.g.* Similarly, B u r n e t t (1992) and G o o s e m (2001), reported that larger and more mobile rodents crossed the roads more often than smaller species.

To conclude: roads, and in particular the wide ones, have a “species filtering” effect (K o z a k i e w i c z 1993) in the sense that they apparently act as an effective barrier for *S.a.*, but as a penetrable barrier for *A.f.* and especially for *C.g.* Among the animals (of both species) that crossed roads of both widths, females and males, adult as well as subadult individuals were registered, therefore it seems that roads do not have an “age filtering” or “sex filtering” effect. However, due to their low numbers, it was not possible to test the differences in sexes or ages. Besides, the studied roads act as a barrier at the individual, not population level in the sense of D o b r o w o l s k i et al. (1993), because they affect only particular individuals, but do not divide the populations.

A c k n o w l e d g e m e n t s

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