Road crossing in bank voles and yellow-necked mice

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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 subdividing the populations adjacent to the roads. The paper examines to what extent a narrow (2-lane) and a wide (4-lane) highways represent barriers for two small mammal species: bank voles *Clethrionomys glareolus* Schreber, 1780 and yellow-necked mice *Apodemus flavicollis* Melchior, 1834, and whether displaced rodents are able to return across roads of different widths. The study was performed at four sites in the Czech Republic. The capture-mark-recapture method was used to determine crossing rates. At two sites, the animals captured close to the road were transferred to the other side and released, to compare return movements across the roads with the movements made by the non-transferred animals. We found that the narrow highway did not prevent movement of neither of the species, although voles crossed only after they had been transferred. Wide highways, on the other hand, completely prevened crossing of both species. While the narrow highways acted at individuals level, the wide highways affected the population subvision.

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Introduction

Roads, railways, and power lines contribute to habitat fragmentation (Reed *et al*. 1996, Goosem 1997, Forman 2000), and are one of the most obvious and extended anthropogenic impacts in the natural areas (Forman and Alexander 1998, Seiler 2001, Spellerberg 2002). The strongest negative influence on wildlife is caused by animal casualties and barrier effects (Young 1994, Trombulak and Frissell 1999, Seiler 2001, Formann and Sperling 2002). Road mortality was widely studied in amphibians and reptiles (eg, Rosen and Lowe 1994, Fahrig *et al*. 1995, Hels and Buchwald 2001, Gibbs and Shriver 2002), birds (eg, Case 1978, Holbrook and Vaughan 1985), small to medium mammals (eg, Holišová and Obrtel 1986, Huijser and Bergers 2000, Clevenger *et al*. 2001a), and in large mam-

mals (eg, Groot Bruinderink and Hazebroek 1996, Cain *et al*. 2003, Kramer-Schadt *et al*. 2004). The presence of exclusion fences along highways mitigates and reduces wildlife-vehicle collisions (Clevenger *et al*. 2001b, Jaeger and Fahrig 2004) by blocking movement across the roads, but at the same time increases barrier effect. Even if roads are not fenced, the physical characteristics of the road, ie, road surface, gutters, and ditches can inhibit or limit the movement of the animals (Trombulak and Frissell 1999, Seiler 2001). This physical hindrance, called "a barrier effect" is seen as a major negative effect of the roads because it contributes greatly to the overall fragmentation of habitat (Forman and Alexander 1998).

According to Seiler (2001), the barrier effect of roads is a non-linear function of traffic intensity, road width, roadside characteristics, the behavior of animals as well as their sensitivity to disturbances. Different studies have shown that roads inhibit the movement of large mammals (eg, Klein 1971, Mace 1996) medium and small mammals (eg, Oxley *et al*. 1974, Mader 1984, Clarke *et al*. 1998, Rondinini and Doncaster 2002), birds (eg, van der Zande *et al*. 1980, Kuitunen *et al*. 1998), reptiles and amphibians (eg, Gibbs 1998, Gibbs and Shriver 2002, Shine *et al*. 2004). The barrier can significantly affect dynamics as well as demographic and genetic properties of the population (Seiler 2001). When roads act as impermeable barriers, they may divide the populations into smaller isolated subpopulations (Saunders *et al*. 2002), reducing gene flow, and may result in an increased extinction risk because of decreased genetic diversity (Frankham 1995, Keller and Waller 2002).

In the particular case of small mammals, it is believed that they are usually not significantly affected by presence of highways, that populations living close to the highways and roads are large enough for long term survival and that small mammals have plenty of possibilities to cross the roads and highways (eg, underpass tubes – Dodd *et al*. 2004). However, even though small mammals might be able to use narrow culverts to cross roads and highways (McDonald and St. Clair 2004a) literature indicates that when crossing structures are not present, roads

and highways either inhibit crossing movements completely (Kozakiewicz 1993, Oxley *et al*. 1974), or act as partial barriers (Kozel and Fleharty 1979, Bąkowski and Kozakiewicz 1988, Richardson *et al*. 1997, Clark *et al*. 2001, Goosem 2001, Rico *et al*., in press) depending on the road width and particular behavioral responses of the species. Thus, little is known about the movement behavior of animals crossing roads or the frequency of these crossings (Formann and Sperling 2002). Rico *et al*. (in press) observed that narrow roads (less than 10 m wide), did not represent a barrier in the crossing movement of two species of forest rodents, while wider roads (less than 20 m wide), although did not prevent, intensely limited it.

Depending on the number and frequency of successful crossings, a population could maintain the genetic variation with at least one crossing in the animals' lifetime, and maintain popu-lation size thus minimizing local extinction by more frequent cross movements (Formann and Sperling 2002).

In this study, we focused on the barrier effects of wide (more than 40 m) roads in small mammals. We had two aims: (1) to determine to what extent narrow (2 lane) and wide (4 lane) highways represented a barrier for two small forest mammal species, and (2) to ascertain whether displaced rodents were able to return across roads of different widths and whether there were differences between species, sexes, and age categories in this respect.

Study area

The study was conducted at four sites in the Czech Republic. Three, HW1, HW2 and HW3, were located on Highway D1 (Prague-Brno), a four-lane, 50 m wide paved highway with a central dividing strip and high traffic volume (around 40 000 vehicles per day – Hoření *et al*. 2005). Their regularly mown grassy verges ranged from 10 to 20 m in width. These sites were at least 15 km apart from each other: HW1 (49°27'N, 15°35'E), HW2 (49°36'N, 15°09'E) and HW3 (49°48' N, 15°09' E). The fourth site was on the county road No. 105 close to the Hluboká township (49°07'N, 14°23'E). This is a relatively narrow road, 19 m wide including both verges (mown), with a traffic intensity around 12–14 000 vehicles per day (Hoření *et al*. 2005).

The type of vegetation of all the four sites was a deciduous pine dominated forest, where the canopy was domi-

nated by Norway spruce *Picea abies*, Scots 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, whose density increased towards forest edges, were red raspberry *Rubus idaeus*, common blackberry *Rubus fruticosus*, dog rose *Rosa canina*, common filbert *Corylus avellana*, and black elder *Sambucus nigra*. The herb layer included mainly tall oatgrass *Arrhenatherium elatius*, quack grass *Agropyron repens*, stinging nettle *Urtica dioica*, thistle *Carduus* sp., white clover *Trifolium repens*, streamside lupine *Lupinus polyphyllus*, and coltsfoot *Tussilago farfara*.

The forest at all sites supported the occurrence of two species of small forest mammals: bank voles *Clethrionomys glareolus* Schreber, 1780 and yellow-necked mouse *Apodemus flavicollis* Melchior, 1834.

Material and methods

Experimental design

At each site, we placed 100 live traps (a wooden version of the Sherman trap) 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 (called "road lines" in the following), and the other one 5 m further inside the unmown vegetation or forest (called "forest lines" in the following). Each line consisted of 25 live traps placed at 5 m intervals (Fig. 1). Traps contained hay as bedding and were baited with a mixture of oats and sardines.

Each site was trapped in summer 2004, and then once more in autumn 2004. At each site, the traps were open over four consecutive nights, with three inspections per day: the 1st one between 20:00 and 21:00 (sunset in sum-

mer), the 2nd one two hours later, and the 3rd one at 5:00 (at dawn).

The capture-mark-recapture (CMR) methodology was used. Each animal captured was marked by toe-clipping, and the weight, sex, age-class (estimated in two categories: subadult and adult on the basis of weight and external reproductive characteristics), and reproductive status were recorded. All animals were released at the point of capture in HW1 and HW2. In HW3 and Road 105, during the first two nights in summer all animals were released at the point of capture, whereas from the third night on in summer and during the first three nights in autumn all animals captured were transferred to the other side of the road and released at the corresponding point at the opposite side. The numbers of animals that crossed back to the original side of the road were then recorded. Animals captured in the forest lines were released at the point of capture.

Analysis

We tested the hypotheses that populations at both sides of the road are of similar size, that the animals of both sexes are equally likely to be captured, and that animals have no extra motivation to cross the road deliberately. We assumed that population size was proportional to the number of catches. We used analysis of variance (ANOVA) to analyze differences in population size among sites and between sides during the sampling; χ^2 goodness-of-fit tests were used to reveal biases from the 1:1 sex ratio and to compare the numbers of animals captured and marked at each side of the road.

Crossing rates of individuals were calculated as the percentage of individuals that were recaptured at the side of the road opposite to where they were first captured out of all recaptured individuals. Differences between crossing rates within one site and among highway segments, as well as between sexes and age classes for each species, were then tested by χ^2 contingency analysis. We distinguished
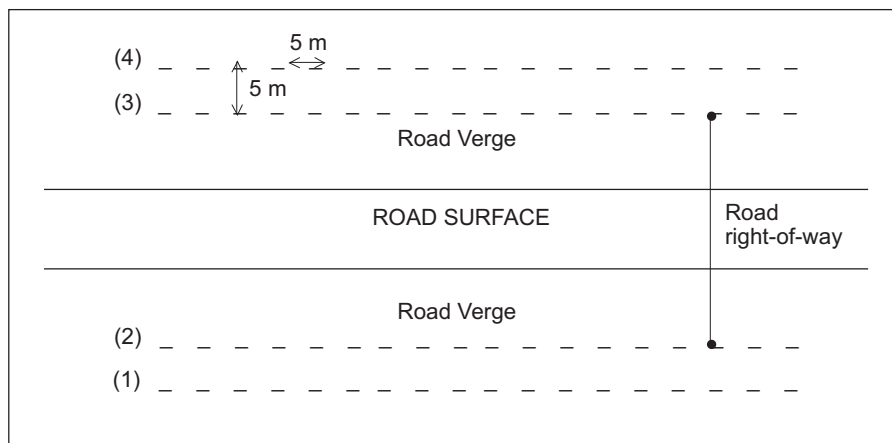

Fig. 1. Live traps positions along the road. The dashed lines represent the live-traps separated by 5 m and the numbers in the brackets are line numbers.

between deliberate crossing rates (those of non-transferred animals recaptured at the opposite side to where they were previously captured) and returning crossing rates (transferred animals recaptured close to place where they were originally captured). A Yates continuity correction was applied to data sets with small counts (Zar 1999). For these analyses, the data were pooled from summer and autumn sampling periods. All animals captured at least once after their marking and release were considered in these analyses.

Results

Species captured

In the summer, a total of 406 different individuals were captured during 1600 trap-nights, 61% of these (245 individuals) were recaptured at least once. Five species were captured: *Clethrionomys glareolus, Microtus arvalis, Apodemus flavicollis, A. sylvaticus,* and *Sorex araneus*. However, only *C. glareolus* and *A. flavicollis* were sufficiently abundant for statistical analyses: these two species represented more than 90% of all captures.

Eight species (*C. glareolus, M. arvalis, M. agrestis, A. flavicollis, A. sylvaticus, S. araneus, S. minutus,* and *Crocidura suaveolens*) were captured in the autumn. During 1600 trap-nights, 590 different animals were captured, of which 59% (347 individuals) were recaptured at least once. Although more species were found and a larger number of individuals captured in the autumn, compared with the summer, the same pattern in species composition as in summer was

found: *C. glareolus* and *A. flavicollis* represented more than 70% of all the captures.

Numbers of captured animals

Populations of *C. glareolus* and *A. flavicollis* inhabited the four sites under study. The number of captured and marked voles was lower than the number of mice at all sites (Table 1). A total of 178 individuals of *C. glareolus* were captured and marked at all sites and both seasons together. Out of them, 60% were recaptured at least once, most frequently two or three times, but some animals were recaptured even 14 times. Out of 581 marked mice, 62% were recaptured, mostly between 2 and 4 times and at most 16 times.

Neither the captures of voles, nor those of mice differed significantly among the highway segments and Road 105 (Table 2), even though the number of captured voles was the lowest in HW2 (Table 1). Across all sites and both seasons, 6 voles were captured on average per 100 trap-nights. The lowest number of individuals per 100 trap-nights (2 individuals) was captured in HW2, but this number was not significantly lower than that at other sites (ANOVA, $F_{3,4} = 2.11$, $p = 0.24$). Across all sites and both seasons, on average 8.5 individuals of mice per 100 trap-nights were captured, with no significant differences among the sites (ANOVA, $F_{3,4} = 6.42$, $p = 0.052$). There were no significant differences in the numbers of animals captured during the

Table 1. Numbers of captured and marked *Clethrionomys glareolus* and *Apodemus flavicollis* individuals and their relative density at all sites. Data pooled over summer and autumn samples at each of the sites.

	Site	Total number of captures	No of marked animals	Relative density per 100 trap-nights	No of recaptured animals	Mean movement distance (SE) (m)	Maximum movement registered (m)
C. glareolus	HW 1	189	54	8	40	14.24 (1.32)	95
	HW 2	34	16	2	8	17.19 (1.88)	30
	HW 3	209	45	5.63	31	18.55 (1.56)	110
	Road 105	130	63	7.88	27	17.61 (2.50)	55
A. flavicollis	HW 1	544	180	22.5	101	18.14 (0.96)	115
	HW 2	380	119	14.86	69	23.97 (1.4)	120
	HW 3	379	99	12.38	67	18.52 (1.25)	115
	Road 105	634	183	22.88	122	11.18 (0.86)	120

Table 2. Results of the two-way analysis of variance of the numbers of captured *Clethrionomys glareolus* and *Apodemus flavicollis*, at all sites, with Site and Season as factors. Degrees of freedom (df) are the same in all species interactions.

	C. glareolus		A. flavicollis		df	
	F	p-level	F	p-level	effect	error
Site	2.11	0.242	6.42	0.052	3	4
Season	5.97	0.071	1.07	0.360	1	4
Site*Season	3.89	0.111	2.35	0.214	3	4

summer and autumn seasons (Table 2). Thus, the seasonal data were pooled for further analyses.

There were no significant differences in the numbers of voles and mice captured per 100 trap-nights between sides of the road (ANOVA, when side was nested in site, *C. glareolus* $F_{4,8}$ = 0.56, p = 0.69. *A. flavicollis* $F_{4,8}$ = 0.42, p = 0.79) independently of site for any of the two species. A significant sex bias was found in voles only in the autumn sample in road 105 (χ^2 goodness-of--fit test; side A: sex ratio 0.15, p < 0.0001; side B: sex ratio 0.10, p < 0.0001), even if females predominated in HW1, HW2 and Road 105. There were more males than females in HW3, with a significant bias from 1:1 at side B during the autumn sample (χ^2 goodness-of-fit test; side B: sex ratio 0.791; p = 0.032). Mostly no significant differences were found between the number of captured males and females in *A. flavicollis*, no matter which season, site or side of the road was considered. Significant biases from the 1:1 sex ratio were found only in HW2 in autumn, but only at side B (χ^2 goodness-of-fit test: sex ratio 0.85; p = 0.002).

Barrier effects

Even though these species were highly mobile and able to move more than 100 m (Table 1), none of the 383 recaptured animals of both species crossed deliberately (without prior translocation) any of the three highway segments, and only four *A. flavicollis* out of 149 recaptured animals crossed the county road 105. Out of these four mice, three were females (2 adults and one subadult), and one was an adult male.

One adult female crossed the road twice, the rest only once.

Animal transfer experiments

A total of 27 voles and 67 mice were transferred across Road 105. Half of the transferred mice (52%), and 33.5% of the voles successfully returned, and were recaptured at the side of original capture, 5 (18.5%) voles and 13 (19.5%) mice were recaptured at the side of the road where they were transferred, and 13 (48%) voles and 19 (28.5%) mice were not recaptured (Fig. 2). A similar number of individuals of each species was transferred to the other side of the road. There was no significant difference in the rate of returning animals between the sides of the road: 35% of voles (56% of mice) returned from side A to B and 30% (48% of mice) returned from side B to A (χ^2 = 0.02, df = 1, p = 0.89 for voles and χ^2 = 0.15, df = 1, p = 0.70 for mice). None of the 6
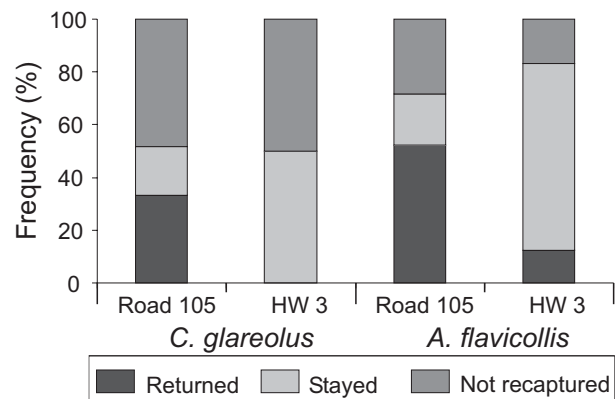

Fig. 2. Percentages of the animals that: returned to their original side of the road, stayed at the side they were transferred to, and which were not recaptured.
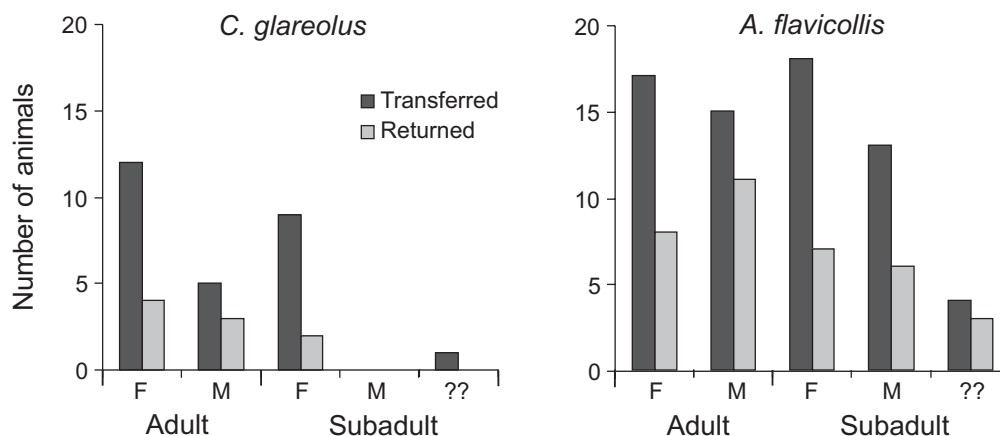
Fig. 3. Comparison of the numbers of adults and subadults as well as males and females of *Clethrionomys glareolus* and *Apodemus flavicollis* individuals that were transferred to the opposite side of the roads and the animals that returned to their original side in Road 105; ?? represents young animals, for which it was not possible to determine their sex. M – male, F – female.

transferred voles but 3 (13.6%) of the 22 transferred mice on the HW3 returned to the original side of the road. Three (50%) voles and 15 (68%) mice stayed on the side to which they were transferred, and the rest of the animals (three voles and four mice) were not recaptured (Fig. 2).

The percentage of transferred voles that returned did not significantly differ between HW3 and Road 105 (χ^2 = 1.33, df = 1, p = 0.25), perhaps due to the low number of transferred voles in HW3, but the percent of mice differed significantly (χ^2 = 8.57, df = 1, p = 0.003).

On the Road 105, the number of voles and mice that crossed the road spontaneously (non-transferred animals) to the other side, was significantly lower than the number of transferred animals that crossed the road returning to their side of origin (*C. glareolus*: χ^2 = 8.5, df = 1, p = 0.003; *A. flavicollis*: χ^2 = 60.3, df = 1, p < 0.0001).

In HW3, where no non-transferred mice crossed, this difference in mice was also significant (χ^2 = 5.37, df = 1, p < 0.017), because four individuals returned to their original side.

The number of crossings on Road 105 did not significantly differ between males and females in both voles and mice (*C. glareolus*: χ^2 = 0.65, df = 1, p = 0.42; *A. flavicollis*: χ^2 = 0.02, df = 1, p = 0.89; Fig. 3), or between adults and subadults (*C. glareolus*: χ^2 = 0.5, df = 1, p = 0.48; *A. flavicollis*: χ^2 = 0.76, df = 1, p = 0.38; Fig. 3).

Discussion

Crossing rates of animals may of course be influenced by road and traffic conditions (eg, Oxley *et al*. 1974, Burnett 1992, Goosem 1997, Richardson *et al*. 1997, McDonald and St. Clair 2004b), but also by two non-road related factors: (1) difference in population densities between individual sides of the road, as the animals may tend to move from more to less populated side of the road; (2) population sex ratio, as females normally are more territorial and therefore more sedentary, while males are more mobile in searching for females. In our data, the number of captured animals at each side of the road at all sample sites was similar and no significant biases from the 1:1 sex ratio were found in any of the subpopulations. Thus these two factors would not likely affect animal movements across the roads.

The transfer experiments were conducted because one can expect that resident individuals, after being transferred, would have a strong motivation to cross the road back and reoccupy their original territories (Richardson *et al*. 1997). Thus by transfers it is possible to determine, whether the roads and highways constitute a hindrance to the species' mobility. Only animals that were captured in the lines closer to the road were transferred, because we assumed

that these animals were resident there. That was supported by the large percentage of adults captured there. We are aware, however, that among the animals captured close to the road there might have also been a certain amount of dispersers (Stamps *et al*. 1987).

Both species crossed the 20 m wide road, although voles were less likely to do so. Rico *et al*. (in press) conducted experiments with the same protocol (without transfer) in 2003 on Road 105. In their experiments, 4.35% of voles and 5.08% of non-translocated mice deliberately crossed the road. Their results were not statistically significantly different from those reported here (*C. glareolus*: χ^2 = 0.13, df = 1, *p* = 0.71; *A. flavicollis*: χ^2 = 0.03, df = 1, *p* = 0.86). This suggests that the crossing rates measured in our experiments are consistent among years.

In Road 105, half of transferred mice, and 30% of voles, successfully returned to the side of the road where they were first captured. The high percentage of transferred mice that returned indicates that this road does not constitute a complete barrier, even though it appears to limit the movement of this species. On the other hand, no deliberate (without prior transfer) crossing movements, and the lower returning (after prior transfer) crossing rates registered for voles, suggest that for this species this road constitutes a partial barrier, and considerably limits its movements. Studies made with the same species in roads less than 30 m wide (Mader 1984, Bąkowski and Kozakiewicz 1988, Rico *et al*., in press) indicated that roads of this width limited the movements of *C. glareolus* and *A. flavicollis*, and that small mammals crossed narrower roads more often than wide ones (Oxley *et al*. 1974, Kozel and Fleharty 1979, Burnett 1992, Goosem 2001). Seiler (2001) stated that depending on the number of successful crossings relative to the size of the population, the barrier effect can significantly affect population dynamics, and demographic or genetic properties. We did not detect a negative effect on local demographic parameters, such as density or sex ratio, although, in the long-term run, population dynamics of voles might be affected, because the exchange of individuals in this species was reduced.

C. glareolus is less mobile than *A. flavicollis* (Rajska-Jurgiel 1992) and this may be the reason, why the roads represented a stronger barrier to movements for the voles in our experiments. Similar results were obtained by Burnett (1992), Goosem (2001) and McDonald and St.Clair (2004b), who reported that larger and more mobile rodents species were more successfully crossing wider roads than smaller and less mobile ones.

Very wide roads – highways wider than 70 m – like our D1, act as totally impenetrable barriers for certain species (Kozel and Fleharty 1979, Wilkins 1982, Garland and Bradley 1984), even in the rare cases when traffic intensity is low there (Oxley *et al*. 1974). Considering deliberate cross movements, our results are in general agreement with these tendencies. However, in HW3, the three transferred mice, apparently successfully crossed this four-lane highway with heavy daytime traffic. Several studies (Oxley *et al*. 1974 on *Peromyscus leucopus* and *Tamias striatus*, Garland and Bradley 1984 on 6 rodent species, Mader 1984 on *A. flavicollis*) did not detect any movement of small mammals across highways. However, Kozel and Fleharty (1979) and McDonald and St. Clair (2004b) reported that transferred *Peromyscus maniculatus* were able to cross the Interstate 70 (Kansas – USA) and the Trans Canada Highway (Banff National Park – Canada) and return to the side they were captured without using crossing structures.

The HW3 site was 100 m apart from an underpass (spanning bridges), which – in theory – could be an alternative route of return. Clevenger *et al*. (2001a) and Ng *et al*. (2004) reported the use of these underpasses by small mammals, even though small mammals are more prone to cross through narrow culverts than through wider underpasses (McDonald and St.Clair 2004a), particularly when culverts are covered by vegetation at both ends (Goosem 2001). The underpass of the HW3, even if it was more than 5 m wide and 4 m high, had a drain at both sides with bush cover at both ends. It is therefore possible that the three individuals that successfully returned used this underpass for crossing, which indicates that they were very well familiar with their surroundings. Considering the high mobility of this species

(Szacki and Liro 1991, Rajska-Jurgiel 1992, Szacki *et al.* 1993), which, in this study, were able to move up to 120 m, this seems reasonable. However, although we tested it by livetrapping in the underpass we failed to prove it. Nevertheless, highways appear to represent a real barrier. This prevents random breeding and might cause genetic isolation of subpopulation at each side of the road with the concomitant genetic separation of subpopulations (Kozakiewicz 1993, Gerlach and Musolf 2000). The risk for inbreeding effects will increase rapidly with possible local extinctions (Seiler 2001). Nevertheless, the presence of some kind of underpasses or bridges, that makes the crossing possible for at least one animal, in particular a male, could satisfactory maintain the genetic variation, although it might not be enough to maintain the population size and then minimize local extinctions (Formann and Sperling 2002).

The transfer experiment on Road 105 has also shown that voles, and particularly mice, successfully return to the original side of the road after being transferred, irrespectively of gender or age. Thus, after transfer, these roads do not act as selective barriers (Dobrowolski *et al.* 1993; Kozakiewicz 1993). The same phenomenon was observed by Bąkowski and Kozakiewicz (1988) in the same species and by Merriam *et al.* (1989) in *Peromyscus leucopus*.

We expected a higher return of adults compared with subadults, because of the territoriality of adults, who have their territories at the original side of the road, while young animals might be expected to be more prone to disperse and find new places for maturation and reproduction (Bujalska 1970, Gliwicz 1988, 1993). However, these differences were not born out by our data, even though only 20% and 40% of subadult voles and mice returned across the road. These animals have probably established their home ranges and then homed back.

Females were reported to be more territorial than males (Bujalska 1970). Thus one could hypothesize females to have a higher tendency to cross the roads back after transfer for two reasons: (1) to take care of the offspring, because the breeding season of *C. glareolus* and *A. flavicollis* spans from March to end of October

(Montgomery 1979, Andera and Horácek 1982, Pucek *et al.* 1993, Dungel and Gaisler 2002); (2) the transferred females are expected to be repelled by "native" ones. According to another hypothesis, sexually active males tend to be more mobile than females, because they are searching for females (Rajska-Jurgiel 1992) and therefore they may be more likely to cross the roads. In our data, only 28 and 40% of female voles and mice respectively, while more than 60% of males of both species were recaptured at their own side. This supports the latter hypothesis.

More than 75% of all transferred animals of both species were recaptured at the side at which they were originally captured within 24 hours from the capture. This quick return to their "home" side suggests the crossing back was due to homing, not due to repellence by "native" animals, as the latter process would take much more time (Kozel and Fleharty 1979).

Among individuals that were recaptured at the side they were transferred to, particularly voles were recaptured close to the traps where they were released; this may be interpreted as animals seeking refuge in the traps (Kozel and Fleharty 1979). A homing intention could be ruled out, because almost all individuals were recaptured either in the forest lines (they moved there from the road lines, where they were released), or several times around a specific trap, no matter whether it was close to the place at which the animal was released or further away. These subsequent recaptures could indicate that displaced individuals are establishing a new home range at the place that they found "vacant", an empty space left by a transferred animal that did not return.

In conclusion, this study indicates that stable populations of mice and voles live along roads, but that the road surface inhibits their movements. Narrow roads act as a partial barrier at the individual, not population level, without gender or age filter, while highways act as a partial barrier at the population level, affecting not only individuals, but dividing and isolating populations (Dobrowolski *et al.* 1993).

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