ARE NON-WILDLIFE UNDERPASSES EFFECTIVE PASSAGES FOR WILDLIFE?

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Abstract

In order to mitigate barrier effects of highways and exclusion fences on wildlife, many countries have invested in specific wildlife crossing structures placed at selected strategic locations. While such structures may be significant to species conservation or management at local scale, they may not necessarily suffice to maintain landscape connectivity at broad scale. Conventional, non-wildlife road bridges, tunnels and culverts, however, are usually abundant along the major infrastructure corridors and are known to be used by animals at least occasionally. Given the large number and density of such passages, their accumulative effect may well be underestimated. On the other hand, there is uncertainty about how effectiveness of wildlife passages should be judged, because clear objectives and performance targets are undeveloped. We used track inventories to study the relative use of a total of 57 conventional road underpasses in south-central Sweden by common wildlife species such as moose (*Alces alces*), roe deer (*Capreolus capreolus*), red fox (*Vulpes vulpes*), badger (*Meles meles*) and hares (*Lepus* spp.). We studied the influence of passage dimensions, design, human disturbance and landscape factors and derived recommendations on limits in size and openness based on selected multiple regressions. Our results support earlier findings in that ungulates are more sensitive to underpass dimensions as medium-sized carnivores and hares. In general, moose and, to some degree also roe deer, used underpasses much less than expected from their occurrence in the surrounding habitat, whereas badgers and foxes, in particular, showed clear preference towards the underpasses. Openness appeared as a strong predictor for the relative use by most species, but also traffic within the underpasses and distance to nearest forest cover were important variables. Landscape attributes, such as habitat composition within 500 m around the passage or the distance to the nearest alternative crossing option, were of less significance to the relative use of underpasses. We estimated that underpasses with a relative openness of 2.3 (and minimum width of 11m), with limited human and vehicular traffic (12 passages per day) and nearby forest cover (distance <15 m) are likely to be used by moose at random, i.e., as much as expected from moose activity on control track beds. Smaller animals, including roe deer, will use such passages more frequently. We propose establishing random passage use (use as expected) as a performance target for non-wildlife crossing structures. Higher targets should be set for adapted wildlife passages. Additional, ecologically scaled performance targets must address the distance between adjacent crossing facilities. We conclude that, at least in Sweden, only a minor proportion of conventional road underpasses built for local access roads provide effective passages to roe deer and smaller species, and only very few to moose. It is worthwhile studying, however, whether other facilities can be created to provide safe passage for wildlife across roads or whether additional protective features can increase the attractiveness of existing structures and thereby provide more cost-efficient mitigation than the investment in new, adapted wildlife passages.

Introduction

For more than three decades, exclusion fencing to prevent wildlife-vehicle collisions has become a standard for new highways in Sweden (Almkvist et al 1980). Over 7000 km of public roads are fenced by now and more is planned as part of road upgrading and traffic safety programs (Anders Sjölund, Swedish Road Administration, pers. comm.). Recently, however, road planners started to acknowledge barrier effects on wildlife induced by fencing and realized that not all major roads can be fenced without providing passages to wildlife (Björckebaum and Mossberg 2007). The first deer overpasses have been built (Olsson, Widén and Larkin 2008, Olsson & Widén 2008), and there is evidence, that already conventional road bridges and underpasses may reduce the risk for moose-vehicle collisions (Seiler 2004), suggesting that combining fences with passages may both enhance traffic safety and safeguard wildlife movements (Ward 1982, Dodd et al 2009). Mitigation action plans are now under development to counteract the increasing barrier effects of roads on animals as well as on humans (e.g., Swedish Road and Rail Administrations 2005).

Given the extent of the fenced road network in Sweden, however, it may not suffice, to install a few well-designed ecoducts or green bridges. Neither will it be necessary to invest in wildlife passages every two to three kilometers. Rather, it appears more effective and desirable to integrate wildlife crossing solutions in the regular road-planning scheme and use them as part of a more general landscape permeability concept (Iuell et al. 2003). This may include various options including automated deer-warning systems installed in fence openings (Huijser and McGowen 2003), traffic rerouting and calming (Jaarsma and Willems 2002), speed reduction (Seiler 2005), and the adjustment of conventional road crossings for a combined use by humans and wildlife (e.g., Rosell et al. 1997, Mata et al. 2008).

In Sweden, thousands of non-wildlife underpasses (and bridges) separate highway traffic from privately owned local access roads, human and cattle trails. Many more underpasses exist for creeks and rivers, while a few viaducts span over entire valleys or wetlands. Although presumably none of these structures has been build with respect to wildlife or provides any fauna adjustments, they may nevertheless be used to a varying degree by deer and other larger mammals. Anecdotal observations (by the authors) and unpublished inventories from Sweden (Seiler & Rydin 1998) suggest that even moose (*Alces alces*) may eventually use pedestrian culverts as small as 2 meter in diameter, while roe deer (*Capreolus capreolus*) may regularly utilize unprotected road bridges (4 m width and 40 m length) over motorways. Also other studies have documented a more or less frequent use of conventional, non-wildlife road passages by animals (e.g., Olbrich 1984, Yanes et al 1995, Rodriquez et al 1996, Ng et al. 2006, Mata et al. 2008). Given the large number of existing road passages in the Swedish countryside and the relative low degree of disturbance by humans or local traffic, the beneficial effect of these unintended crossing structures might thus be underestimated.

However, the mere occurrence of animal tracks within an underpass does not automatically imply that the structure is efficient for the species in question. The observed pattern could simply result from a high animal abundance in the surrounding habitat but still express avoidance behavior. To control for this, the number of tracks found in an underpass must be related to some measure of animal abundance or activity outside the passage (Clevenger and Waltho, 2000, 2005). At a proximate level, when the number of tracks going through a passage is equal or higher than expected from chance, i.e., from the species' occurrence in the surrounding, the passage could be considered as at least locally effective. Ultimately, however, this does not imply that this single structure will be efficient in preventing genetic isolation or demographic divergence at large. To achieve this, many more effective passages may be needed along the barrier line.

While the understanding of passage effectiveness is still weak, knowledge about the use of crossing structures by wildlife and the factors that discourage or promote their use is quickly increasing (see Glista et al. 2009, for review). Three main classes of factors determining passage use can be distinguished: passage structure and dimension, surrounding landscape features including habitat distribution, and human disturbances (e.g., Rodriguez et al. 1997, Cain et al. 2003, Clevenger and Waltho 2000, Ascensão and Mira 2007). The effect of these variables is highly species specific. Ungulates, for example, are generally more reluctant to use narrow road underpasses than medium-sized carnivores (e.g. Mata et al. 2008), whereas larger carnivores may be more sensitive to human disturbances in crossing structures than to dimensions (Clevenger and Waltho 2000). However, only few of all relevant variables can be addressed in the planning of conventional road passages. In practice, it is mainly the width of an underpass, the vegetation cover at its immediate surrounding, the fencing of the road above, and additional structural components such as noise or light shields, that can be adjusted by road engineers with relative ease. All other variables are either limited by constraints for traffic safety, road standard or other technical matters, or cannot be controlled for by the transport sector (habitat composition, topography, human use of underpass).

In our study, we therefore put special emphasis on the effect of underpass dimensions but included other ecologically meaningful parameters as well, such as distance to nearest alternative passage or frequency of vehicles and humans trespassing the underpass. Our main concern was to evaluate whether or not, and under what conditions, conventional road underpasses can be regarded as effective wildlife passages. We conclude by proposing limit values for passage dimensions that at least will ensure a random use by wildlife.

Materials and Methods

Study Sites

During 1997 to 2005, we conducted a series of inventories of the use of conventional road crossing structures by wildlife. Here, we present results from 57 typical minor road underpasses built under 6 major motorways, (E4, E6, E18, E22, RV40, RV44) in southwestern and southeastern Sweden (figure 1). The locations were selected in order to be representative for road underpasses made for forestry or agricultural local access roads under motorways, while maximizing the variation in passage dimensions (figure 2) and reducing the variation in road characteristics, traffic volume, habitat composition, and species occurrences. The underpasses were located in areas dominated by coniferous, semi-boreal forest, with no permanent housing in immediate vicinity and with no or only very limited trespassing vehicular traffic or human disturbance. None of these passages, except one large culvert (E6-9), was originally designed for wildlife and none was equipped with protective shields to reduce disturbance of animals by traffic noise or light. Most passages (N=49) were standard concrete bridges (figure 3), while some contained steel-tunnels built primarily for pedestrians (N=8). Some underpasses (N=12) consisted of two adjacent constructions separated by a small opening for the central reserve between the motorway lanes, but most were closed, single buildings. A few underpasses contained both road or trail and a small watercourse (N=5), while the majority was dry (N=52). All structures were considered large enough to at least in theory provide passage for moose, i.e., their opening was larger than 2 m in diameter. All motorways were fenced against larger wildlife (standard moose fences of 2 m in height), and carried a traffic load above 10,000 vehicles per average day (National Road Database 2007). Local traffic, pedestrians, as well as larger animals were not supposed or able to cross the motorways at grate.

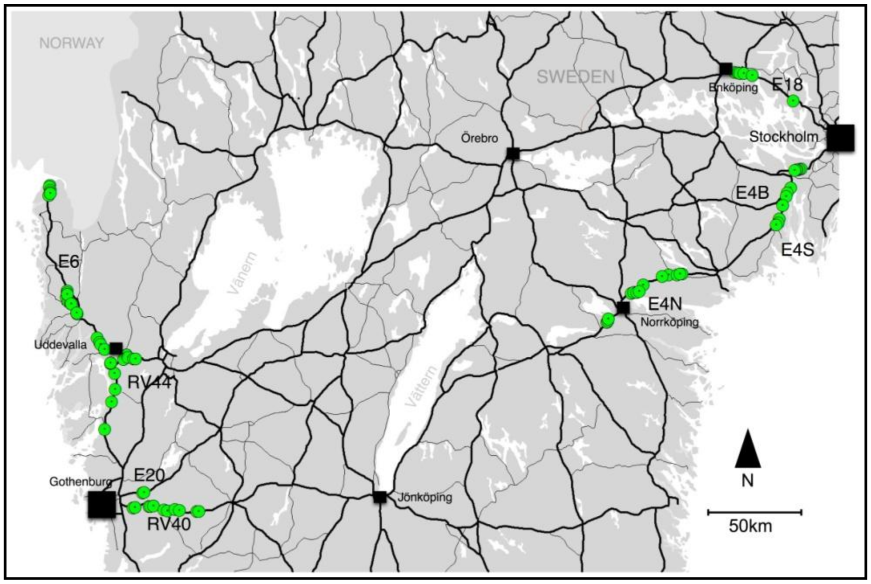

Figure 1: Map over south-central Sweden with study sites.

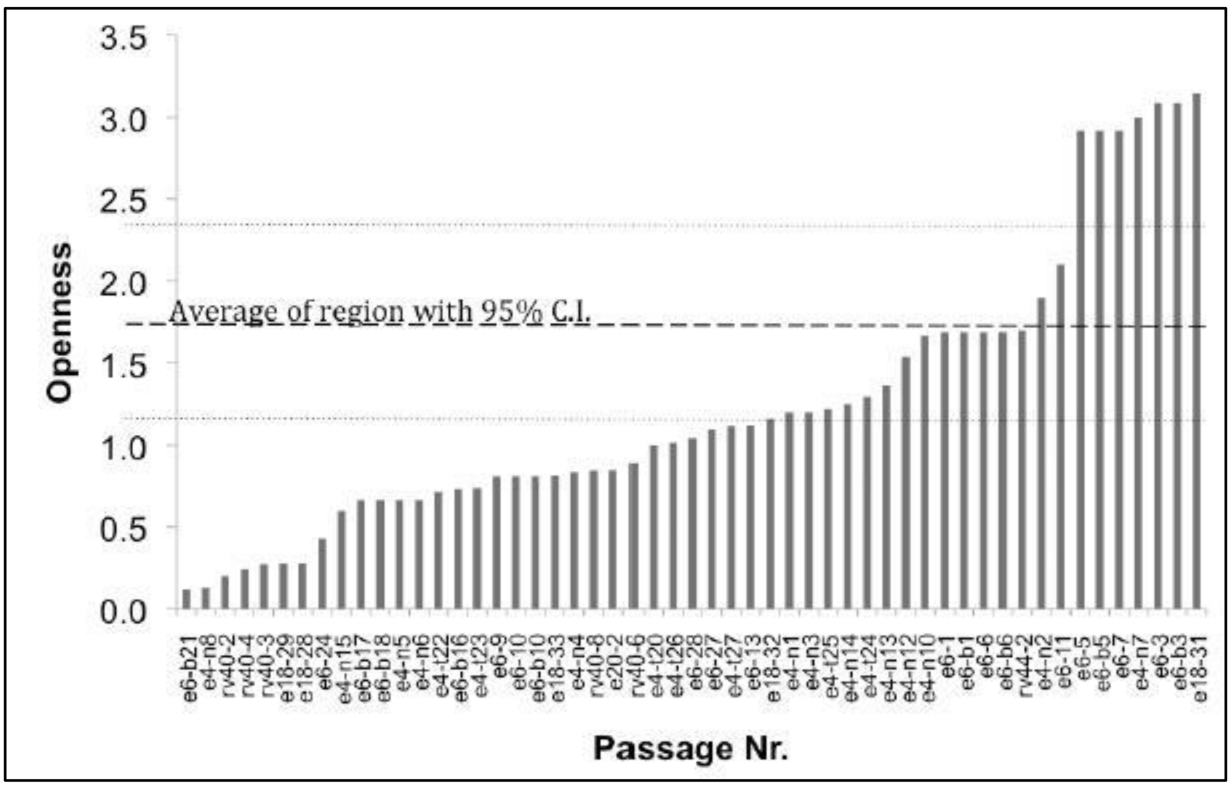

Figure 2: Variation in openness among the studied underpasses.
Dotted lines indicate the average openness calculated for all similar underpasses (N=185) under motorways in the region VMN of the Swedish Road administration (SRA bridge database 2007).

Figure 3: Picture of a typical road underpass for local but publicly used gravel road in Sweden. The picture shows underpass E4N-12 (width 8m, height 5m, length 26m, openness 1.54) that has been completely avoided by moose (U=0), but used to some degree by roe deer (U=0.32), more often by foxes (U=0.63) and very frequently by hares (U=0.96). Photo Andreas Seiler.

On each location (table 1), we measured the structural dimensions of the underpass, and the distance to the nearest bridge, tunnel or fence opening that eventually could be used by wildlife to cross the highway. Vehicular traffic passing through the underpasses was estimated based on vehicle counts made during the inventories and specific visits, averaged as number of vehicles per daytime hour. Land cover proportions (within 200 m distance from underpass) and the number of and the distance to houses and nearest continuous forest (within 500 m distance) were quantified from topographic satellite maps (Swedish Land Survey, SMD maps). Road and road traffic data was obtained from the National Road Database of the Swedish Road Administration (SNRA 2007).

Variable	Description
Tracks on test bed	Averaged number of tracks found per day on the sand bed within the underpass
Tracks on controls	Averaged number of tracks found per day on all control sand beds
Usage of underpass	Response variable, Proportion of tracks in underpass of all tracks recorded
LENGTH	length of the underpass ceiling (in meter)
WIDHT	maximum width of the underpass (in meter)
HEIGHT	maximum height of the underpass (in meter)
OPEN	Openness = width * height / length
TRAFFIC	Average number of cars recorded per hour within the underpass
HOUSES	Number of buildings within 500 m from the underpass (on topographic map)
HOUSE_DIST	Distance to the nearest building (on topographic map)
FOREST_DIST	Distance to nearest forest cover (on topographic map)
FOREST_RATIO	Ratio of forest cover within 200 m between the opposite road sides
PASS_DIST	Distance to the nearest crossing structure (tunnel, bridge, end of fence)
ROADS	Density of roads within 500 m radius from the underpass (km/km2)
URBAN	Percentage of urban land cover within 200 m radius
AGRICULT	Percentage of agricultural land within 200 m radius
FOREST	Percentage of forest within 200 m radius (sum of dec, con, mix)

Table 1: Description of measured variables. Land cover percentages and usage proportions were arcsine transformed.

Tracking

We used track beds to record animal movements within and nearby the selected road underpasses. Track beds consisted of sand layers (1 m in width, about 3-5 cm in depth, and length equal to the diameter of the underpass) placed within each underpass (test bed) and in the nearer surrounding on either side of the road (control beds). Depending on topography and vegetation, one to three control beds of the same size as the test bed were placed on either side within 100 m from the entrances of the passage. Animal tracks recorded on the control beds of a given site were averaged over all controls and both roadsides.

The track beds were re-visited for new tracks on a weekly basis in intervals of usually 1-3 days. Each track was identified and counted, if the sand layers were found operational, that is not disturbed by heavy rain, vehicles or animals. However, it was not possible to determine the number of individuals that crossed each bed. After each visit, the sand beds were raked smooth in preparation of the next visit.

A total of 57 road underpasses were studied in this way, however, the final sample that could be used in the analysis for each respective species was smaller (table 2). In order to combine data collected during different years and by different field personnel, we imposed the following qualitative and quantitative restrictions:

- Only data from inventories made during June to November was used, which was the period of year where data existed in all passages.
- Each location must have been re-visited and measured at least 9 times independently.
- For a location to be included the analysis of one species, it had to be visited at least 3 visits by the species in question (i.e., tracks were found on either test or control beds).
- Inventories were considered valid when the time interval between consecutive measurements was 1-3 days, in moose <7 days, however, provided that the sand layers were found operative.

Species	N sites studied	N repeated visits	Mean N of visits per site	N tracks in underpass	N tracks in mean control
Moose	26	912	35	77	204
Roe deer	51	1344	26	306	777
Badger	18	667	37	130	195
Red fox	25	905	36	203	231
Hares	10	466	47	75	106

Table 2. Sample sizes (*number* of sites and number of visits) and number of visits where animal tracks were found on either test or control sand beds, respectively.

On average, we obtained 36 operative visits per location and between 10 to 51 valid sites per species (table 2). Various wildlife species including wild boar (*Sus scrofa*), lynx (*Felis lynx*), red deer (*Cervus elaphus*), otter (*Lutra lutra*) were found to use some of the sites occasionally, but only moose, roe deer, red fox (*Vulpes vulpes*), badger (*Meles meles*) and hares (*Lepus europeaus and Lepus timidus*) produced sufficient data to be included in this analysis.

Index of Use

We calculated the relative use of an underpass by a given species as the ratio of tracks found in the underpass per operative day to all tracks found in underpass and control beds combined. Hence, the relative use is given as $U = P / (P + C)$, where P is the number of tracks found on the test bed within the underpass per day and C is the average number of tracks per day found on all control beds combined. The index value ranges hence from zero to one, with 0.5 indicating that the passage was used as much as what could be expected from the controls. In other words, if $U = 0.5$, the underpass is neither repelling nor attracting wildlife and has the same chance of being visited as an average control sand bed in the surroundings. For the regression analysis, U values were arcsine transformed to compensate for the skewed distribution (Zar 1998) and averaged over all measurements per location and species.

Statistical Analysis

We used Mann-Whitney U tests to distinguish different types of underpasses in their effect on passage use by wildlife (concrete rectangular underpass versus steel tunnel; closed versus divided passage; dry passage versus combined with water). However, since we did not find a differential effect on passage use in any of these pairs (minimum p-value=0.235, U=46, adj. Z=-1.185, N=19,7), passage type was not maintained as predictor variable in the further analysis.

We then used univariate regression models to identify which of the independent (continuous) variables correlated with passage use. To reduce intercorrelation among these predictor variables, we used only the most effective variable of those that, after a sequential Bonferroni correction (Rice 1989), significantly correlated with each other. The remaining variables were entered in general regression models with the response variable being the arcsine transformed relative use per species. The models were ranked using Akaike's Information Criteria (AIC) to identify the most parsimonious subsets (Burnham & Anderson 2002). Among these subsets (difference from model with lowest AIC value < 2), we chose the model that combined most factors that that are subject to road planning, i.e. passage dimensions (width, height, openness), location (distance to nearest alternative passage and distance to nearest forest cover) and human disturbance (trespassing vehicular traffic, vicinity to houses, density of roads). Calculations were performed with the statistical software package STATISTICA (StatSoft 2008).

Results

We observed clear differences among the species in how readily they used conventional road underpasses (table 3). On average, moose was significantly reluctant to cross through the passages (mean U=0.33), while foxes clearly selected using the underpasses. Roe deer and badgers, correspondingly, showed similar but not significant behavior (at 95% level). In all species except hares, the frequency of tracks found within the underpasses was strongly correlated with track frequency on control beds (p<0.001). The relative use, however, was affected by passage dimensions, passage location and the surrounding habitat. As expected, the variables acted differently on the different species. Overall, passage openness provided a better predictor for the relative use than passage width, length or height, individually or combined. Human and vehicles using the underpass were a valuable predictor for the use by most species, whereas the distance to the nearest alternative crossing structure (ca 800 m on average) had little effect on underpass use. As intended by the design of our study, location and landscape variables such as the distance to the nearest building, number of houses, forest cover, etc. (table 4), varied only little and provided therefore weaker predictors.

Species	Mean relative use	SD	t	df	p
Moose	0.33	0.31	-2.84	25	0.009
Roe deer	0.44	0.25	-1.81	50	0.077
Badger	0.63	0.27	1.98	17	0.064
Red fox	0.76	0.12	10.88	24	0.000
Hares	0.63	0.32	1.23	9	0.250

Table 3. Test of means of relative underpass use against the reference constant U=0.5 (relative use as expected from controls).

	MOOSE (N=26)			ROE DEER (N=51)			BADGER (N=18)			FOX (N=25)			HARE (N=10)		
Variable	**Mean ± S.D.**	**R**	***p***	**Mean ± S.D.**	**R**	***p***	**Mean ± S.D.**	**R**	***p***	**Mean ± S.D.**	**R**	***p***	**Mean ± S.D.**	**R**	***p***
Tracks on testbed	0.026 ± 0.036			0.095 ± 0.122			0.066 ± 0.084			0.066 ± 0.051			0.023 ± 0.022		
Tracks on controls	0.025 ± 0.032			0.090 ± 0.091			0.039 ± 0.072			0.017 ± 0.013			0.009 ± 0.010		
Usage of underpass	**0.325 ± 0.314**			**0.437 ± 0.247**			**0.627 ± 0.271**			**0.763 ± 0.121**			**0.626 ± 0.323**		
LENGTH	25.715 ± 3.999	-0.504	*0.009*	26.849 ± 7.105	-0.138	*0.335*	29.122 ± 7.778	0.300	*0.227*	26.028 ± 8.361	0.065	*0.758*	24.960 ± 3.956	-0.558	*0.094*
WIDHT	6.958 ± 3.270	0.409	*0.038*	6.569 ± 3.108	0.257	*0.069*	6.200 ± 2.939	-0.127	*0.617*	6.656 ± 3.144	-0.368	*0.071*	7.700 ± 2.936	0.502	*0.139*
HEIGHT	4.896 ± 0.867	0.167	*0.414*	4.571 ± 1.219	0.200	*0.159*	4.694 ± 1.446	0.003	*0.992*	4.456 ± 1.306	-0.234	*0.261*	5.150 ± 0.280	0.208	*0.564*
OPENNESS	1.462 ± 0.896	0.498	*0.010*	1.269 ± 0.841	0.275	*0.051*	1.153 ± 0.818	-0.127	*0.616*	1.302 ± 0.888	-0.401	*0.047*	1.674 ± 0.810	0.510	*0.132*
TRAFFIC	0.952 ± 2.167	-0.250	*0.219*	0.874 ± 1.761	-0.330	*0.018*	0.524 ± 1.107	-0.651	*0.003*	0.789 ± 1.422	0.205	*0.326*	1.189 ± 1.802	0.279	*0.435*
HOUSES	2.885 ± 2.658	0.258	*0.204*	3.765 ± 4.407	0.345	*0.013*	2.222 ± 1.927	0.183	*0.468*	4.320 ± 4.534	0.017	*0.936*	2.800 ± 2.700	0.236	*0.511*
HOUSE_DIST	294.0 ± 165.8	-0.270	*0.183*	310.3 ± 194.0	-0.037	*0.798*	372.6 ± 187.9	0.042	*0.867*	339.7 ± 234.1	0.134	*0.523*	330.6 ± 206.2	-0.409	*0.240*
FOREST_DIST	5.032 ± 12.178	-0.189	*0.356*	16.468 ± 36.330	0.253	*0.073*	12.667 ± 27.788	0.033	*0.896*	21.822 ± 40.127	-0.072	*0.733*	9.794 ± 18.670	0.002	*0.996*
FOREST_RATIO	0.469 ± 0.134	-0.143	*0.486*	0.501 ± 0.197	0.010	*0.943*	0.504 ± 0.177	0.298	*0.229*	0.476 ± 0.194	0.272	*0.189*	0.503 ± 0.124	0.209	*0.563*
PASS_DIST	812.3 ± 339.9	-0.160	*0.436*	807.9 ± 378.1	-0.129	*0.369*	869.1 ± 368.8	-0.276	*0.267*	831.5 ± 386.1	0.107	*0.611*	837.0 ± 365.0	0.397	*0.256*
ROADS	1.380 ± 0.872	-0.522	*0.006*	1.504 ± 0.789	-0.258	*0.067*	1.330 ± 0.863	-0.456	*0.057*	1.430 ± 0.691	0.067	*0.749*	1.614 ± 1.059	0.114	*0.753*
URBAN	11.878 ± 6.085	-0.551	*0.004*	14.871 ± 6.422	-0.180	*0.207*	14.583 ± 5.927	-0.167	*0.509*	15.513 ± 6.546	0.363	*0.075*	13.907 ± 5.971	-0.249	*0.488*
AGRICULT	21.706 ± 11.320	0.049	*0.814*	23.590 ± 13.668	0.333	*0.017*	24.251 ± 15.065	-0.014	*0.955*	25.258 ± 14.139	-0.165	*0.431*	20.786 ± 8.772	0.627	*0.052*
PASTURE	12.594 ± 7.506	0.167	*0.415*	12.805 ± 7.205	0.318	*0.023*	10.737 ± 7.345	-0.006	*0.980*	11.434 ± 7.067	-0.337	*0.099*	12.039 ± 5.538	0.076	*0.835*
DECIDUOUS	14.549 ± 6.396	0.184	*0.369*	13.015 ± 5.962	-0.171	*0.230*	12.783 ± 4.855	0.018	*0.945*	12.450 ± 5.072	0.054	*0.798*	14.994 ± 3.686	-0.522	*0.122*
CONIFEROUS	39.677 ± 10.152	-0.096	*0.641*	38.423 ± 11.417	-0.282	*0.045*	39.776 ± 12.843	0.103	*0.685*	38.630 ± 11.802	0.101	*0.631*	39.458 ± 9.212	-0.113	*0.755*
MIXED	2.539 ± 2.627	-0.174	*0.397*	2.502 ± 2.806	0.163	*0.253*	3.188 ± 3.104	0.354	*0.150*	2.873 ± 3.091	-0.025	*0.907*	3.047 ± 3.195	-0.643	*0.045*
FOREST	56.765 ± 12.330	-0.021	*0.920*	53.941 ± 13.508	-0.280	*0.047*	55.748 ± 14.412	0.174	*0.491*	53.952 ± 13.665	0.102	*0.629*	57.499 ± 12.152	-0.413	*0.235*

Table 4. Descriptive statistics of the selected variables and their univariate correlation (R-value) with the usage of underpasses by the given species.

Moose

Underpass use by moose increased significantly with openness (R^2=0.248, $F_{1,24}$=7.92, p<0.010) and width (R^2=0.167, $F_{1,24}$=4.82, p<0.038), as well as with reduced passage length (R^2=0.254, $F_{1,24}$=8.17, p<0.008). Openness together with the amount of traffic through the underpass and the distance to the nearest forest cover comprised one of the best variable subsets according to AIC comparison (table 5), but still explained only a small part of the observed variation in use (adjusted R^2 = 0.29). Overall, passage use by moose was adversely affected by human disturbance (roads, houses, agriculture) in the surroundings, by human use of the underpass (traffic), and by the distance to nearest forest cover. However, these variables were only effective if combined with passage dimensions, and decreased only slightly the residual variation.

Roe deer

Roe deer was generally less affected by passage dimensions than moose (OPEN: R^2=0.076, $F_{1,49}$=4.016, p<0.051; WIDTH: R^2=0.066, $F_{1,49}$=3.455, p<0.069), but more sensitive to traffic (R^2=0.109, $F_{1,49}$=5.982, p<0.018). As in moose, openness combined with traffic and distance to forest cover, produced one of the best variable subsets explaining underpass use by roe deer (table 4, adj. multiple R^2=0.184, $F_{4,21}$=4.757, p<0.006). Usage also increased significantly with more houses, more agriculture and less forest cover in the surroundings of the underpass, thus reflecting the species' habitat preferences. However, despite the comparably large sample size in roe deer, these models resolved only little of the observed variation (table 5).

Badger

Badgers appeared indifferent to passage dimensions as they frequently used even the smallest underpasses (R^2=0.055, $F_{1,16}$=0.117, p>0.737). In fact, their tracks were found more often in the underpasses than expected from track frequency on the control beds, although the difference was not significant (table 3). On the other hand, badgers responded negatively to traffic, and as in roe deer, this factor was by far the single most influential predictor of the relative underpass use by this species (table 4; R^2=0.423, $F_{1,16}$=11.790, p<0.003).

Red Fox

Foxes clearly took greatest benefit from road underpasses as they used them on average 50% more often than expected, were not sensitive to trespassing traffic, and seemed overall little affected by location and landscape parameters. However they preferred smaller passages (R^2=0.161, $F_{1,23}$=4.402, p<0.0469).

Hares

In hares, sample size was very limited (N=10). Nevertheless, the best variable subset contained openness, traffic and the proportion of deciduous forest cover in the surrounding landscape (table 5; R^2=0.763, $F_{3,6}$=6.433, p<0.022). Hares seemed to avoid underpasses that were frequently used by foxes (R^2=0.312, $F_{1,8}$=5.093, p<0.054), and when underpass use by fox was included as independent variable in the multiple regression analyses, subsets containing fox, traffic and agriculture ranked second best according to their AIC.

	Regression Coefficients					Model	
MOOSE	Coeff. (B)	S.E	S.E. of B	t-Value	P-Value	DF	F
Intercept	0.122	0.118	0.122	1.036	0.312	3,22	4.40
OPENESS	0.216	0.069	0.536	3.153	0.005	adj. R2	P
TRAFFIC	- 0.053	0.028	- 0.317	- 1.866	0.075	0.29	0.014
FOREST_DIST	- 0.006	0.005	- 0.205	- 1.216	0.237		
ROEDEER	Coeff. (B)	S.E	S.E. of B	t-Value	P-Value	DF	F
Intercept	0.377	0.067	0.377	5.627	0.000	3,47	4.76
TRAFFIC	- 0.054	0.021	- 0.339	- 2.599	0.013	adj. R2	P
OPENESS	0.094	0.044	0.282	2.167	0.035	0.184	0.006
FOREST_DIST	0.001	0.001	0.179	1.370	0.177		
BADGER	Coeff. (B)	S.E	S.E. of B	t-Value	P-Value	DF	F
Intercept	0.611	0.206	0.611	2.958	0.010	2,15	5.38
TRAFFIC	- 0.173	0.060	- 0.579	- 2.901	0.011	adj. R2	P
FOREST_RATIO	0.388	0.375	0.206	1.033	0.318	0.340	0.017
FOX	Coeff. (B)	S.E	S.E. of B	t-Value	P-Value	DF	F
Intercept	1.008	0.067	1.008	15.139	0.000	1,23	4.42
OPENESS	- 0.089	0.043	- 0.401	- 2.102	0.047	adj. R2	P
						0.125	0.047
HARE	Coeff. (B)	S.E	S.E. of B	t-Value	P-Value	DF	F
Intercept			1.229	3.182	0.019	3,6	7.03
DECIDUOUS	- 0.657	0.193	- 0.077	- 3.399	0.015	adj. R2	P
OPENESS	0.613	0.201	0.326	3.054	0.022	0.668	0.022
TRAFFIC	0.431	0.200	0.103	2.158	0.074		

Table 5. Results of selected multiple linear regression models for underpass usage by five game species. For more information about model selection see text.

Limits	Moose	Roe deer	Badger	Fox	Hares
openness	2.3 (**)	1.4 (**)	NA	NA	1.2 (°)
width	11m (**)	7m (**)	ns	ns	ns
length	22m (°)	23m (*)	ns	ns	ns
height	ns	4.5m (*)	ns	ns	ns

Table 6. Recommended dimensions for wildlife adjustments of road underpasses based on multiple regressions (compare table 4). The models include additional predictor variables: TRAFFIC (=0.5 v/h), FOREST_DIST (=15m) and in hares: DECIDUOUS (=15%). Underpass use by badgers and foxes was not limited by passage dimensions within the observed range. Significance levels: NA not applicable, ns p>0.1, ° p<0.1, * p<0.05, ** p<0.01.

Limit Values

Based on the coefficients of the above multiple regression models, the set of conditions can be predicted under which track frequencies in an underpass are likely equal or exceed those expected from controls, i.e., when the underpass can be considered being effective (table 6). In an average situation, that is, when only a few vehicles pass through the underpass (Traffic < 0.5 /h), and forest cover is nearby (< 15m from structure), the underpass should have an openness index larger than 2.3 in order to provide an effective passage for moose, or 1.4 for roe deer, respectively. In hares, given the same conditions as above plus a proportion of deciduous forest cover of 15% within 500m of the location, an openness of 1.2 may probably suffice. These limits for underpass openness include, however, that the width is not smaller than 11 m in moose or 7 m in roe deer, respectively. Already somewhat narrower passages, more traffic, or greater distance to forest cover will start to discourage these animals from using the underpass, whilst not entirely preventing its usage by these species.

In figure 4, we used univariate regressions between openness and relative use by moose and roe deer, to illustrate how usage changes with openness. These regressions are highly significant (Moose R^2=0.639, $F_{1,25}$=44.24, p<0.0001; Roe deer R^2=0.645, $F_{1,50}$= 90.68, p<0.0001), as we excluded the intercept (roe deer: 0.336, moose: 0.072) assuming that an openness of null would not allow any animals to use to passage. However, confidence limits for these predictions are large. In moose, for example, the threshold openness may range from 1.7 to 5.2 (mean 2.4). Note also that these univariate predictions deviate from the limit values proposed in table 6.

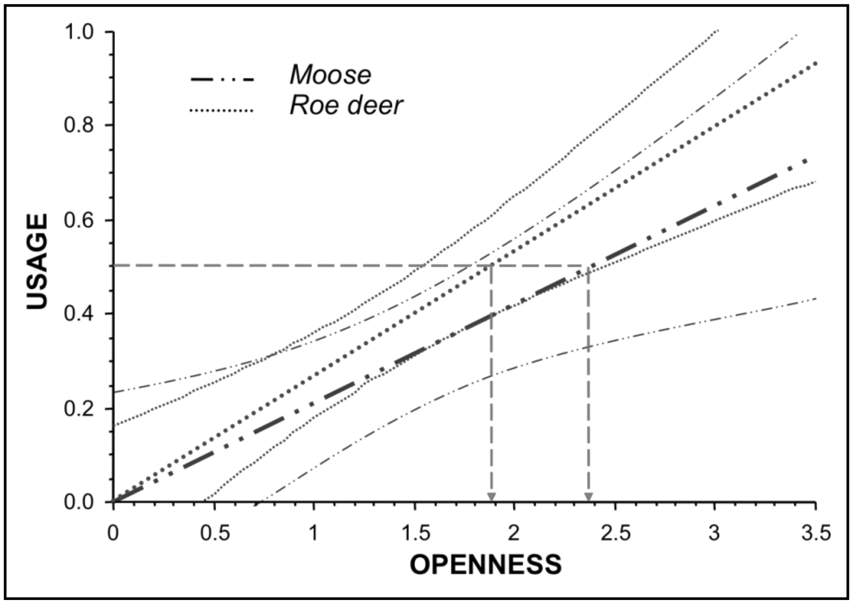

Figure 4. Predicted effect (mean with 95% C.I.) of altered openness on underpass use by moose and roe deer. Predictions were based on univariate regression models with excluded intercepts.

Discussion

Underpass width, and especially openness, appeared to be strong a predictor of the relative use of underpasses by wildlife. Surprisingly, openness was generally more effective than width, height or length taken individually or together. This supports the use of openness as a general criterion in the design of wildlife passages (e.g., Iuell et al. 2003).

Differences between Species Groups

As expected, there were significant differences between the species in how much they preferred or avoided a passage or responded to differences in openness. Moose, as the largest species, was generally more reluctant than roe deer and the smaller species to cross through underpasses and was more sensitive to passage openness and width. Roe deer also preferred wider passages and refrained from using more trafficked underpasses. This is in line with earlier studies suggesting that large mammals, and large ungulates in particular, such as moose (Clevenger et al. 2002), elk (i.e. red deer; *Cervus elaphus*) (Olbrich 1984, Clevenger and Waltho 2005), mule deer (*Odocoileus hemionus*) (Ward 1982, Ng et al. 2004), fallow deer (*Dama dama*) and roe deer (*Capreolus capreolus*) (Olbrich 1984), generally prefer passages that are considerably wider, taller and shorter and less disturbed on average, than the structures that facilitate movements of small and medium sized mammals such as lagomorphs (hares (*Lepus granatensis*) and rabbit (*Orictolagus cuniculus*)), badger, genet (*Genetta genetta*) or red fox (Rodriguez et al. 1996, Rosell et al. 1997, Ascensão and Mira 2007). This may simply be due to their greater body size, but also be related to their biology as prey species. In northern Sweden, Seiler et al. (2003) observed that migratory moose preferred to cross road fences and highway rather than using the (narrow) road underpasses that have been built to reconnect their migration routes. Kusak et al (2008) showed that the ratio of large mammals crossing the highway in Gorski Kotar (Croatia) on wide overpasses was several times larger than compared to narrow underpasses. Iuell et al (2003) recommend therefore building overpasses or viaducts instead of more narrow underpasses as crossing structures for ungulates and other larger mammals.

We observed that foxes did not seem to bother the occasional presence of humans or vehicles near or in the underpass nor its structural features. In fact, foxes were significantly less selective for larger underpasses, while still using them more often than expected by chance. As can be expected from their ground-dwelling activities, foxes and badgers may be more comfortable with smaller passages (Ascensão and Mira 2007), although this pattern might change in smaller passages (Grilo et al. 2008). In general, medium-sized carnivores are frequently reported using drainage culverts or pipes under highways and railway lines (Rodriguez et al 1996, 1997, Rosell et al. 1997, Ascensão and Mira 2007). Similar applies to hares and presumably various other medium-sized to small mammals. Studies suggest that for smaller mammals, the physical dimensions and design of an underpass are generally less important than its placement and surrounding habitat (Rodriquez 1996, Clevenger et al. 2001, Ascensão and Mira 2007, Grilo et al. 2008). Thus, with respect to these species, the typical road underpasses built in Sweden for local access forestry or agriculture roads, do not need any further adjustment to be an effective crossing facility. However this does not imply that their number and distribution suffice to mitigate the barrier or mortality effect of roads and railroads on populations of these species. The problem here may not be that roads impose dispersal barriers but instead kill a significant proportion of the population (e.g., Clarke et al. 1998, Seiler & Helldin 2006).

Evaluating Effectiveness

These general pattern are not astonishing, but must be translated into thresholds and limit values if practical guidance is to be derived for road engineers and planners. Olbrich (1984) concluded from his extensive inventories of 788 crossing structures in Germany, that structures with a relative openness of 0.75 were suitable for roe deer, while red deer and fallow deer were more likely to use passages wider than 1.5. According to the European handbook on Wildlife and Traffic (Iuell et al. 2003), an underpass for large and medium-sized animals should exceed a minimum width of 15 m, height of 3-4 m, and a relative openness of 1.5. Joint usage by wildlife and humans (pedestrians, local traffic) should only be allowed in passages wider than >10m. These recommendations are based on the experience that animals readily use passages with these dimensions, however, without specifying whether the use is lesser or greater than expected from animal abundance or activity nor whether it is sufficient to achieve the management or conservation goal. As stated before, a frequent underpass use by a species does not automatically imply effectiveness, as it could merely reflect the commonness of the species while still being less than expected from its abundance. In order to evaluate effectiveness, performance indices must be established that relate observed to expected frequencies of use (e.g., Yanes 1995, Clevenger and Waltho 2005).

We calculated the relative use of an underpass as the ratio in the number of tracks found in underpass (observed) to averaged control beds (expected) and developed regression models with this index as dependent variable. This allows for estimating the set of parameter values that will produce a certain index level. To illustrate the use of these models and get an idea of the status-quo of road underpasses in reality, we used data on existing road underpasses build for forestry or agriculture (N=113), pedestrians or local access roads (N=68) and cattle (N=4) under motorways in the administrative region of Mälardalen in south-central Sweden (data from Swedish Road Administration). According to the database, the mean dimensions (± 95% C.I.) of these passages were: width = 6.5 ± 0.42 m, height = 4 ± 0.27m, length = 20 ± 1.58m, and mean openness = 1.84 ± 0.63). Applying the limits values proposed in table 6 to these underpasses, suggests that in total only 11 structures out of 185 (6.1%) may be effective for moose, while 55 (30.4%) may be potentially effective for roe deer. Moose and roe deer will probably use more underpasses than these, but likely to a much lesser degree than expected by chance. The question is, however, whether this should be considered as sufficient, acceptable or alarming.

Clearly, the answer depends entirely on the objective for a possible mitigation action and the perspective from which effectiveness is judged. To efficiently prevent genetic or demographic divergence of two adjacent, but separated populations, it may require highly effective passages on many locations (Corlatti et al 2009). For maintaining viable populations of common species while accepting a certain impact on gene flow and population densities, these requirements can probably be eased (Van der Grift 2005). Providing a minimum connectivity across infrastructure barriers for otherwise common species will allow for even fewer and less effective measures. Counteracting deer-vehicle collisions or reducing wildlife road kill by providing safe passages, on the other hand, may require more effective measures again. Thus, in order to develop and implement barrier mitigation plans and invest in new or improved wildlife crossing structures, the objectives for these actions should be clearly stated. Broad environmental quality objectives, as existing in Sweden (Swedish Government 2000), have only little relevance to landscape and infrastructure (Nilsson & Sjölund 2003) and are often not sufficiently detailed to provide guidance for the development of adequate performance targets (Seiler & Sjölund 2005).

Practical Implementation

What is reasonable from a practical planning point of view? We propose using a relative measure of animal movement to evaluate the proximate effectiveness of a crossing facility, i.e. without relating to the ultimate population objective. Such evaluation should comprise an integrated part of the planning of new crossing structures and can also easily be done at existing passages, as in our study. We further propose the level of random use (use as expected by chance or from reference controls, neither avoidance nor preference) as quantifiable performance target for non-wildlife road crossing structures that allow for a use by wild animals. Obviously, this does not apply to crossing facilities where no animals are desired or allowed due to traffic safety reasons. Also, if passages are primarily designed for wildlife, the performance target must be higher (for example 50% more than expected by chance) unless the target is already given by management or conservation objectives (e.g., support winter migration, maintain viable local population).

However, a single crossing structure will not suffice in maintaining habitat connectivity across the landscape. Additional performance targets must therefore be defined with respect to the barrier effect, or better, permeability of the road section or infrastructure network. Several effective passages may need to be distributed at distances that match the mobility of the species in focus. Bissonette and Adair (2008) proposed isometrically scaled distances between adjacent crossing structures, where distances equal the square root of a species' home range ($H^{0.5}$). This measure represents a linear metric for the daily movements of animals and relates also to known dispersal distances of many species ($7*H^{0.5}$) (Bowman et al. 2002). Thus, combining the two performance targets (random use of crossing structures distributed at isometrically scaled distances) in the evaluation of habitat fragmentation due to transport infrastructure may help to define whether and where mitigation efforts are needed to re-create (or maintain) a minimum of landscape permeability and reduce road kill in wildlife.

In southern Sweden, moose home range sizes average about 12-15 km^2 (Olsson et al. 2008), while roe deer home ranges approximate 1 km^2 (Liberg and Cederlund 1995, Kjellander et al. 2004). Applying the $H^{0.5}$ criterion for the distance between crossing structures on these data produces a scaled metric of 3.9 km in moose and 1 km in roe deer. In our data, the mean distance to alternative crossing structures (bridges, tunnels, fence ends) was 800 m, thus well below these limits. However, since only 6-30% of the existing passages under motorways (in Mälardalen, see above) probably meet the performance target for effectiveness, there will likely be several sections along the motorways where adequate crossing facilities are too rare or too distant to provide sufficient permeability.

Whether mitigation actions will finally result in isometrically dispersed adaptations of non-wildlife passages, the building of strategically placed wildlife over- or underpasses (Woess et al. 2002, Herrmann et al. 2007), openings in exclusion fences (with automated warning systems, Huijser et al. 2007), temporally and locally reduced speed limits (compare Seiler 2005), or a re-routing of traffic flow to calm certain rural areas (Jaarsma and Willems 2002), will depend on practical, economic and political constraints. Also, it is still uncertain to what degree extended fences may funnel animals towards a suitable passage, or noise or light shields may increase the attractiveness of existing conventional road underpasses for larger wildlife and thereby provide more cost-efficient mitigation than the enlargement of the construction itself (see Kastdalen 1999). Obviously, more applied research is needed in order to establish a well integrated and effective de-fragmentation approach in transport and landscape planning.

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Biographical Sketches

Mattias Olsson received his Ph.D. from Karlstad University in 2007, with a thesis named "The use of highway crossings to maintain landscape connectivity for moose and roe deer". He has worked as a wildlife biologist since that time, primarily conducting science in the field of road ecology. Currently he is combining his work as a scientist at Karlstad University with a consultant job focusing on ecological adaptations of both present and new road projects.

Andreas Seiler has his PhD in wildlife biology from the Swedish University of agricultural Sciences in 2003 and has worked on animal-vehicle collisions, barrier effects of roads on wildlife, traffic noise disturbance in birds, and landscape fragmentation issues. He has been involved in a number of follow-up studies and monitoring projects of new roads and railroads and worked closely together with the Swedish Road and Rail Administrations on ecological issues. Andreas has recently worked with a research program on sustainable transport and is active in the Infra Eco Network Europe (IENE).

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