The effects of landscape attributes on the use of small wildlife underpasses by weasel (*Mustela nivalis*) and stoat (*Mustela erminea*)

Maarten R. van Vuurde[1,2,*] **& Edgar A. van der Grift**[3,#]

[1] Wageningen University, Department of Environmental Sciences, P.O. Box 47, NL-6700 AA Wageningen, The Netherlands

[2] Holland Railconsult B.V., P.O. Box 2855, NL-3500 GW Utrecht, The Netherlands

[3] Alterra, Wageningen University and Research Centre, P.O. Box 47, NL-6700 AA Wageningen, The Netherlands, e-mail: edgar.vandergrift@wur.nl

---

Abstract: Increasingly wildlife overpasses and underpasses are being constructed along roads and railroads to mitigate against their barrier effect and to restore habitat connectivity. Surveys show that such wildlife crossing structures are used by a variety of mammal species, including weasel (*Mustela nivalis*) and stoat (*Mustela erminea*). Little is known, however, about which attributes of wildlife crossing structures and the surrounding landscape affect their acceptance, and use, by small mustelids. We studied the effect of landscape variables on the crossing rates of small mustelids in 14 small wildlife underpasses along a four-track railroad between the cities of Boxtel and Eindhoven, The Netherlands. Track-plates were used to record animal crossings over a period of eight weeks. We studied three landscape variables: distance to the nearest natural element providing cover (>1.5 m high), distance to the nearest building, and distance to the nearest road parallel to the railroad. Passage length and openness, percentage of the passage length with grates on top, and average number of crossings by animals that predate on small mustelids were studied as co-variables. Small mustelids were found to use 11 underpasses, making a total of 146 crossings (~15% of all animal crossings). We found a significant negative correlation between the crossing rates of small mustelids and the distance to natural cover, while there was an indication of a positive correlation with the distance to buildings. No correlation was found with the distance to the nearest parallel road, the crossing rates by predators, or any of the structural variables of the wildlife underpasses. A correlation with structural variables was not expected, as the selection of underpasses had aimed to minimise such differences. For future research on the identification of variables that affect crossing structure performance we recommend including population density estimations, individual animal movements, the effects of fences on crossing rates, the importance of underpasses for animals on dispersal, and experimental modification of landscape variables around underpasses.

Keywords: landscape attributes, weasel, *Mustela nivalis*, stoat, *Mustela erminea*, carnivores, barrier effect, fragmentation, wildlife passage, railroad, habitat connectivity.

Introduction

One of the main threats to biodiversity in the Netherlands is habitat fragmentation due to anthropogenic induced changes in land use. This threat is caused not only by the direct loss of habitat and hence the loss of area in which wildlife species may occur, but also by a decrease in habitat connectivity. The on-going construction and widening of transport corridors is one of the main causes of the problem of habitat fragmentation. Besides directly contributing to loss of habitat, transport corridors form barriers to wildlife movements, increase wildlife mortality due to collisions, and reduce habitat quality in adjacent areas due to e.g. disturbance or pollutants (Forman & Alexander 1998, van der Grift & Kuijsters 1998, Trombulak & Frissell 2000,

---

[*] *Present address:* Westerkade 33a, NL-3511 HC Utrecht, The Netherlands

[#] *Corresponding author.*

Spellerberg 2002, Forman et al. 2003). As a result, population viability may be reduced or (local) populations may even become extinct (Opdam et al. 1993, van der Grift et al. 2003, Trocmé et al. 2003).

For many terrestrial mammal species, the barrier effect of roads and railroads is evident (van der Grift 1999, Spellerberg 2002). This may be the result of either the physical characteristics of the infrastructure (e.g. the presence of fences, concrete barriers, noise screens) that simply prevent animals from crossing, or may be caused by inducing a change in animal behaviour (e.g. Huijser 2000, James & Stuart-Smith 2000, Goosem 2002, Chruszcz et al. 2003, Kaczensky et al. 2003). The disturbance created by traffic in the transport corridor, the danger of getting killed by passing traffic or the risk of predation while crossing the linear clearing, may make animals reluctant to cross the infrastructure or even lead to them avoiding the (rail)road area altogether. In case of physical obstacles the barrier is absolute. In case of shifts in behaviour the barrier is usually only partial: animals do cross, but less than they would if the (rail)road was not there. In both cases, however, roads and railroads divide habitats, reduce the exchange of animals between (local) populations and often reduce gene flow, all of which affect population viability.

Increasingly wildlife crossing structures, e.g. overpasses and underpasses, are being incorporated in transport corridor schemes to mitigate the barrier effect and restore habitat connectivity. Surveys show that such wildlife crossing structures are used by a variety of mammal species, usually soon after construction (see e.g. Bekker et al. 2001, Trocmé et al. 2003). Little is known, however, about how the attributes of these structures and of the surrounding landscape affect their acceptance and use by wildlife (Romin & Bissonette 1996, but see Hunt et al. 1987, Brandjes et al. 2001, Ng et al. 2004). Furthermore, most studies that do address these questions focus on large mammal species, such as ungulates and large carnivores (i.e. Foster & Humphrey 1995, Clevenger & Waltho 2000, Cain et al. 2003, Clevenger & Waltho 2005).

Several studies show that wildlife crossing structures such as badger pipes, drainage culverts and amphibian underpasses are used by small mustelids, such as stoat (*Mustela erminea*) and weasel (*Mustela nivalis*) (Yanes et al. 1995, Brandjes et al. 2001, Clevenger et al. 2001, an overview in Brandjes et al. 2002). Both species of carnivore are likely to be sensitive to habitat fragmentation by infrastructural barriers as they often have large home ranges and consequently have to cross roads and railroads frequently during their daily territorial movements. In addition these small mustelids, especially young males, run the risk of getting killed during dispersal (Van Gompel 1992). Road mortality is considered to be one of the reasons for the decline in number of stoats in the Netherlands (Pelzers 1992a).

Several studies have addressed the question of the effectiveness of wildlife crossing structures for *Mustela* species. Landscape attributes are likely to be of particular importance for such small carnivores, because of their preference for cover and avoidance of open areas (Pelzers 1992a, Pelzers 1992b, Canters & Broekhuizen 1998). Yanes et al. (1995) showed that for all studied carnivores – including weasel – crossing frequency was negatively correlated with the underpass length and the height of boundary fences situated between the underpasses and the surrounding landscape. Vegetation in the surrounding area was not found to have a discernible effect (Yanes et al. 1995). Brandjes et al. (2002) found similar results. They also showed a negative correlation between underpass length and use by *Mustela* species. Landscape attributes, e.g. the percentage of cover adjacent to the underpass or the distance to cover, did not seem to have an effect. Elsewhere the same authors have proven landscape openness to affect underpass use by weasel significantly, with the highest crossing rates in half-open landscapes (small-scale agricultural landscape), medium crossing rates in open landscapes (large-scale agricultural landscape) and the lowest crossing rates in closed landscapes (forests and (sub)urban areas) (Brandjes et al. 2001). Furthermore, they showed that the widening of ledges in culverts significantly increased weasel crossing rates. However, neither of these factors had an effect on stoats (Brandjes et al. 2001). Clevenger & Waltho (1999) and Clevenger et al. (2001) found a positive correlation between underpass use by *Mustela* sp. and underpass length, traffic volume and culvert height. They found a negative correlation for the percentage of forest cover adjacent to the underpasses, the distance from the underpass to cover, the underpass age, its aperture (i.e. through-underpass visibility), underpass openness (i.e. width x height / length), mean snow depth and noise level (Clevenger & Waltho 1999, Clevenger et al. 2001). Obviously there are some ambiguities within these studies: the effect of underpass length has been assessed differently and only Clevenger & Waltho (1999), Clevenger et al. (2001) and, to some extent, Brandjes et al. (2001) assessed effects of landscape attributes on crossing rates by small mustelids. It is hard to arrive at definitive conclusions because of the limited number of studies.

Without pretensions to answer all questions raised in earlier studies, the objective of our study, which can be classified as a pilot-study, was to explore the possible impact of landscape attributes on the use of small wildlife crossing structures by stoat and weasel. Furthermore, we aimed to provide recommendations for future research to support the planning and design of effective wildlife underpasses for small mustelids.

Materials and methods

Study area

We selected 14 wildlife crossing structures which are more or less similar in design, all along a twelve kilometre stretch of railroad between the cities of Boxtel and Eindhoven in the south of the Netherlands (51°29'N, 5°25'E; figure 1). The railroad is four-track with carrying an average of 26 trains per hour. In this area the railroad passes through woodlands, small-scale agricultural land and suburban areas (Bakker 1997). Weasel and stoat were known to be present here (Pelzers 1992a, Pelzers 1992b).

Wildlife underpasses

All 14 underpasses are rectangular with an identical width (0.6 m) and height (0.3 m) (table 1; photo 1). Their length varied between 19 and 32 m (table 1). Some were designed with grates on top positioned between the railroad tracks and/or on the ends of the passageway (table 1; photo 2). These grates were placed to improve visibility, which was expected to increase underpass acceptance and use by amphibians and reptiles (Bakker et al. 1991). The underpasses were constructed between 1998 and 2003 when the railroad was expanded from two to four tracks (table 1). Animal-proof fences, to keep animals off the railroad and simultaneously guide them towards the wildlife underpasses, were not constructed.

Eight of the underpasses were situated in rural areas: two in woodlands and six in small-scale farmland with patches of woodland and hedges (table 1). The other six were situated in the suburban area of Eindhoven: four near a golf-course, industrial zone and some small-scale farmland with small patches of woodland and two in woodland with sports fields and some scattered buildings (table 1).

Underpass attributes

Our interest was in identifying whether (and to what extent) landscape attributes influence mustelid use of wildlife underpasses. By selecting underpasses of one single type, which were all located underneath the same railroad, we aimed to minimise differences in structural variables of the underpasses as well as differences in barrier-related variables, i.e. characteristics of the transport infrastructure itself, such as traffic volume, noise level and railroad width. The underpasses were too small for human use, hence anthropogenic variables, such as differences in human co-use, could also be avoided. This approach helped us to decrease co-variables.

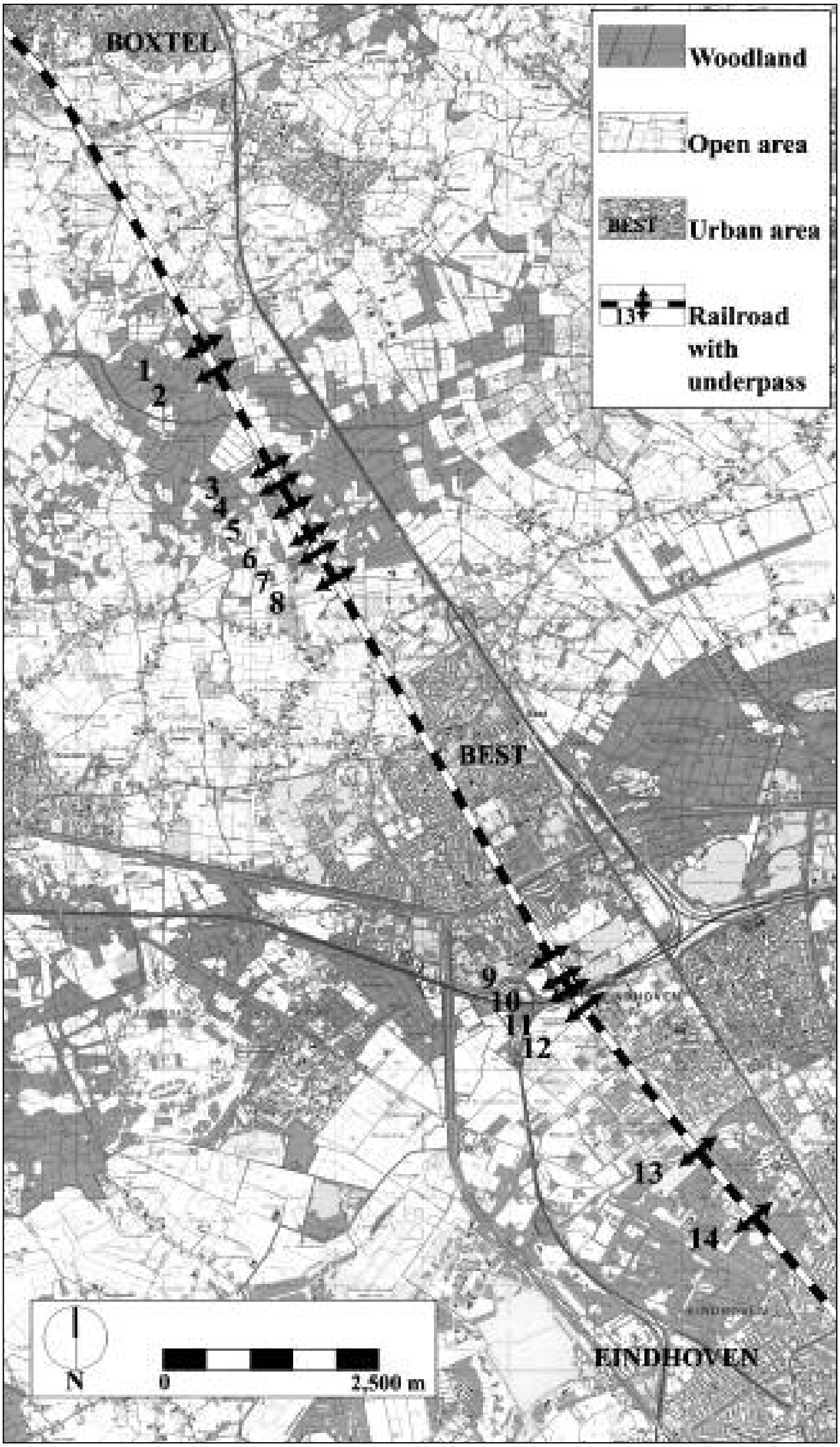

Figure 1. Locations of the 14 underpasses across the four-track railroad between Boxtel and Eindhoven.

Table 1. Location and design characteristics of the selected underpasses along the railroad between Boxtel and Eindhoven. W = width; H = height; L = length.

Underpass	Position along railroad	Year of construction	Design				Landscape type	
			W (m)	H (m)	L (m)	grate (m)	Code	Land use
1	Km 43.34	1998	0.6	0.3	32	9	A	rural - woodland
2	Km 43.73	1998	0.6	0.3	30	9	A	rural - woodland
3	Km 44.97	1998	0.6	0.3	22	2	B	rural - small-scale farmland
4	Km 45.13	1998	0.6	0.3	31.5	0	B	rural - small-scale farmland
5	Km 45.48	1998	0.6	0.3	19	2	B	rural - small-scale farmland
6	Km 45.85	1998	0.6	0.3	19.5	2	B	rural - small-scale farmland
7	Km 46.11	2003	0.6	0.3	20	2	B	rural - small-scale farmland
8	Km 46.46	2003	0.6	0.3	20	2	B	rural - small-scale farmland
9	Km 51.57	2003	0.6	0.3	28	2	C	suburban - farmland, golf, industries
10	Km 51.83	2003	0.6	0.3	23	2	C	suburban - farmland, golf, industries
11	Km 52.00	2001	0.6	0.3	21	0	C	suburban - farmland, golf, industries
12	Km 52.25	2001	0.6	0.3	21	0	C	suburban - farmland, golf, industries
13	Km 54.36	2001	0.6	0.3	22.5	2	D	suburban - woodland, sports fields, houses
14	Km 55.40	2001	0.6	0.3	22.5	4	D	suburban - woodland, sports fields, houses

We studied the correlation between underpass use by small mustelids and three landscape variables: distance to cover (LC), distance to nearest building (LB), and distance to nearest parallel road (LP) (table 2). Two structural attributes, underpass length (SL) and percentage of underpass covered by grates (SG), and one ecological attribute, crossing rate of predators (EP), varied between underpasses and were thus included as co-variables (table 2). Because width and height were identical for all underpasses, SL also reflects underpass openness (= width x height / length). The ecological co-variable EP was selected after it had become clear that some underpasses were used by feral cats (*Felis catus*) and red fox (*Vulpes vulpes*), which are known to kill weasels and stoats (Dijkstra 2000, Lange et al. 1994). The values for LC, SL and SG were measured in the field. LB and LP were measured in the field if the distance was <20 m. LB and LP were measured from topographic maps with a scale of 1:1,000 if the distance was 20-150 m and maps with a scale of 1:25,000 if the distance was >150 m (see table 3). If the values of landscape variables differed between both sides of an underpass, we expected that the ‘unfavourable’ landscape would be the one limiting the number of crossings in both directions. In such situations the most unfavourable values were the ones recorded and used in the analysis.

Recording of crossings

We monitored animal crossings in all underpasses from 28 August 2003 through to 23 October 2003. Tracks were collected by using trackplates (width = 0.6 m, length = 2.4 m) with an ink-bed in the middle, made of cloths saturated with a blend of paraffin oil and pulverised charcoal, and wall-paper on both sides to record the prints of passing animals (Brandjes & Smit 1996, Smit 1996, Huijser & Bergers 2000, Brandjes & Veenbaas 1998, Brandjes et al. 2002; figure 2). This method, using a neutral ink, is considered unlikely to affect the health of medium-sized mammals, such as mustelids (Brandjes

Photo 1. One of the 14 studied wildlife underpasses. *Photograph: Maarten van Vuurde.*

Photo 2. Grates on top of the wildlife underpasses. *Photograph: Maarten van Vuurde.*

Table 2. Studied variables and their expected correlation with the crossing rate of weasel and stoat: + = positive correlation expected; - = negative correlation expected; 0 = no effect expected.

Variables	Code	Definition	Expected correlation
Landscape attributes			
Cover	LC	Distance to the nearest natural cover (m), e.g. shrubs, hedges, trees (height >1.5 m), connected to larger habitat patches or linear elements (>100 m^2)	–
Building	LB	Distance to the nearest building (m)	+
Parallel road	LP	Distance to the nearest parallel road (m)	+
Structural attributes			
Length	SL	Underpass length / openness (m)	–
Grate	SG	Proportion of underpass with grate on top (%)	0 (-?)
Ecological attribute			
Predator use	EP	Average number of crossings by feral cat/red fox (day^{-1})	–

et al. 1999). We collected the two pieces of paper from every track-plate after an average of eight days (photo 3). One track-plate was used at each underpass and was placed about one metre inside the underpass. Long ink-beds (length = 0.6 m) were used to reduce the chance of animals jumping over them. No baits were used.

Data analyses

We identified all the animal tracks on the track-papers following Lange et al. (1986), Lange et al. (1994), Oord (1996) and Van Diepenbeek (1999). It is known there is an overlap in size between the tracks of weasel and stoat, especially of male weasel and female stoat. We therefore considered both species as one group: ‘small mustelids’. The behaviour and preferred habitat are known to be quite similar for both species (Lange et al. 1994), hence, we presumed the influence of landscape variables on the crossing rates of the two species to be the same. For each underpass we estimated the number of track sets per animal species (or species group) and crossing direction. We defined the crossing rate as the mean daily number of track sets (in both directions) detected in an underpass. Operative days were the days in which recording of tracks was done successfully.

Table 3. The values of studied landscape, structural and ecological attributes for each underpass.

Underpass	LC (m)	LB (m)	LP (m)	SL (m)	SG (%)	EP (day^{-1})
1	0	375	750	32.0	28	0.00
2	0	675	775	30.0	30	0.00
3	4	128	600	22.0	9	0.00
4	1	23	850	31.5	0	0.36
5	4	90	850	19.0	11	0.00
6	4	250	875	19.5	10	0.00
7	4	250	9.5	20.0	10	0.00
8	9	44	9	20.0	10	0.11
9	7	26	44	28.0	7	0.00
10	18	50	46	23.0	9	0.00
11	0	150	400	21.0	0	0.00
12	1	40	850	21.0	0	0.00
13	16	135	260	22.5	9	0.00
14	18	54	5.5	22.5	18	0.04

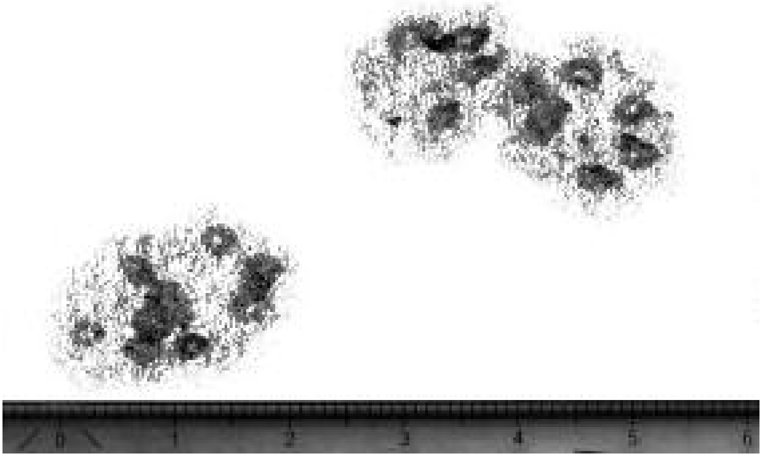

Figure 2. Weasel and stoat tracks were recorded as ink-prints on track-plates (scale in cm).

Differences in crossing rates between underpasses may just be a reflection of differences in mustelid densities within the study area, about which nothing was known. Therefore, we tested for correlations between the crossing rates of mustelids and differences in landscape type (types A-D; see table 1). Mustelid densities, as well as size and shape of home ranges, are known to vary between landscape types (Murphy & Dowding 1994) and correlations between underpass use and landscape type have been assessed before (see Brandjes et al. 2001).

We analysed the number of crossings with a loglinear regression model, a generalised linear

Photo 3. The two pieces of paper on the track-plates were collected and replaced after an average of eight days. *Photograph: Els van Vuurde.*

model with a Poisson distribution and a logarithmic link function (McCullagh & Nelder 1989). We thus modelled the relationship between the mean μ of the Poisson distribution and the variables by $\log(\mu)$ = constant + predictor variables. Over-dispersion was accounted for by inflating the variance with an over-dispersion parameter. Consequently, deviance ratios were employed for significance testing. We assumed that the number of crossings was proportional to the number of operative days per underpass and thus we used the logarithm of the number of operational days as an offset in the regression model. The predictor variables LB and LP had a very large range (table 3) and so we log-transformed them.

Results

In total we recorded 941 crossings for all animal species (table 4). Weasel and stoat used underpasses in all four landscape types: 146 weasel and stoat crossings were detected in eleven underpasses (table 5). Hence, mustelid crossings comprised 15.5% of all crossings, found in 78.6% of the underpasses. The highest number of crossings (38) by small mustelids was found in underpass 7. Crossing rates varied between 0.00 and 0.68 (average: 0.19) crossings per underpass per day. Track set numbers of small mustelids differed from 0 to 8 at individual inspections. The underpasses were used by at least 10 other animal species or species groups (table 4), with each underpass being used by an average of 3.6-4.1 species (groups). In underpasses (n=11) used by small mustelids, the average number of species (groups) using the underpass was 3.9-4.5. Feral cats were recorded 27 times, using only underpasses 4, 8 and 14. Red fox was recorded only once: in underpass 4. Predator crossings comprised 3.0% of all crossings (table 4).

No significant differences in crossing rates between landscape types were found (P=0.523). Although the number of observations was relatively small, we assumed population densities to be equal across the whole study area and hence did not use landscape type as a forced factor in the correlation analyses. We found a negative correlation between the crossing rates of small mustelids and the distance to cover (LC: P=0.019; b=-0.15, se=0.07). Although not significant, there was an indication of a positive correlation between crossing rates and the distance to the nearest buildings (logLB: P=0.067; b=0.56, se=0.28). No correlation was found between the use of underpasses by stoat and weasel and the distance to parallel roads (logLP: P=0.756). No correlation was found between crossing rates and the co-variables SL, SG and EC. Adding these co-variables, logLB or logLP to the regression model with LC did not produce significant improvements of the model with LC. Similarly, adding the co-variables LC or logLP to the regression model with logLB did not produce significant improvements of the model with logLB.

Discussion

Weasel and stoat used a large proportion of the studied underpasses (~80%) and the number of mustelid passages comprised a substantial part of all crossings (~15%). By comparison, Brandjes et al. (2002) found that 44% of studied underpasses (circular wildlife tunnels; n=50) were used by small mustelids, and small mustelid crossing numbers comprised no more than ~8% of all crossings. These differences may possibly be a result of their inclusion of extremely long (>40 m) underpasses. The high number of small mustelid crossings in our study was even more surprising, because no animal-proof fences had been constructed along the railroad that would prevent the animals from crossing the railroad elsewhere and which would also guide the animals to the underpasses. Although no information is available about how many small mustelid crossings still take place over the railroad tracks, it appears that the underpasses offer an attractive passageway, at least for some individuals.

Although our survey period was limited to eight weeks in August-October, a period in which young animals show high dispersal rates

Table 4. Number of track sets of all species/species groups per underpass. Ranges in track set numbers (reflecting minimum and maximum number of track sets) are due to difficulties in interpreting track recordings. N = number of operative days.

Underpass	N	Species (groups)												Total of all species	Total number of species (groups) recorded
		Western hedgehog	Rabbit	Mice, voles and shrews	Brown rat	Weasel and stoat	Western polecat	Pine and stone marten	Red fox	Feral cat	Newts	Toads	Frogs		
1	49	0	0	43-44	2	9	0	0	0	0	4	0	0	58-59	4
2	56	0	0	73-74	7	25-27	0	0	0	0	54-66	25-38	3-4	187-216	6
3	56	0	0	24-26	0	7	0	0	0	0	0	0-1	2	33-36	3-4
4	56	0	0	3	4	6	0	8	1	19	0	0	0	41	6
5	56	0	0	23	0	1	0	0	0	0	0	0	3	27	3
6	56	11-12	0	108	0-1	13	0-1	0	0	0	0	0	2	135-136	4-5
7	56	0	0	55	0	38	0	0	0	0	0-1	0-2	3-4	96-100	3-5
8	56	1	0	3	0	0	0	0	0	6	0	0	5	15	4
9	56	0	0	6-14	0	0	0	0	0	0	0	0-1	1	7-16	2-3
10	56	0	0	39	0	2	0	0	0	0	0	0	2-3	43-44	3
11	56	0	0	6-7	0	14	0	0	0	0	0	0-2	0	20-23	2-3
12	56	0	6	0	142	24-30	0	0	0	0	0-2	0	0	172-180	3-4
13	56	0	0	58-59	0	0	0	0	0	0	1	0	0	59-60	2
14	56	0	7	1	0	3	0	0	0	2	0	1-2	2-5	16-20	6
Total		12.5	13	449	155.5	146	0.5	8	1	27	66.5	36	26	941	–
Number of underpasses used		2	2	13	4-5	11	0-1	1	1	3	3-5	2-6	9	14	–

Table 5. The number of operative days, the total number of crossings and the crossing rates of weasel and stoat for each underpass.

Underpass	Number of operative days	Total number of crossings by weasel and stoat (both directions)	Average number of crossings by weasel and stoat (day^{-1})
1	49	9	0.18
2	56	26	0.46
3	56	7	0.13
4	56	6	0.11
5	56	1	0.02
6	56	13	0.23
7	56	38	0.68
8	56	0	0.00
9	56	0	0.00
10	56	2	0.04
11	56	14	0.25
12	56	27	0.48
13	56	0	0.00
14	56	3	0.05
Total	777	146	–
Average	–	–	0.19

(Van Gompel 1992), we believe that crossing rates in our survey reflect life history traits of both weasel and stoat in general. There is no particular period or season in which these mustelids show (extremely) low activity. The high metabolism rates of weasel lead to high levels of day and night time activity, interspersed with short breaks, throughout the whole year (Verkem et al. 2003). High levels of day time activity can also be seen in female stoats with young (Lange et al. 1994). Yanes et al. (1995) found little seasonal variability in use of underpasses by carnivores, including weasel, although crossing numbers in spring were lower. Both species often have large home ranges (weasel: up to 25 ha; stoat: up to 50 ha) and consequently the animals frequently have to cross roads and railroads during their daily territorial movements. Home range size is found to be largely dependent on prey densities (Lange et al. 1994). Hence, in years with high prey densities crossing rates at transport barriers may decrease.

Crossings of small mustelids were found in tunnels of all age classes, which differed between 0 (*n*=4), 2 (*n*=4) and 5 (*n*=6) years (see table 1). Apparently, small mustelids quickly become habituated to the new crossing structures.

We assumed that every small mustelid recorded on the track-plates did cross the railroad, and did not only visit the underpass and leave again on the same side. This assumption was supported by the fact that there were often differences between the number of track sets of animals going in opposite directions at single inspections of single track-plates. Furthermore, no tracks were recorded of animals which had turned around at the track-plates. Mud prints instead of ink prints on the track-plates could have indicated that animals were jumping over the ink-beds (see e.g. Brandjes et al. 2002), thus reflecting a ‘barrier-effect’ by the ink-beds. However, we found no such evidence.

We found that differences in crossing rates of small mustelids were significantly correlated with the distance to the nearest natural element providing cover. As expected, there were more crossings by weasel and stoat when shrubs, hedges and woodlands were close by. Our results generally correspond with earlier studies by Clevenger & Waltho (1999) and Clevenger et al. (2001) in which distance to cover, trees or shrubs >1.5 m high, was a significant factor, with a negative correlation for underpass use by small mustelids. By contrast, Brandjes et al. (2002) did not find a significant effect of distance to cover on crossing rates by weasel or stoat. A possible explanation for these differences is different data treatment. Brandjes et al. (2002) averaged distances to cover on both sides of the passages, thus averaging extreme distance values, while in our study the most unfavourable distance of both underpass sides was used in the analysis.

A twofold explanation can be provided for the effect of distance to cover on crossing rates: (1) species that prefer habitats with abundant cover for hiding would feel an even stronger need for protective vegetation in inhospitable environments, such as open railroad corridors (see also Clevenger & Waltho 2005), and (2) landscape elements that provide cover, simultaneously direct the animals towards the underpass entrances and thus help them find the passageways. The high number of crossings suggests that daily use by local animals (home range movements) is more important than underpass use by dispersing animals. If this assumption is true, we believe that the effect of distance to cover on small mustelid crossings was mainly a result of the preference for cover, and less a result of guiding the animals.

Although distance to buildings was not significantly correlated with crossing rates, we did find an indication of a positive correlation, as we had expected. Crossing rates seemed to decrease when buildings were close by. Human activity around buildings is believed to decrease the attractiveness of an underpass for small mustelids. We assume that the effect of distance to buildings might be proven to be significant if the underpasses are monitored for a longer period.

Distance to roads parallel to the railroad did not show a correlation with crossing rates. This may be due to the fact that all the roads at short distances from the underpasses (<100 m) were local roads, with (very) low traffic volumes after dark. Telemetry studies showed that such roads form little to no barrier for small mustelids, due to their mainly nocturnal life style and mobility (Murphy & Dowding 1994).

We did not find any significant correlation between crossing rates and the structural or ecological co-variables. This is not surprising because in selecting the underpasses we had tried to standardise these variables as much as possible. Although underpass length and openness were likely to affect crossing rates (see e.g. Yanes et al. 1995, Clevenger & Waltho 1999), these variables showed no correlation, due to the small variation in underpass length in our study (maximum difference: 13 m). Brandjes et al. (2002) had found that tunnel length, split in two classes (≤40 m and >40 m) was the only attribute which showed a significant negative correlation with crossing rates of small mustelids who preferred underpasses of ≤40 m.

No correlation was found for crossing rates and the percentage of underpass length with grates on top. The impact of grates on the crossing rates of small mustelids is hard to predict. No research has yet been published which studies this relationship. Although the absence of a correlation can be the result of the (intended) small difference in grate length between the studied underpasses, we hypothesized that grate length would have no effect on underpass use by small mustelids. Grates were constructed in order to reduce the ‘tunnel effect’ for amphibians and reptiles and improve micro-climate in the passageway. It is unlikely that small mustelids, which often use underground tunnels dug by mice and moles, are sensitive to such effects (King 1989). One may even argue that underpasses without grates on top would be more suitable for small mustelids. Other studies have revealed that some mammal use of highway underpasses was negatively affected by the presence of openings between the lanes, because of increased noise levels in the underpass (Clevenger & Waltho 2005). Noise from passing trains may stress the animals while passing through the underpasses and potentially restrict their acceptance of the tunnels as passageways.

A comparison of crossing rates of underpasses that show large variance in grate length (0-100%) is needed to fill these knowledge gaps.

There is some evidence that wildlife crossing structures can be used by predators to capture prey (Little et al. 2002, Cain et al. 2003, Little 2003). This may lead to prey species avoiding using the passageways. However, we found no indications for such behavioural responses in prey species. Underpasses with high crossing rates for small mustelids also often had high crossing rates by their prey species, such as mice, voles, shrews or amphibians. The use of underpasses by weasel and stoat, themselves frequently killed by feral cat and red fox, also showed no correlation with the crossing rates of their potential predators. The absence of such a correlation may be due to the small number of feral cat and red fox crossings and their use of only a limited number of underpasses. Even with a much larger sample size, however, Brandjes et al. (2002) did not find a significant effect of co-use by feral cats on the crossing rates by weasel or stoat.

Recommendations for future research

We indirectly tested for differences in the densities of small mustelids within the study area by using landscape type as a variable. We did so for practical reasons: data on mustelid densities around the studied railroad were unavailable. However, we do recommend including animal density estimations in studies that seek to identify variables that affect crossing structure performance (see also Hardy et al. 2003). In study areas where snow tracking in winter is not an option, referential track-plates can be used (see e.g. Yanes et al. 1995, Brown & Miller 1998, Huijser & Bergers 2000, Brandjes et al. 2002) or capture-mark-recapture studies can be set up. The advantage is that corrections for (even small) differences in mustelid densities can be made in the correlation analyses between crossing rates and landscape variables.

The use of track-plates provides results in crossing rates by species or species group, but usually cannot provide information about the number of individuals that used the underpasses (Brandjes & Smit 1996). Such information is essential, however, to draw any conclusions about the effectiveness of underpasses as habitat connectors and measures to ensure the viability of (local) populations. The use of subcutaneous radio tags, i.e. Passive Integrated Transponders (PIT), may be a helpful tool for studying the use of underpasses by individual animals. These allow the recording of the exact number of crossings made by one individual, by using receivers inside the passages (Kenward 2001). An even better option, although more time-consuming, is the use of radio collars. Individual animal movements can be followed more precisely, both within and outside the railroad corridor, which may provide information about habitat use, home range size, underpass preference, crossing rates in underpasses, frequency and locations of crossings elsewhere over the railroad tracks, and mortality due to collisions with trains (see e.g. Murphy & Dowding 1994, Foster & Humphrey 1995, James & Stuart-Smith 2000, Miller et al. 2001, Millspaugh & Marzluff 2001). Radio-tracking also facilitates studying the importance of wildlife underpasses for dispersing animals, which is important, as it is assumed that dispersing animals will find it more difficult to discover an underpass than local animals. Hence, the effects of wildlife underpasses on the persistence of (meta)populations will be better understood (Chruszcz et al. 2003, Veenbaas et al. 2003). Such studies can also help in the identification of locations for the construction of new wildlife underpasses, by using knowledge about successful or unsuccessful railroad crossing locations in areas where the viability of the population is at risk (Romin & Bissonette 1996, van der Grift & Pouwels 2006).

Special research attention is recommended for the effect of fencing on crossing rates through underpasses. Fences can either enhance or reduce population viability, depending on the degree of railroad avoidance of a species and the mortality rates of animals that try to cross the tracks (Jaeger & Fahrig 2003). Hence, conclusions about the need for fenced, or fenceless, railroad corridors can only be drawn if all small mustelid crossings (successful or unsuccessful) are known, both through the underpasses and across the tracks. A first step may be to compare crossing rates in underpasses before and after the construction of fences.

The construction and maintenance of animal-proof fences is costly. Hence, if animals can be encouraged to use underpasses without need for guiding fences, this would be an important advantage. Different measures for optimising underpass use, without the construction of animal-proof fences, may be considered. Changes in the landscape around underpasses may positively affect their use. These could include the development of guiding landscape elements and cover at underpass entrances. Other measures could involve a decrease in the distance between underpasses, or the removal of natural cover close to the transport corridor at sections between wildlife crossing structures (see also Huijser 2000). Experiments with such measures are recommended, with attention paid to a variety of species, because of differences in behaviour and preferences.

Conclusions

This study shows that small rectangular wildlife underpasses have the potential to restore habitat connectivity and reduce traffic-related mortality for a variety of small vertebrates, including small mustelids. Even without the construction of animal-proof fences, the studied underpasses were used frequently by weasel/stoat. No data exist on the number of crossings over the railroad tracks and in consequence the proportion of crossings that take place through the underpasses can not be estimated. The high crossing rates suggest that the small mustelids consciously use underpasses, despite the absence of fences, to avoid crossing the inhospitable railroad clearing.

The small sample number (*n*=14 underpasses) and short research period (8 weeks) of this pilot-study, the absence of data on the behaviour of the animals inside the underpasses (crossings versus visits), and the lack of information about the densities of small mustelids within the study area, force us to be cautious in our conclusions about factors affecting the performance of wildlife underpasses. Our study does, however, indicate the importance of landscape elements in providing cover close to underpass entrances. The number of crossings by small mustelids is likely to increase when shrubs, hedges and trees are close by. By contrast, crossing rates are expected to be lower when underpasses are situated close to buildings. Long-term monitoring of wildlife crossing structures, preferably combined with capture-mark-recapture or radio-tracking studies, is needed to verify these conclusions and to be able to predict the impact of underpass use on population viability of small mustelids.

Acknowledgements: We would like to thank Tjeerd Kooij (Holland Railconsult B.V.), who was one of the initiators of this study, assisted us with the field work and the necessary permits to conduct the monitoring in the railroad corridor, and commented on an earlier draft of this paper. We would also like to thank ProRail for their financial support for this study and especially Mariëtte van Rooij (ProRail) for her help. We thank Paul Goedhart (WUR, Plant Research International) for his help with the statistical analyses and Paul Opdam (WUR, Alterra) for his critical and valuable comments on a previous draft of this manuscript. Finally, we are very grateful to Annemarie van Diepenbeek for her help with the identification of the animal tracks and to Els van Vuurde for her help with the data collection.

References

Bakker, R. 1997. Reinforcement of environmental values along railway-infrastructure: An integrated approach. In: K. Canters (ed.). Proceedings of the International Conference on Habitat Fragmentation, Infrastructure and the Role of Ecological Engineering, 17-21 September 1995, Maastricht/Den Haag, Netherlands: 316-326. Ministry of Transport, Public Works and Water Management, Road and Hydraulic Engineering Division, Delft, The Netherlands.

Bakker, R., A. van Daatselaar, G. Roorda & M. van der Zwan 1991. Landschapsonderzoek Boxtel-Eindhoven. Ingenieursbureau Nederlandse Spoorwegen, Utrecht, The Netherlands.

Bekker, G.J., R. Cuperus, C.F. Jaarsma, D.A. Kamphorst & R.J.M. Kleijberg 2001. Dealing with fragmentation: prevention, mitigation and compensation. In: A.A.G. Piepers (ed.). Infrastructure and nature; fragmentation and defragmentation. Dutch State of the Art Report for COS activity 341: 77-98. Defragmentation Series 39A. Ministry of Transport, Public Works and Water Management, Road and Hydraulic Engineering Division, Delft, The Netherlands.

Brandjes, G.J. & G.F.J. Smit 1996. Overzicht onderzoeksmethoden gebruik faunapassages. Ontsnipperingsreeks 30. Rijkswaterstaat Dienst Weg- en Waterbouwkunde, Delft, The Netherlands.

Brandjes, G.J. & G. Veenbaas 1998. Het gebruik van faunapassages langs waterwegen onder rijkswegen in Nederland. Een oriënterend onderzoek. Ontsnipperingsreeks 36. Rijkswaterstaat Dienst Weg- en Waterbouwkunde, Delft, The Netherlands.

Brandjes, G.J., G. Veenbaas & G.J. Bekker 1999. Registreren van het gebruik van faunapassages. De Levende Natuur 100 (1): 6-11.

Brandjes, G.J., G. Veenbaas, I. Tulp & M.J.M. Poot 2001. Het gebruik van faunapassages langs watergangen onder rijkswegen. Resultaten van een experimenteel onderzoek. Ontsnipperingsreeks 40. Rijkswaterstaat Dienst Weg- en Waterbouwkunde, Delft, The Netherlands.

Brandjes, G.J., R. van Eekelen, K. Krijgsveld & G.F.J. Smit 2002. Het gebruik van faunabuizen onder rijkswegen. Resultaten literatuur- en veldonderzoek. Ontsnipperingsreeks 43. Rijkswaterstaat Dienst Weg- en Waterbouwkunde, Delft, The Netherlands.

Brown, J.A. & C.J. Miller 1998. Monitoring stoat (*Mustela erminea*) control operations: power analysis and design. Science for Conservation 96: 1-21.

Cain, A.T., V.R. Tuovila, D.G. Hewitt & M.E. Tewes 2003. Effects of a highway and mitigation projects on bobcats in Southern Texas. Biological Conservation 114: 189-197.

Canters, K.J. & S. Broekhuizen 1998. Soortsbeschrijvingen Wezel (*Mustela nivalis*) & Hermelijn (*Mustela erminea*). De Levende Natuur 99: 168, 200.

Chruszcz, B., A.P. Clevenger, K.E. Gunson & M.L. Gibeau 2003. Relationships among grizzly bears, highways, and habitat in the Banff-Bow Valley, Alberta, Canada. Canadian Journal of Zoology 81: 1378-1391.

Clevenger, A.P. & N. Waltho 1999. Dry drainage culvert use and design considerations for small- and medium-sized mammal movement across a major transportation corridor. In: G.L. Evink, P. Garrett & D. Ziegler (eds.). Proceedings of the Third International Conference on Wildlife Ecology and Transportation: 263-277. FL-ER-73-99. Florida Department of Transportation, Tallahassee, USA.

Clevenger, A.P. & N. Waltho 2000. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. Conservation Biology 14: 47-56.

Clevenger, A.P. & N. Waltho 2005. Performance indices to identify attributes of highway crossing structures facilitating movement of large mammals. Biological Conservation 121: 453-464.

Clevenger, A.P., B. Chruszcz & K. Gunson 2001. Drainage culverts as habitat linkages and factors influencing passage by mammals. Journal of Applied Ecology 38: 1340-1349.

Diepenbeek, M.A.J. van 1999. Veldgids diersporen. Sporen van gewervelde landdieren. Stichting Uitgeverij KNNV, Utrecht, The Netherlands.

Dijkstra, V. 2000. De huiskat als predator van kleine marterachtigen. Zoogdier 11(4): 19-21.

Forman, R.T.T. & L.E. Alexander 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29: 207-231.

Forman, R.T.T., D. Sperling, J.A. Bissonette, A.P. Clevenger, C.D. Cutshall, V.H. Dale, L. Fahrig, R. France, C.R. Goldman, K. Haenue, J.A. Jones, F.J. Swanson, T. Turrentine, T.C. Winter 2003. Road ecology – Science and solutions. Island Press, Washington, USA.

Foster, M. & S.R. Humphrey 1995. Use of highway underpasses by Florida panthers and other wildlife. Wildlife Society Bulletin 23: 95-100.

Goosem, M. 2002. Effects of tropical rainforest roads on small mammals: fragmentation, edge effects and traffic disturbance. Wildlife Research 29: 277-289.

Grift, E.A. van der 1999. Mammals and railroads: Impacts and management implications. Lutra 42: 77-98.

Grift, E.A. van der & H.M.J. Kuijsters 1998. Mitigation measures to reduce habitat fragmentation by railway lines in the Netherlands. In: G.L. Evink, P. Garrett, D. Zeigler & J. Berry (eds.). Proceedings of the International Conference on Wildlife Ecology and Transportation: 166-170. FL-ER-69-98. Florida Department of Transportation, Tallahassee, USA.

Grift, E.A. van der & R. Pouwels 2006. Restoring habitat connectivity across transport corridors: Identifying high-priority locations for de-fragmentation with the use of an expert-based model. In: J. Davenport & J.L. Davenport (eds.). The ecology of transportation: managing mobility for the environment: 205-231. Springer, Dordrecht, The Netherlands.

Grift, E.A. van der, J. Verboom & R. Pouwels 2003. Assessing the impact of roads on animal population viability. In: C.L. Irwin, P. Garrett & K.P. McDermott (eds.). Proceedings of the International Conference on Ecology and Transportation: 173-181. Centre for Transportation and the Environment, North Carolina State University, Raleigh, USA.

Hardy, A., A.P. Clevenger, M. Huijser & G. Neale 2003. An overview of methods and approaches for evaluating the effectiveness of wildlife crossing structures: Emphasizing the science in applied science. In: C.L. Irwin, P. Garrett & K.P. McDermott (eds.). Proceedings of the International Conference on Ecology and Transportation: 319-330. Centre for Transportation and the Environment, North Carolina State University, Raleigh, USA.

Huijser, M.P. 2000. Life on the edge. Hedgehog traffic victims and mitigation strategies in an anthropogenic landscape. PhD thesis. Wageningen University, Wageningen, The Netherlands.

Huijser, M.P. & P.J.M. Bergers 2000. The effect of roads and traffic on hedgehog (*Erinaceus europaeus*) populations. Biological Conservation 95: 111-116.

Hunt, A., H.J. Dickens & R.J. Whelan 1987. Movement of mammals through tunnels under railway lines. Australian Zoologist 24 (2): 89-93.

Jaeger, J.A.G. & L. Fahrig 2003. Under what conditions do fences reduce the effects of transportation infrastructure on population persistence? In: Proceedings Infra Eco Network Europe (IENE) Conference, *Habitat fragmentation due to Transportation Infrastructure*. Institute of Nature Conservation, Brussels, Belgium.

James, A.R.C. & A.K. Stuart-Smith 2000. Distribution of caribou and wolves in relation to linear corridors. Journal of Wildlife Management 64: 154-159.

Kaczensky, P., F. Knauer, B. Krze, M. Jonozovic, M. Adamic & H. Gossow 2003. The impact of high speed, high volume traffic axes on brown bears in Slovenia. Biological Conservation 111: 191-204.

Kenward, R.E. 2001. A manual for wildlife radio tagging. Academic Press, London, UK.

King, C. 1989. The natural history of weasels & stoats. Christopher Helm, London, UK.

Lange, R., A. van Winden, P. Twisk, J. de Laender & C. Speer 1986. Zoogdieren van de Benelux. Herkenning en onderzoek. Jeugdbondsuitgeverij, 's-Graveland, The Netherlands.

Lange, R., P. Twisk, A. van Winden & A. van Diepenbeek 1994. Zoogdieren van West-Europa. KNNV Uitgeverij, Utrecht, The Netherlands.

Little, S.J. 2003. The influence of predator-prey relationships on wildlife passage evaluation. In: C.L. Irwin, P. Garrett & K.P. McDermott (eds.). Proceedings of the International Conference on Ecology and Transportation: 277-292. Centre for Transportation and the Environment, North Carolina State University, Raleigh, USA.

Little, S.J., R.G. Harcourt & A.P. Clevenger 2002. Do wildlife passages act as prey traps? Biological Conservation 107: 135-145.

McCullagh, P. & J.A. Nelder 1989. Generalized Linear Models, second edition. Chapman & Hall, London, UK.

Millspaugh, J.J. & J.M. Marzluff 2001. Radio tracking and animal populations. Academic Press, San Diego, USA.

Miller, C., M. Elliot & N. Alterio 2001. Home range of stoats (*Mustela erminea*) in podocarp forest, south Westland, New Zealand: implications for a control strategy. Wildlife Research: 165-172.

Murphy, E.C. & J.E. Dowding 1994. Range and diet of stoats (*Mustela erminea*) in a New Zealand beech forest. New Zealand Journal of Ecology 18: 11-18.

Ng, S.J., J.W. Dole, R.M. Sauvajot, S.P.D. Riley & T.J. Valone 2004. Use of highway undercrossings by wildlife in southern California. Biological Conservation 115: 499-507.

Oord, J.G. 1996. Herkenning van diersporen en –prenten bij kleinwildtunnels. Buro voor faunatechniek Oord, Wittelte, The Netherlands.

Opdam, P., R. van Apeldoorn, A. Schotman & J. Kalkhoven 1993. Population responses to landscape fragmentation. In: C.C. Vos & P. Opdam (eds.). Landscape ecology of a stressed environment: 147-171. Chapman & Hall, London, UK.

Pelzers, E. 1992a. Hermelijn, *Mustela erminea*. In: S. Broekhuizen, B. Hoekstra, V. van Laar, C. Smeenk & J.B.M. Thissen (eds.). Atlas van de Nederlandse zoogdieren: 138-141. Stichting Uitgeverij KNNV, Utrecht, The Netherlands.

Pelzers, E. 1992b. Wezel, *Mustela nivalis*. In: S. Broekhuizen, B. Hoekstra, V. van Laar, C.

Smeenk & J.B.M. Thissen (eds.). Atlas van de Nederlandse zoogdieren: 142-145. Stichting Uitgeverij KNNV, Utrecht, The Netherlands.

Romin, L.A. & J.A. Bissonette 1996. Deer-vehicle collisions: status of state monitoring activities and mitigation efforts. Wildlife Society Bulletin 24: 276-283.

Smit, G.F.J. 1996. Het gebruik van faunapassages bij rijkswegen. Overzicht en onderzoeksplan. Ontsnipperingsreeks 29. Rijkswaterstaat Dienst Wegen Waterbouwkunde, Delft, The Netherlands.

Spellerberg, I.F. 2002. Ecological effects of roads. Science Publishers Inc., Enfield, USA.

Trocmé, M., S. Cahill, J.G. de Vries, H. Farrall, L. Folkeson, G. Fry, C. Hicks & J. Peymen 2003 (eds.). COST 341 – Habitat Fragmentation due to transportation infrastructure: The European Review. Office for Official Publications of the European Communities, Luxembourg, Luxembourg.

Trombulak, S.C. & C.A. Frissell 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14: 18-30.

Van Gompel, J. 1992. Kleine marterachtigen in de Uitkerkse Polder. Zoogdier 3: 3-8.

Veenbaas, G. & J. Brandjes, G. Smit & E. van der Grift 2003. Effectiveness of fauna passageways at main roads in the Netherlands. In: Proceedings Infra Eco Network Europe (IENE) Conference, *Habitat fragmentation due to Transportation Infrastructure*. Institute of Nature Conservation, Brussels, Belgium.

Verkem, S., J. De Maeseneer, B. Vandendriessche, G. Verbeylen & S. Yskout 2003. Zoogdieren in Vlaanderen. Ecologie en verspreiding van 1987 tot 2002. Natuurpunt Studie / JNM-Zoogdierenwerkgroep, Mechelen / Gent, Belgium.

Yanes, M., J.M. Velasco & F. Suárez 1995. Permeability of roads and railways to vertebrates: the importance of culverts. Biological Conservation 71: 217-222.

Samenvatting

Het effect van landschappelijke kenmerken op het gebruik van kleine faunatunnels door wezel (*Mustela nivalis*) en hermelijn (*Mustela erminea*)

Steeds vaker worden faunapassages, zoals ecoducten en faunatunnels, aangelegd om de barrièrewerking van verkeers- en spoorwegen te mitigeren en de uitwisseling van dieren tussen leefgebieden aan weerszijden van de infrastructuur te herstellen. Onderzoek heeft aangetoond dat dergelijke faunavoorzieningen door een scala aan zoogdiersoorten wordt gebruikt, inclusief wezel (*Mustela nivalis*) en hermelijn (*Mustela erminea*). Er is echter weinig bekend over welke kenmerken van faunapassages en het direct aangrenzend landschap de acceptatie en het gebruik van de voorzieningen door kleine marterachtigen beïnvloeden. Wij onderzochten het effect van landschapsvariabelen op het gebruik door kleine marterachtigen van 14 kleine faunatunnels onder een viersporige spoorlijn tussen Boxtel en Eindhoven. We gebruikten sporenplaten om passages van dieren door de tunnels gedurende acht weken vast te stellen. We onderzochten drie landschapsvariabelen: afstand tot het dichtstbijzijnde dekkingbiedend landschapselement (>1.5 m), afstand tot de dichtstbijzijnde bebouwing en afstand tot de dichtstbijzijnde weg, parallel aan de spoorlijn. Lengte en openheid van de faunatunnels, het percentage van de tunnels dat is afgedekt met lichtroosters en het gemiddelde aantal passages per dag van diersoorten (hier: huiskat en vos) die prederen op kleine marterachtigen zijn in de studie meegenomen als co-variabelen. Kleine marterachtigen maakten gebruik van 11 faunatunnels met een totaal van 146 passages (~15% van alle passages). We vonden een significante negatieve correlatie tussen het gebruik van de tunnels door kleine marterachtigen en de afstand tot dekking, terwijl er een indicatie was voor een positieve correlatie tussen het gebruik en de af-

stand tot de dichtstbijzijnde bebouwing. Er is geen correlatie gevonden met de afstand tot de dichtstbijzijnde parallelweg, het gebruik door predatoren of een van de structuurkenmerken van de faunatunnels. Een correlatie met structuurkenmerken was ook niet de verwachting, omdat bij de selectie van faunapassages het streven was geweest om verschillen in structuurkenmerken minimaal te houden. Voor toekomstig onderzoek naar factoren die het functioneren van faunapassages beïnvloeden adviseren we onderzoek naar (verschillen in) populatiedichtheden in de studie op te nemen, evenals onderzoek naar bewegingen van individuele dieren, het effect van rasters op het gebruik van de tunnels, het belang van faunapassages voor dieren op dispersie en experimenten waarbij landschapsvariabelen rond faunapassages kunstmatig worden aangepast.

Received: 12 December 2005
Accepted: 2 March 2006