Use of wildlife passages by invertebrate and vertebrate species

Bertram Georgii[1], Verena Keller[2], Hans Peter Pfister[2], Heinrich Reck[3], Elke Peters-Ostenberg[4], Michael Henneberg[4], Mathias Herrmann[5], Heiko Mueller-Stiess[5], Lothar Bach[6]

Abstract

Presented are the results of two studies (1993-97 and 2003-06) considering the use of different kinds of wildlife and non-wildlife over- and underpasses (green bridges, viaducts, culverts, etc.) by invertebrates and mammals. The passages varied considerably in width (1-200 meters) and age (3-16 years). Animal groups studied were ground beetles, grasshoppers, butterflies, burnet moths, spiders, voles, shrews, dormice, bats, medium sized mammals (European hare, predators) and ungulates. Methods applied depend on the species investigated: trapping, mark and recapture, bat detectors, direct and infrared camera observations, track counts, telemetry etc. With a few exceptions, all species investigated used at least the wider over- and underpasses. This applies especially for the medium sized and large mammals which showed a strong preference for green bridges and viaducts. The larger box-shaped wildlife underpasses and those for small mammals unexpectedly were used only moderately. On the other hand even insects able to fly, like butterflies and burnet moths, and birds showed a preference for overpasses when crossing a road compared to adjacent parts of the roads. Ground beetles, grasshoppers, spiders, mice, shrews and bats can use a green bridge effectively when species-specific habitat elements are present on the bridges especially when these elements are connected to the corresponding habitats in the neighbourhood of the road. There was a general trend to more open-habitat adapted species on the overpasses even when they lie within forests. Statistical analyses, which was possible with the data of green bridges and larger mammals only (20 buildings, intensive frequentation), showed that especially width and age and to a lesser extent position were of positive influence on the use of the bridges. By contrast, dense canopy, traffic noise, the number of gravel roads, intensity of human use and nearby buildings lessen the frequentation of the bridges. For the effectiveness of wildlife passages it is important to choose the right target species, to develop habitat structures on, under and near the passageways which strongly meet the habitat requirements of the target species and to avoid as much human disturbances as possible.

[1] Vauna Consulting, D-82487 Oberammergau

[2] Swiss Ornithological Institute, CH-6204 Sempach

[3] Arbeitsgruppe fuer Tieroekologie und Planung, D-70794 Filderstadt; now: Ecology Centre, Department of Landscape Ecology, University of Kiel, Olshausenstrasse 75, D- 24118 Kiel

[4] Steinbeis Transfer Center Applied Landscape Planning c/o University Rostock, D-19059 Rostock

[5] Oeko-Log, D-16247 Parlow & D-66482 Zweibruecken

[6] Freilandforschung, D-28357 Bremen

1 Introduction

During the last three decades the effects of infrastructure (roads, railways and waterways) on nature and wildlife have become a growing concern (Ellenberg et al. 1981, Brigth 1993, Bennett 1997). They can have negative impacts on animals or their habitats up to a distance many times the width of the road (Reck & Kaule 1994, Reijnen et al. 1997, Trombulak & Fissel 2000, Forman et al. 2003). One aspect, the barrier effect of roads, has been neglected for a long time but is meanwhile being discussed as one of the most severe threats to nature conservation, because it leads to habitat fragmentation and as a consequence for some species to population isolation and local population decline or even extinction (Soule 1983).

Currently the western parts of Europe have one of the densest infrastructure networks of the world. Since the late 1980s nature conservationists, infrastructure planers and road construction agencies especially in France, The Netherlands, Switzerland and Germany have developed numerous techniques to mitigate the barrier effect: wildlife overpasses ("green bridges", tunnels) as well as wildlife underpasses (viaducts, culverts, small mammal underpasses, amphibian tunnels, etc.). At the same time there was a growing body of investigations on the effectiveness of these mitigation measures (see e.g. reviews by Trocmé et al. 2003, Ree et al. 2007, Huijser et al. 2007). This has resulted in a European handbook (Iuell et al. 2003) followed by handbooks at national levels (e.g. SETRA 2005, Ministerio de Medio Ambiente 2006, FGSV 2008).

In this paper we focus on two comprehensive investigations carried out in Germany and adjacent countries. The first one from 1991 to 1996 was a before-during-after-study along a new highway called B31new including investigations on overpasses in France, Switzerland and The Netherlands (Pfister et al. 1997). This report consisted of 16 different papers, dealing with large, medium-sized and small mammals, invertebrates, birds and amphibians. The second one from 2003 to 2006 was a re-evaluation of the passages on the B31new but included additional crossing structures from other parts of Germany not investigated so far (Georgii et al. 2006) and investigated especially large and medium-sized mammals, dormice and bats. Here we combine the two studies. We present some main results and compare both time periods where possible.

At the centre of the field investigations were green bridges and the question as to what extent especially insects, unable to fly, as well as mammals use green bridges and how often. Most of these studies follow a more qualitative approach; only in some cases the methods of data sampling allowed inferential statistical treatment.

2 Study area

The 1991-1996 study was carried out mainly on the B31new and B33new highways near Lake Constance in Baden-Wuerttemberg (southern Germany), and some additional green bridges in The Netherlands, France, and Switzerland. The 2003-2006 study included the green bridges on the B31new and B33new again as well as green bridges and other crossing structures at three motorways (A8, A96, A98), one more highway (B464), and three

state main roads (L113new, L1100, L1207) in Baden-Wuerttemberg and along a section of the A20 motorway in Mecklenburg-Vorpommern (northern Germany).

The study areas differ in landscape character, with the environment around the roads in Baden-Wuerttemberg, the Alsace, Switzerland, The Netherlands, and France showing normally plain or slightly hilly terrain with a small-scale mixture of meadows, fields and forests whereas the landscape around the A20 in Mecklenburg-Vorpommern is mainly plain and consists of large-scale farm land with only scarce forests. The road density varied between 0,43 and 0,78 km/km², the traffic volume from only about 1.700 to more than 63.000 vehicles per 24h. All motor- and highways are fenced, apart from state main roads.
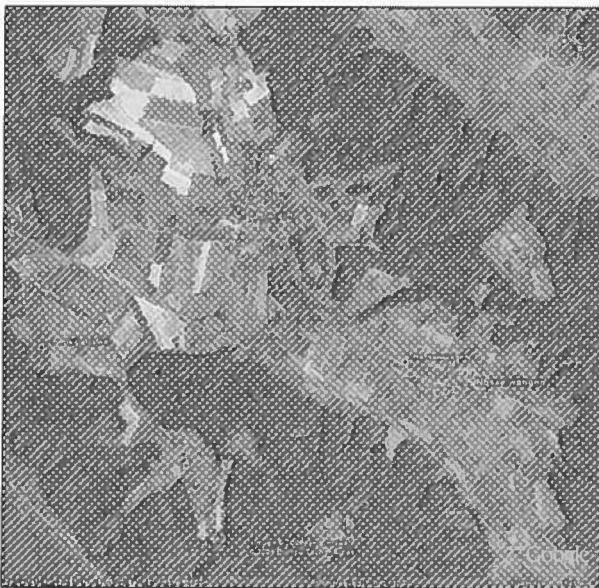
Baden-Württemberg *Mecklenburg-Vorpommern*

3 Material and methods

The studies involved 20 green bridges, 10 viaducts, 7 wildlife underpasses for large animals, some 20 underpasses for small mammals, 6 river crossings or culverts as well as non-wildlife over- and underpasses (for use by farmers, foresters or public traffic, n = 38). Their age ranges from three to sixteen years according to the age of the roads. Vegetation on the green bridges or below the viaducts varied from nearly pure meadow, open parts mixed with shrubs to completely wooded. Most crossing structures contained gravel (in some cases also paved) roads which were used by humans (for some more detail see Table 1).

Animal groups studied were ungulates, European hare, medium sized predators (on all roads); mice, voles and shrews, dormice and bats, ground beetles, grasshoppers, birds and amphibians (mainly on the B31new). Some additional studies on voles, ground beetles, grasshoppers and especially the investigations on butterflies, burnet moths and spiders took place on two green bridges at the A36 in France (Alsace). We applied a variety of methods depending on the species investigated (Table 2).

crossing structures	quantity	width[1] (meters)	height (meters)	length (meters)	vegetation
green bridges (gb)	20	23 - 201	--	23 - 120	pure meadow, totally wood, mixed
viaducts (vd)	10	58 - 440	5,5 - 55	*	pure ground, mainly meadow, partially shubs and wood
large mammal underpasses (lu)	7	6 - 44	2,4 - 8	45 - 95	pure ground, partially meadow
culverts[2] (cu)	6	3,2 - 15	1,8 - 4,3	35 - 68	mainly pure ground, some stoned
small mammal underpasses[2] (su)	20	0,8 - 2,0	0,8 - 2,0	35 - 55	pure ground

[1] from the perspective of the animals (between fences or walls)
[2] circular and box shaped
* equal to road with

Table 1 The main wildlife passages involved in the study; further crossing structures were non-wildlife passages for use by farmers, foresters, recreationists or even public traffic (joint-use passages); parentheses show abbreviations used in figures

Concerning the roads and crossing structures we collected data describing the dimensions of the passages, roads, vehicle frequency, traffic noise, human use and vegetation structure on and under the passages as well as in their surroundings.

For most crossing structures their number were too small or the use by animals too low for statistical treatment. Only the methodological approach of the 2003-2006 study and the intensive use of the green bridges by medium sized and large mammals (including the data of 1991-1996) allowed some statistical analyses. Carrying out multiple regression analysis (Zar 1999) we investigated the influence of 28 independent variables on the species' use of the 20 green bridges (see Table 5). We defined the intensity of passage use as the number of animals from each species seen on the videos per night or the amount of tracks in snow per 24h-day. We used models including the whole group of mammals as well as models regarding only roe deer, red fox and hare (the three most frequent mammal species). Differences between mean values were tested by simple or paired t-test (Zar 1999) and aspects of use of vegetation structure by compositional analysis (Aebischer et al. 1993). In some cases the regression results explain differences in the intensity of species' passage use with relatively high R^2-values (0,56 to 0,86).

	road	years of investigation	methods	intensity of investigation
insects unable to fly	B31new B33new A36	1991, 1992, 1996	determination of species with lines or grids of pitfall traps (ground beetles) or by their songs with frequency recorders and with insect nets (grasshoppers); capture-mark-recapture experiments with species of both groups on two bridges and in reference areas; elytra marking (beetles) and colour marking (grasshoppers)	several-week periods from March-October
insects capable to fly	B31new A36	1992	semi-quantitative counts on the green bridges or adjacent areas, observation of flight patterns via the green bridges and the intermediate road sections in May, June, July and September	several-day observations in each month
ground-dwelling mammals	B31new B33new A36	1991, 1992, 1993, 1994, 1996	capture-recapture in lines of box traps in July, September, October on three (B31new) and two (A36) green bridges and in their surroundings; marking of the animals by toe-clipping	14 days each month
spiders	A36	1992, 1993	capture of animals from April-October using lines of pitfall traps from two green bridges into the adjacent forests	two-week intervals
dormice	B31new	1991, 1992, 1994, 1996 2004, 2005	capture-recapture in box traps in June, July, August, September, October on one green bridge and in its surroundings; search for nests, controls of nesting boxes, counting of calls, telemetry (47 animals)	13-20 days each month
bats	B31new B464 A8	2004, 2006	in May, July, August, September observation by binoculars and bat detectors (during day light) and by headlights, night-vision devices and automated echolocation call loggers (during night) on eight green bridges; telemetry on one green bridge (4 animals)	4 x 3 days each summer
birds	B31new	1991, 1996	mapping along transects and of territories during the breeding season, in September and December; flight counts via the green bridges and the intermediate road segments	3-4 counts each season
large and medium sized mammals	B31+33new, B464; L113, 1100, 1207; A8,96,98,20	1991, 1993, 1994, 1996, 2004, 2005	direct observation during spring and autumn of all species and telemetry with 5 badgers on the B31new and in its surroundings; track counts along transects in winter, interviews with hunters, foresters an other people experienced with the situation (all roads); infrared video recordings on green bridges and some non-wildlife passages at the B31new in 1994 (May, September) and 1995 (March); track counts at all roads (Winter), infrared video recordings on green bridges and remote cameras at most of the small mammal passages and non-wildlife passages in 2004 and 2005 (March/April)	camera monitoring 5 days per period

Table 2. Roads investigated, years of investigations and methods used to study the different groups of species

4 Results

4.1 Use of green bridges by invertebrates

From 1991 to 1996 we investigated the use of green bridges on the B31new, the B33new and on the A36 (Alsace, France) by different invertebrate species (Pfister et al. 1997).

4.1.1 Ground beetles

In 1991, before construction of the B31new, and in 1996 after the road, five green bridges and several culverts had been completed, 108 species of ground beetles were found in the sampling plots alongside the road and in its surroundings and 73 species on the green bridges (Rietze & Reck 1997). In the centre of two culverts we found 2 species whereas near the entrances of the culverts 35 species could be found.

To evaluate the roaming patterns of ground beetles around the green bridges and roads an extensive capture-mark-recapture study at one of the B31new bridges and an adjacent road section was carried out. In 1991, 5,993 individuals from 62 species were marked, and 7,827 from 64 species in 1996. In 1991 the recapture results showed that there was an intensive exchange between the habitats on and around the strip of the planned road with some individuals moving up to 500 meters (Fig. 1). In the same year 25% out of these animals crossed the position of the planned green bridge whereas in 1996 only 15% of the recaptured specimens were found on the meanwhile built overpass. Furthermore in 1996 only 1% crossed the adjacent road section (i.e. one single male of *Carabus violaceus* was found across the road).
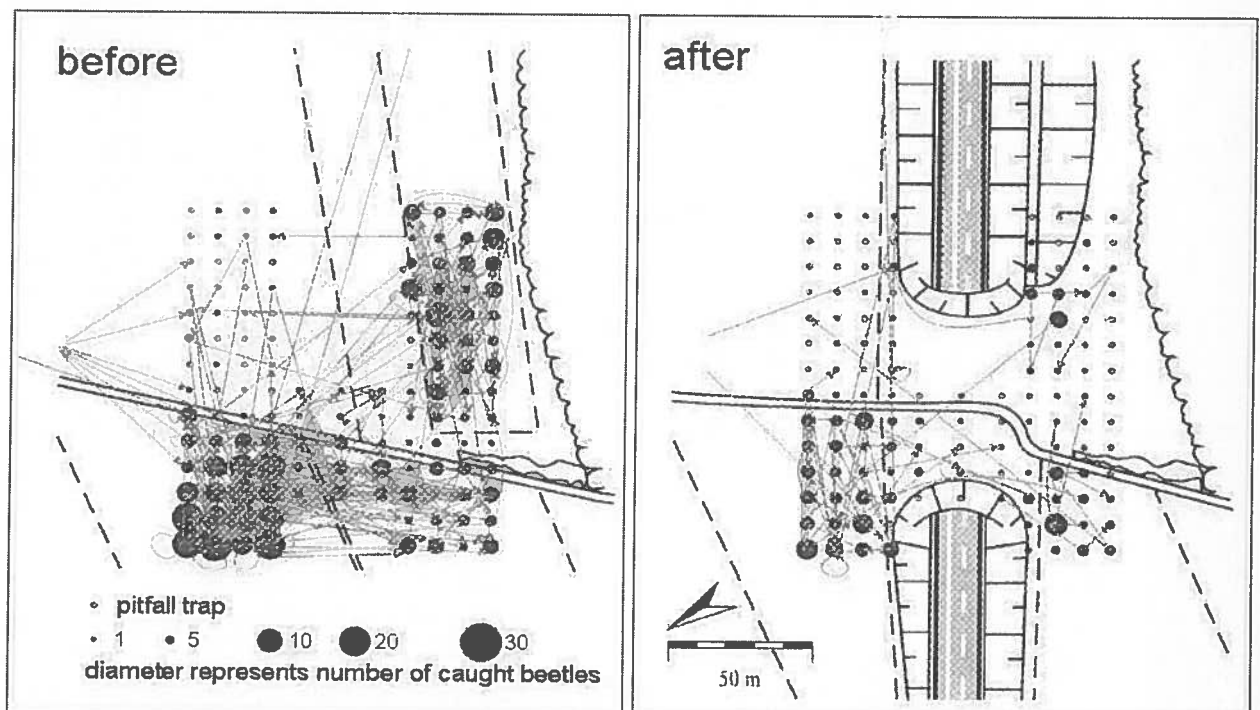

Fig.1 *Grids of pitfall traps on a segment of the planned B31new (before; 1991) and on the green bridge in the same position after the road had been completed (after; 1996). Lines between the pitfalls show movements of marked male beetles of the species* Carabus cancellatus

	B33new-1	B33new-2	A36	railway
sampling plots	63	49	57	36
green bridge	57	46	36	43
gb % of plots	90	94	63	119

Table 3 Number of ground beetle species on four green bridges: B33new-1 (near forest), B33new-2 (open fields), A36 (within forest), railway (within forest) and in nearby sampling plots

To evaluate the species composition on the overpasses in 1992 four additional green bridges at the B33new, the A36 and a high-speed railway as well as road and rail sections adjacent to the bridges were investigated (Reck et al. 1992). Altogether, 113 species were found in the different habitat types near and on the green bridges. On the green bridges across roads less species (63-94%), in the case of the overpass at the railway even more species (119%) were recorded than in the surrounding habitats (Table 3). In general the results clearly indicated a trend to more open-habitat adapted species on the green bridges probably because most of the latter ones were young with only scarce canopy. So, even on the green bridges at the A36, which lie in a large deciduous forest and showed a rather dense canopy, only few woodland species and more open-habitat species were found (Fig. 2; Zangger 1995a), probably having immigrated along the road embankments with open habitat. This was especially true for two green bridges at the B33new and the one across the railway, which lie within forests also but showed only little canopy cover or for one passage far away from forests, within fields.
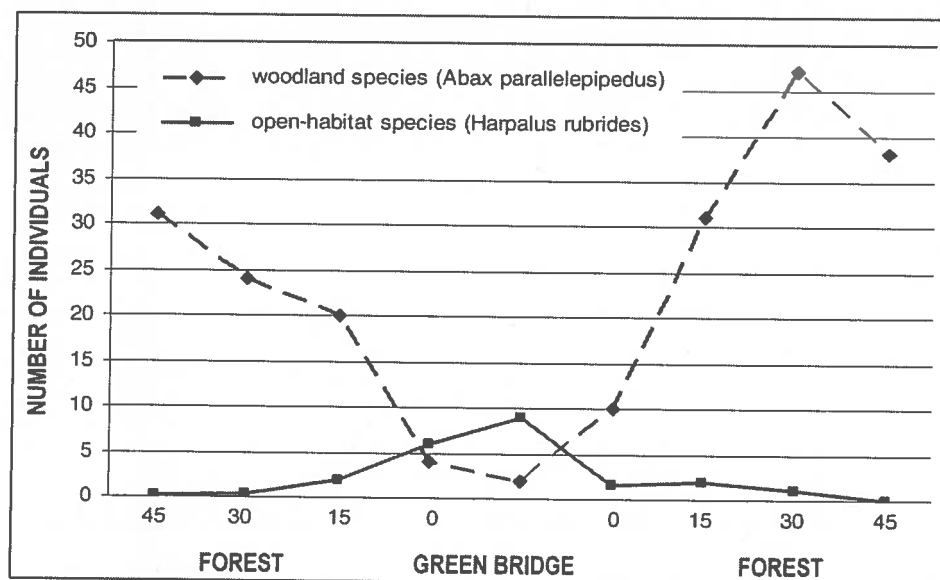

Fig.2 Numbers of ground beetles captured on one of the A36 green bridges and in the adjacent forests

4.1.2 Grasshoppers

In 1991 and 1996 grasshoppers were studied using the same sampling plots and crossing structures on the B31new (Rietze & Reck 1997) and, in addition, near one green bridge on the B33new (Rietze & Reck 1993, Leisi 1992). Moreover, two further capture-mark-recapture studies were carried out.

On the B31new sampling plots 26 species were identified, out of which 16 have been found on the green bridges as well as in the surroundings. In the capture-recapture experiment 4,425 and 3,896 individuals in 1991 and 1996 respectively, from 13 species, were marked in a rather humid grassland habitat (e.g. water-meadow grasshopper *Chorthippus montanus* and steppe grasshopper *C. dorsatus*). In 1991, 2,073 animals were recaptured from which 86 had crossed the strip of the planned road. By contrast, despite recapturing no less than 2,348 individuals in 1996 none had crossed the meanwhile completed and opened road and none was found on the green bridge some 300 m away from the capture habitat. The reason for this probably is that the habitats along the road had changed to become rather dry ones. Hence the animals were no longer able to cover the distance of about 300 m to the green bridge, as they had to move through unsuitable habitat and suitable habitat corridors were missing (Fig. 3). Furthermore, the direction of movements changed. Whereas in 1991, before the road's construction, no preference in the direction of the movements
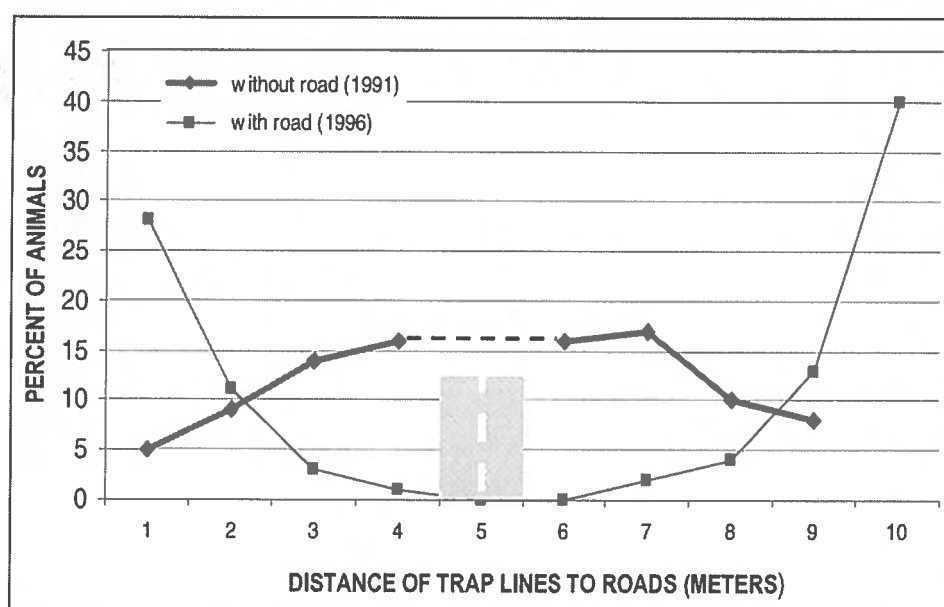

Fig.3 Distribution of grasshoppers of the species Chorthippus albomarginatus *in different distances from the road captured in the same sampling plots before and after the road has been constructed*

could be detected, in 1996 about 70% of the movements of adults were directed away from the road and only 30% towards the road (e.g. 66 out of 92 recorded movements of the steppe grasshopper (*C. dorsatus*) and 43 out of 59 of the lesser marsh grasshopper (*C. albomarginatus*).

On the B33new some 3,000 marked individuals from 13 species (especially the meadow grasshopper *Chorthippus parallelus* and the bow-winged grasshopper *Chorthippus biguttulus*) were translocated 50, 125, 225, and 275 m away from a green bridge. 677 animals were recaptured with five individuals found on the bridge perhaps crossing it. Probably because of a narrow but continuous strip of suitable habitat from the bridge to the release patches, one of the individuals moved 275 m and was recaptured on the overpass.

In addition, in 1992 these two green bridges were compared with those on the A36 and the high-speed railway (Reck et al. 1992[8]). There, 28 species in the habitats around the bridges were determined with 47-83% of these found also on the green bridges (Table 4).

	B33new-1	B33new-2	A36	railway
sampling plots	12	12	16	19
green bridge	9	15	9	8
gb % of plots	75	83	50	47

Table 4. Number of grasshopper species on four green bridges (gb) and in nearby sampling plots (compare Tab.3

The European mole cricket (*Gryllotalpa gryllotalpa*) was the only grasshopper species observed in small mammal culverts too.

4.1.3 Butterflies and burnet moths

These two groups of insect species were studied along the A36 only (Reck et al. 1992). In the whole area we found 41 butterfly species and one burnet moth species. 29 of these species were recorded on the overpasses as well. In July and August we observed during one hour each flight patterns of the animals at one of the overpasses and at a distance of 100 m. During the two hours 75 individuals from 20 species were crossing the overpass (width: 10 m) and 13 individuals from 5 species could be detected crossing the motorway in a sector 5 times longer than the width of the overpass. 3 of these 13 individuals were killed by cars (Fig. 4).
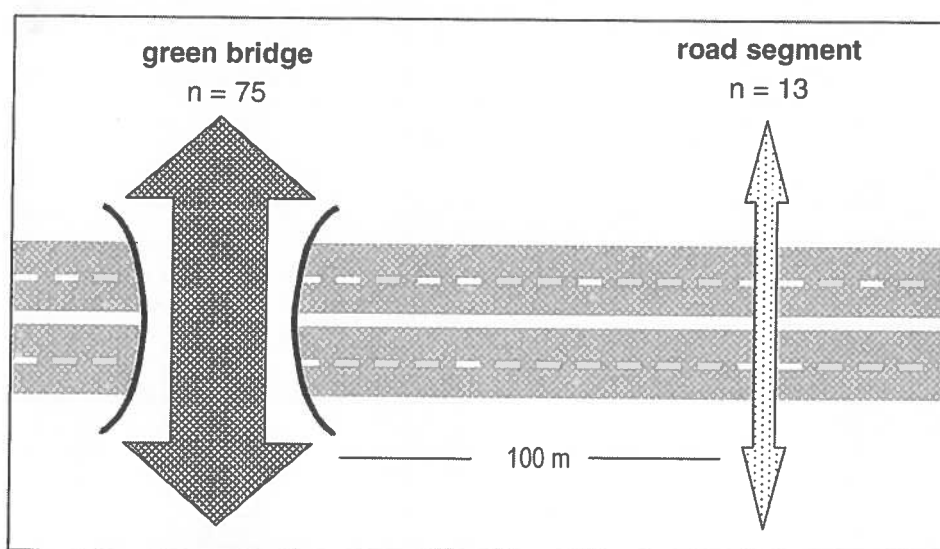

Fig.4 Experimental design and results of motorway crossings by butterflies via the observed green bridge and nearby road segments without overpasses (one hour of observation each during Juli and August, respectively)

4.1.4 Spiders

During the vegetation period in 1993 pitfall samplings of epigeic spiders, especially cursorial species, were taken along a transect from a green bridge at the A36 to the adjacent forest area (Zangger 1995b). In total 4,660 individuals out of 47 species or eight families, respectively, were inventoried. Although the overpass was partly landscaped with a hedgerow the data showed a clear gradient in the abundance of forest dwelling species along the transect towards the overpass. Few individuals of forest species could be found under shrubs on the bridge. On the contrary, species preferring warm habitats and forest edges mainly inhabited the overpass, such as e.g. Aulonia albimana (Fig. 5). Species assemblages found on the green bridge were thus similar to the catches from the fully exposed roadside verges. Due to the inconvenient microhabitats on the bridge only a weak linkage between forest floor arthropod communities on both sides of the motorway was postulated.
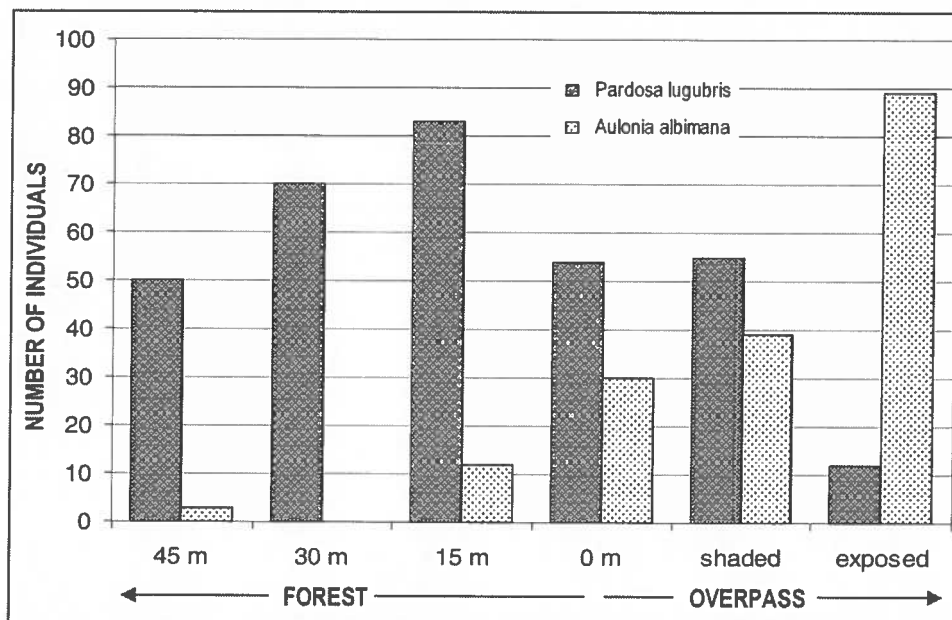

Fig.5 Comparison of mean abundance of two species of spiders along the forest-overpass transect

4.2 Use of green bridges by small mammals

4.2.1 Mice, voles and shrews

On three green bridges at the B31new and two at the A36 three species of mice (*Muridae*) and voles (*Arvicolidae*) each and four species of shrews were found (*Soricidae*; Wilhelm & Paliocha 1997). Species composition varied considerably from bridge to bridge. Their relative density was normally higher in the adjacent habitats than on the green bridges and higher on older than on younger bridges (Fig. 6). This was partially due to the habitat requirements of the species with the ecological more generalistic species like the common vole (*Microtus arvalis*) or the long-tailed field mouse (*Apodemus sylvaticus*) found on all green bridges whereas the bank vole (*Chletrionomys glareolus*) did only use the wooded
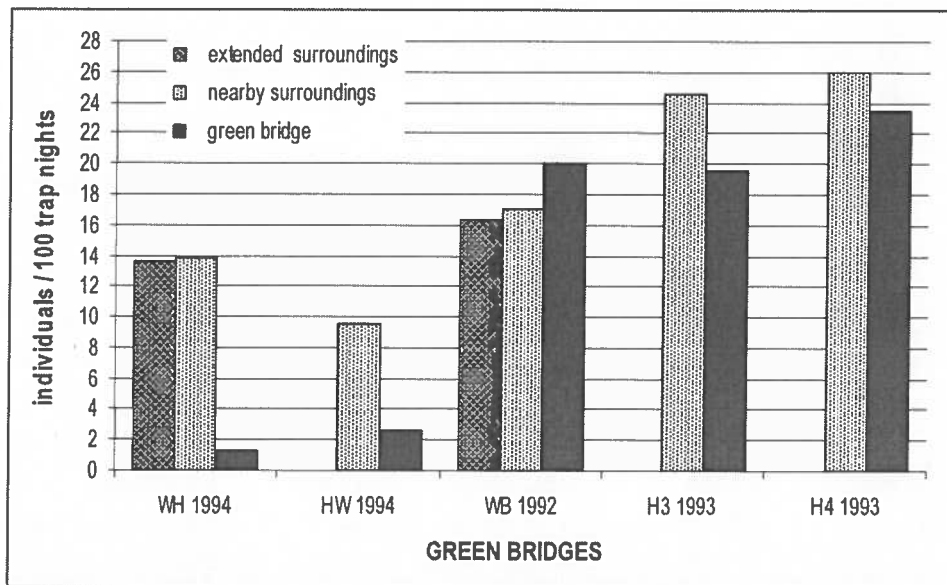
Fig.6 Relative densities of the seven mice, vole and shrew species investigated in 1992, 1993 and 1994 on five green bridges and in their surroundings (WH, HW = B31new; WB = B33new; H3, H4 = A36; age of bridges increasing from left to right)
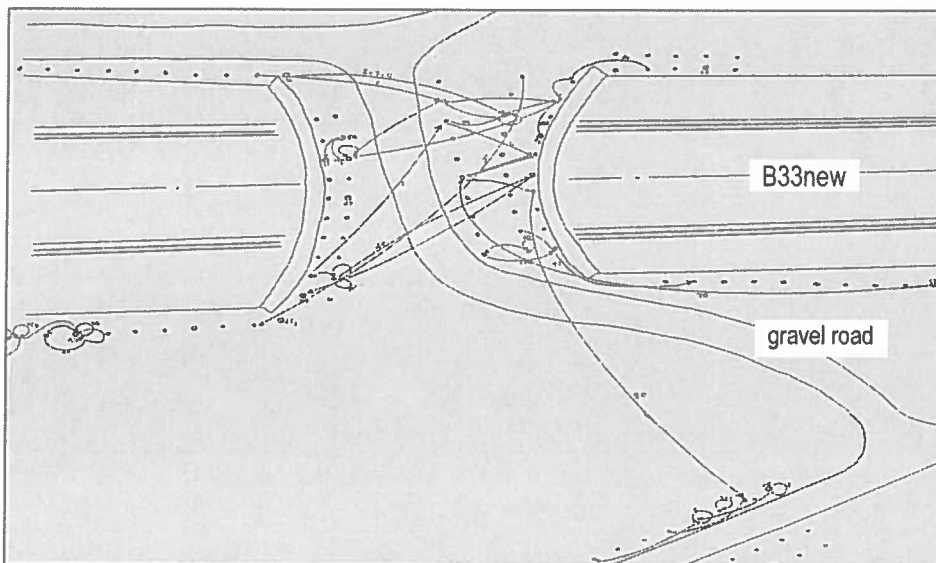

Fig.7 Roaming patterns of the common vole (*Microtus arvalis*) at one of the green bridges on the B33new (with a gravel road); points show trap lines

buildings (H3, H4 at A36), because it is closely adapted to shrubs. The capture-recapture experiments showed that some animals have at least parts of their home ranges on the bridges (Fig. 7) but roam in the nearby adjacent areas too. In contrast others primarily used the green bridges to cross the road. Shrews were found on the bridges only in small numbers.

4.2.2 Dormice

With the investigation of two dormice species, the hazel dormouse (*Muscardinus avellanarius*) and the edible dormouse (*Glis glis*), both with a strong affinity for trees and shrubs, we especially addressed the question whether a totally reforested green bridge allows the species to move between forest patches (Mueller-Stiess & Herrmann 1997). In 1991, before construction of the B31new, we studied the distribution of the two dormice species in the still undissected forest. In 1993 after a green bridge had been completed in this place but was not yet reforested and even in 1996 when first trees and shrubs had grown neither of the two species was found on the bridge (Fig. 8). However, ten years later, in 2005, when the bridge was covered by a continuous layer of trees and shrubs of about eight meters in height some 15 animals were found on the bridge, four of which were equipped with transmitters (Mueller-Stiess 2005). Two of these animals, translocated over a small paved road adjacent to the bridge, did not return, probably because of the road, whereas the two others used the bridge as part of their home ranges.
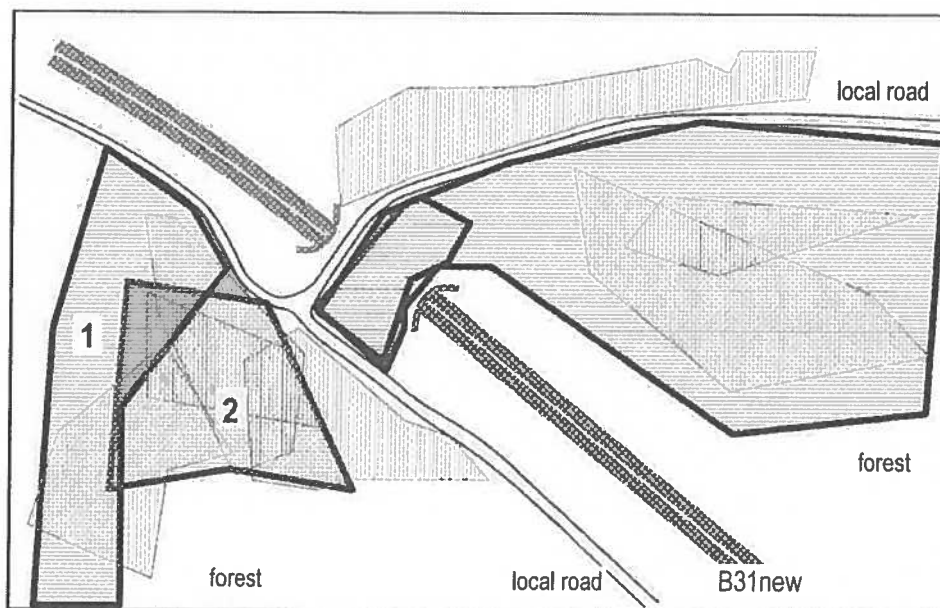

Fig.8   Home ranges of seven dormice in 1991 (shaded vertically, thin outlines) adjacent to the green bridge and of four dormice in 2004 (shaded horizontally, thick outlines) partially lying on the green bridge as well as of the two dislocated animals (1, 2)

4.2.3 Bats

At eight of the green bridges and six other crossings structures in Baden-Wuerttemberg ten bat species were found (Bach & Mueller-Stiess 2005). Seven of these species used the green bridges both to cross the roads and as a feeding habitat. This applies especially for those species which orient themselves in their flights using vertical landscape elements, e.g. the common pipistrel (*Pipistrellus pipistrellus*) or the natterer's bat (*Myotis nattereri*). The others were observed crossing the bridges only, e.g. the common noctule (*Nyctalus noctula*) or the serotine bat (*Eptesicus serotinus*). When comparing the green bridges it seems that those with linear structures out of trees and shrubs were more intensively frequented than those with more scattered structures (Fig. 9). As for the non-wildlife under- and overpasses

the former ones were more intensively used than the latter ones. However, these findings should be dealt with caution because samples were only small and no statistical treatment possible.
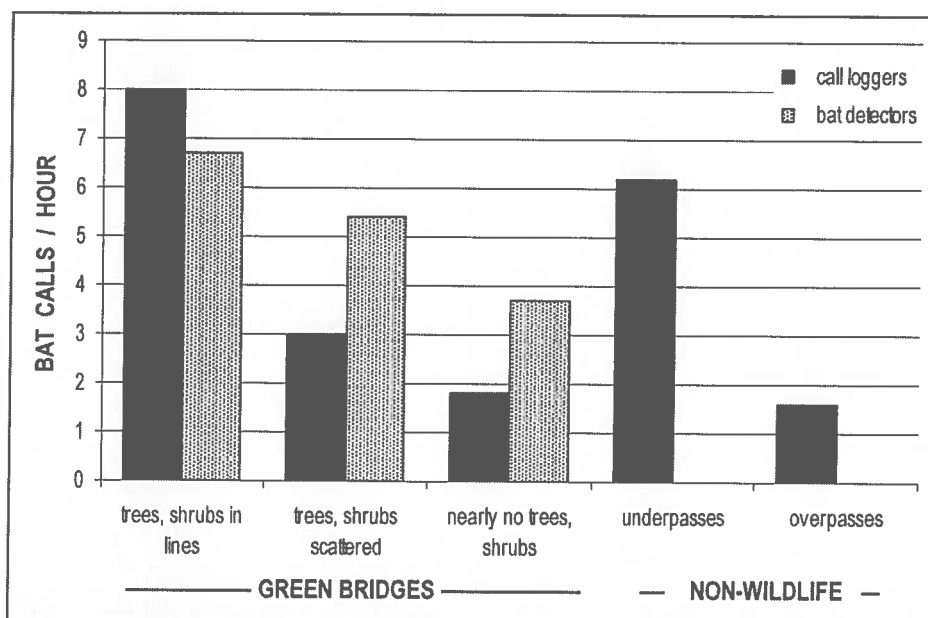

Fig.9   Use of green bridges and non-wildlife passages by bats as a function of the vegetation structure on the bridges or near the other passages

4.3   Use of over- and underpasses by medium sized and large mammals

4.3.1   Species

Summarizing the 335 video nights in 1993-1997 (Pfister et al. 1997) and 117 video nights as well as 43 tracking days in 2003-2006 (Georgii et al. 2006) we recorded a total of 1,835 animals in the first study period and of 3,567 animals in the second, crossing the different types of passages. As Fig. 10 shows, roe deer (*Capreolus capreolus*), hare (*Lepus europaeus*) and fox (Vulpes vulpes) accounted for 72% (videos) and 85% (tracks) of the records.

The second most frequent species were badger (*Meles meles*), martens (pine marten *Martes martes* and beech marten *Martes foina*, species not distinguished, and polecat *Mustela putorius*) and wild boar (*Sus scofa*). Red deer (*Cervus elaphus*), fallow deer (*Dama dama*), otter (*Lutra lurta*) and racoon dog (*Procyon lotor*), which were present only in the 2003-2006 study on the A20 in Mecklenburg-Vorpommern, made up 2-3% of all species recorded.

Comparing the data from the 1993-1997 study with those of the 2003-2006 study the overall proportion of the different species is rather similar. The category "others" comprises mainly domestic cats. Two species, otter and polecat, are endangered in Germany.
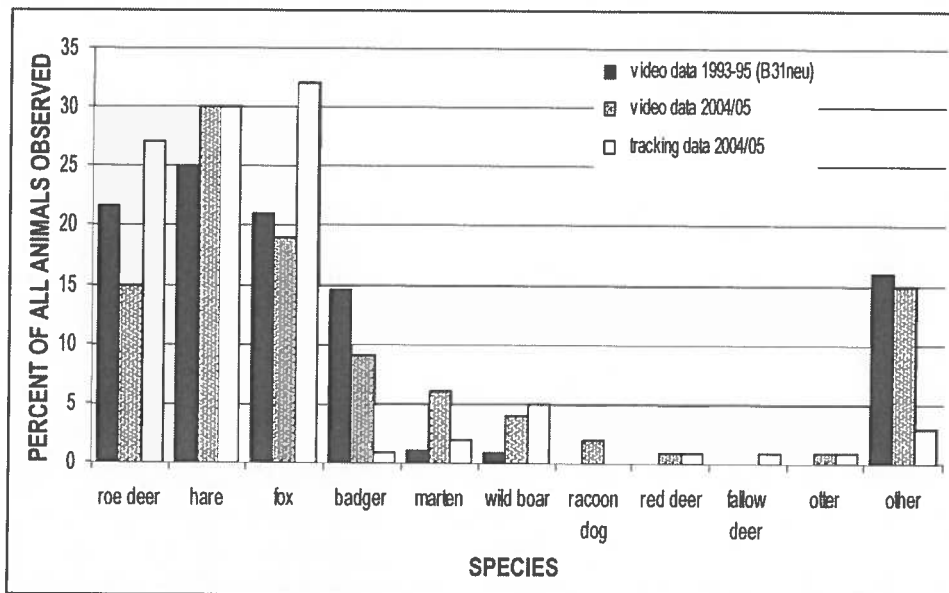
Fig.10 Frequency of ten mammal species on 20 green bridges; data from infrared video recordings (animals per night) and track counts during snow (animals per 24h-day); "others" are mainly domestic cats

4.3.2 Use of different passage types

When analysing the video and track data of the 2003-2006 study, both reveal green bridges and viaducts as the crossing structures most intensively used by the species studied (Fig. 11), despite the fact that some green bridges and all viaducts have not been build primarily as wildlife passages. In detail this means, that most of these passage types have been used at least by about ten animals, some by up to 20 and one even by about 50 animals per night. These differences are partly due to the size, to the age or to the position of the buildings (see below). Unexpected was the only moderate use of the large mammal under-
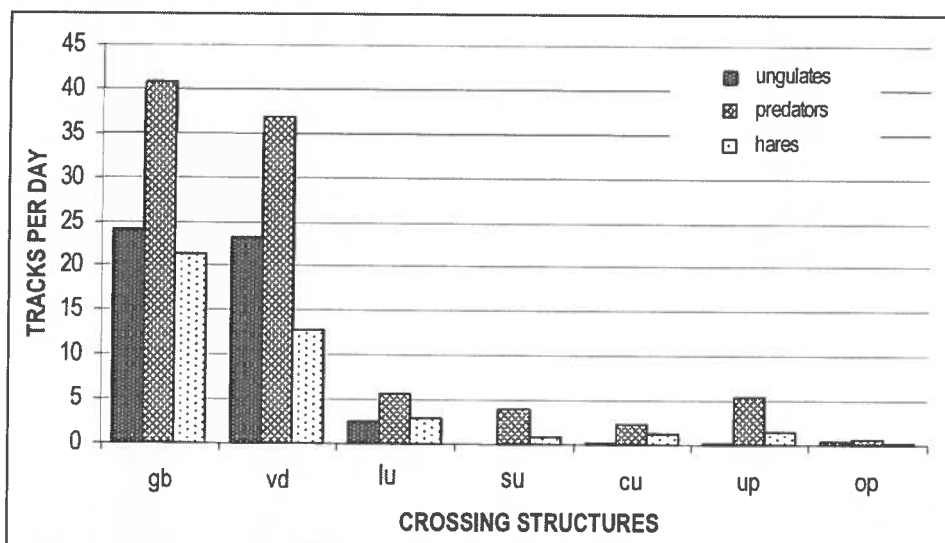

Fig.11 Use of different wildlife and non-wildlife crossing structures by the three groups of mammal species contained in Fig. 10 too; data from track counts (gb = green bridges, vd = viaducts, lu = large mammal underpasses, su = small mammal underpasses, cu = culverts, up = non-wildlife underpasses, op = non-wildlife overpasses)

passes by ungulates and of the culverts and small mammal passages by medium sized animals with five, less than five or even less than two animals per night or day, respectively, although they have been build especially for these species. On the other hand use of all underpasses, the non-wildlife passages included, showed that predators (fox, badger, martens, otters, racoon dogs) and in some cases also hares had no problems to use even the narrower and longer ones.

Besides wild boar, which often run when crossing (especially smaller) passages, most other species showed "relaxed" behaviour. Moreover in the videos roe deer, hare, badger and fox used the green bridges as feeding habitats and have been observed leaving scent or urine marks.

When comparing the distribution of tracks near the green bridges with that in the intermediate road segments it became obvious that discrete tracks as well as track paths concentrate funnel-shaped already from far apart towards the bridges (Fig. 12). Along the intermediate road segments density was only about half of that at the green bridge entrances.
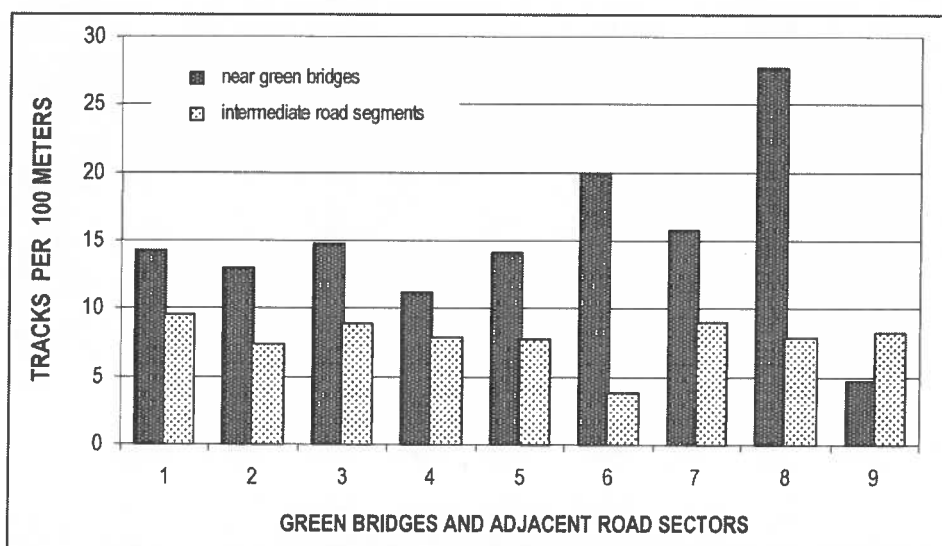

Fig.12 Density of tracks in snow per 100 meters at the entrances of nine green bridges and in the adjacent road segments

4.3.3 Influence of constructional and environmental attributes on the use of green bridges

Analysing the use of green bridges by treatment with statistical methods we tested 28 independent variables, eight of which proved to be of influence on the use of this kind of overpass in some cases (Table 5).

WIDTH

Both studies, from 1991-1995 and 2003-2006, showed that the intensity of use of green bridges by medium-sized and larger mammals increases according to the width of the buildings. In the later investigation this could be confirmed with the multiple regression

analysis using the track data for all species (P = 0.015; but not with the video data). When using the video data of roe deer only a significant negative reaction to the length of the green bridges was found as well (P = 0.020).

For all other crossing structures there seems to be a relation between use intensity and width too, but without statistical significance.

Attribute	video data			
	beta	SE	P-value	rank
all species	$R^2 = 0.56$			
gb_age[1]	-0.552	0.063	0.000	1
gb_wood[2]	-0.042	0.007	0.000	2
anth_use[3]	-0.579	0.233	0.038	3
roe deer	$R^2 = 0.76$			
road_numb[3]	-0.722	0.235	0.013	1
gb_length[4]	-0.040	0.014	0.020	2
build_envir[5]	-0.149	0.074	0.074	3
red fox	$R^2 = 0.65$			
gb_age[1]	-0.203	0.054	0.004	1
anth_use[3]	-0.804	0.301	0.023	2
attribute	track data			
	beta	SE	P-value	rank
all species	$R^2 = 0.86$			
build_envir[5]	-0.086	0.027	0.009	1
road_numb[6]	-0.449	0.147	0.012	2
gb_width[7]	0.007	0.002	0.015	3
gb_noise[7]	-0.041	0.017	0.040	4

[1] date when build (1989, 1990, ...)
[2] amount of wooded area on green bridges (percent of whole surface)
[3] number of people or cars per 24h-day in three categories (1, 2, 3)
[4] from entrance to entrance
[5] number of buildings in the nearer environment of green bridges
[6] number of paved or unpaved roads on green bridges
[7] in meters between the fences
[8] dB(A) in the middle of green bridges

Table 5 *Eight out of some 28 independent variables which proved to be significant factors explaining the green bridge use by medium-sized and larger mammals (using multiple regression analysis); all other variables failed or nearly failed to be of significance. Rank is based on sum of squares (relative importance) of this variable*

AGE

With the video data the multiple regression revealed age of the green bridge to be a significant factor explaining green bridge use by all observed mammal species (P = 0.016): the younger the buildings the less intensive was the frequentation by the animals. This was confirmed by the fox data alone (P = 0.004). On the other hand there exists a strong correlation between the age and the amount of wooded area on the green bridges (r = 0.802): the older the bridges the more of the surface was covered with shrubs and trees. The regression analysis showed that this is of influence on the age-dependent use of the overpasses because a higher amount of wooded area results in lesser animals crossing the green bridges (P < 0.001).

This can dampen the effect of age so far that there is no difference recognizable between younger and older performance data. This became obvious when we compared the actual data with those from 1993-1997 of the same seven green bridges (Fig. 13). Notwithstanding the ten year difference in the vegetation development there is a highly significant correlation between the number of species' passages in 1993-1997 and 2003-2006 (r = 0.905, P < 0.005).

POSITION

When analysing the video data it became evident that the position of green bridges seems to play a role for the use by the mammal species investigated (Fig. 14). So bridges at forest edges apparently were most intensively frequented and bridges within forest more than such in open habitats (meadows, fields etc.). Similarly, green bridges nearer to canopy are more intensively used than bridges far away. However, these differences proved not to be of statistical significance.
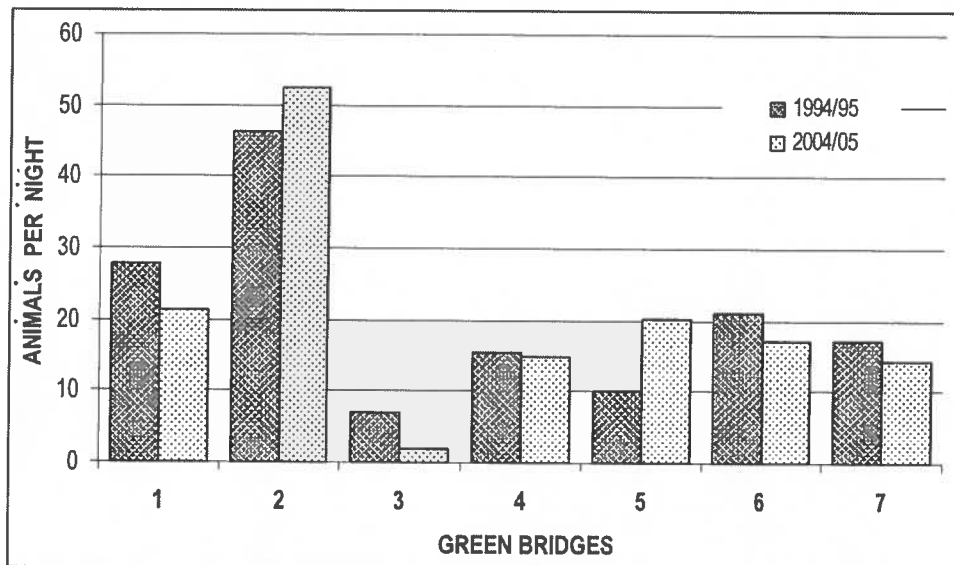

Fig.13 Intensity of use of seven green bridges on the B31new and B33new during 1994/1995 and 2004/2005, data from infrared video recordings
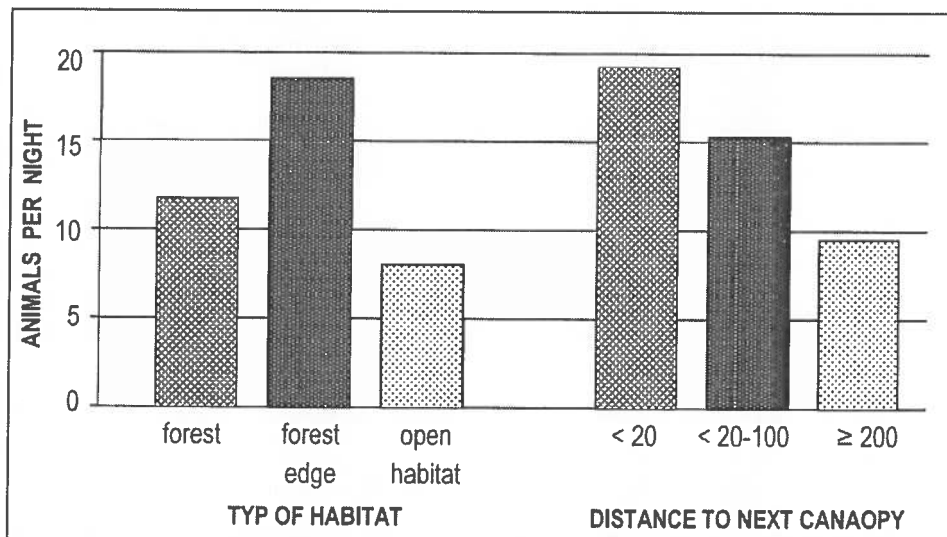

Fig.14 Use of green bridges located in different types of habitat and dependent of distance to next canopy (in meters); lines show standard errors

VEGETATION AND OTHER STRUCTURAL FEATURES

Another influence of vegetation as well as other structures became apparent when we compared the use of the different structural features on the green bridges such as wooded areas, meadows or open parts respectively, gravel roads and the earth mounds at the outer edges. So, for example, the animals used the open parts of the green bridges more and the wooded areas less intensively than it would be expected from the percentage of bridge surface covered by these structures (Fig. 15). Especially hares, badgers, and foxes preferred to walk on the gravel roads. Compositional analysis (Aebisher et al. 1993) of these data showed a clear ranking for the preference of the different structures (P = 0.0073): open parts > gravel roads > wooded parts > earth mounds.
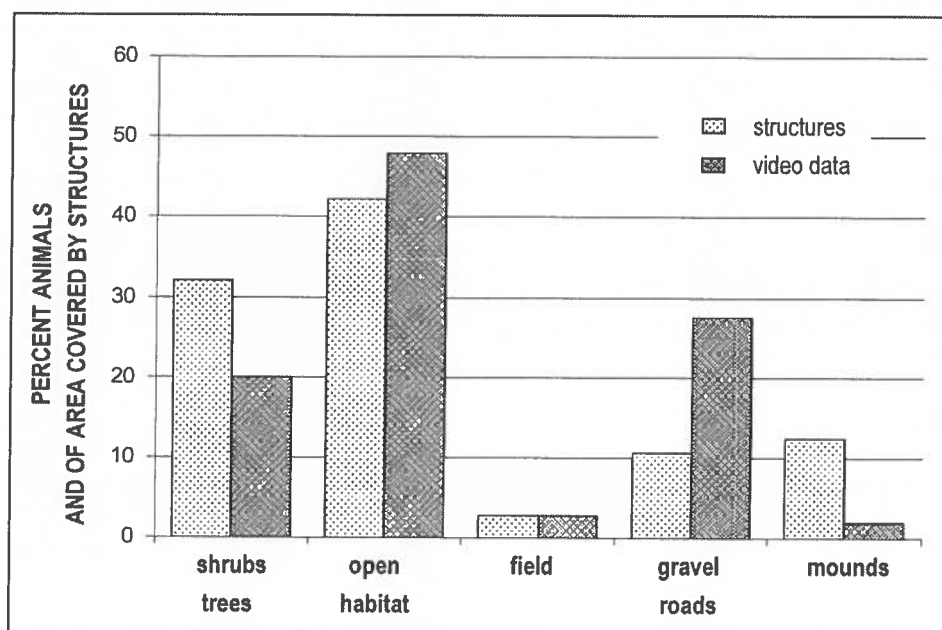

Fig.15 Use of five different types of structures on the green bridges by the mammal species investigated; intensity of use in relation to the amount of area covered by the structures

TRAFFIC NOISE

In both studies we measured noise on the green bridges and at the road verges nearby using hand-held noise meters (Integrating Impulse Sound Level Meter, Type 2226, Brueel and Kjaer, Denmark) with special emphasis on irregular noise bursts (e.g. extra noisy high-speed vehicles, trucks). Because of the noise-lowering effect of earth mounds or screens on the overpasses these traffic noise peaks were about 17 to 39 dB(A) lower on the green bridges than at the road side (73 to 98 dB).

Applying multiple regression analysis to the track data of all species studied showed that less noisy green bridges were used significantly more intensively than more noisy ones (P = 0.040). With the video data this relation was only nearly significant (P = 0.070).

HUMAN PRESENCE

Twelve of the 20 green bridges are joint-use passages mainly with gravel but in some cases with smaller traffic roads also. Furthermore, in the nearby surroundings of most over- and underpasses there were additional roads as well as buildings like farm houses or barns. This enhances the presence of people at the crossing structures, mainly during (the second half of the) day, but also during dusk and dawn.

In the case of green bridges the multiple regression analysis with the *video data* of all species revealed that the recorded human activities on the bridges has a significant negative influence on their frequentation by wild animals ($P = 0.038$). The same was true for the fox ($P = 0.023$). On the other hand, when regarding the *track data* of all species and the *video data* of roe deer the more indirect indices showed the same effect: the higher the number of gravel roads leading to the green bridges or of buildings in their nearby neighbourhood the less the bridges were used by the species observed ($P = 0.012$ and $P = 0.009$) as well as by roe deer ($P = 0.013$ and $P = 0.074$).

4.4 Use of green bridges by birds

In 1992 we investigated the flight patterns of birds at one green bridge lying in farmland (B33new) and at two green bridges lying within forests (A36-1, A36-2; Keller et al. 1996). We compared the intensity of flights via the bridges with those via the road segments in between them during the spring breeding season and the autumn bird migration respectively, using the same study design as for butterflies (see Fig. 4).
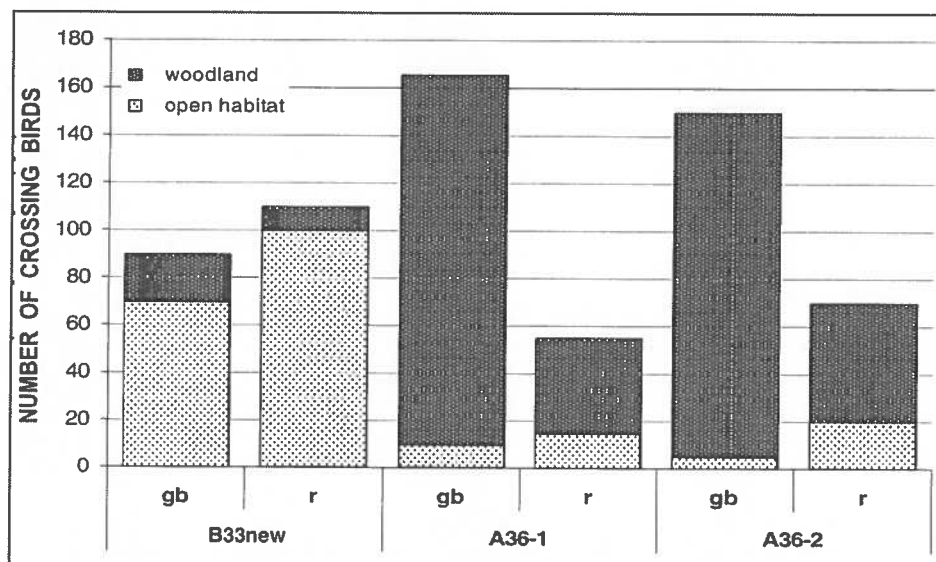

Fig.16 Crossings of the motorways by open-habitat bird species and woodland bird species across the green bridges (gb) and nearby road segments without overpasses (r) in spring (15 hours of observations for each sector); B33new = open habitat; A36-1, A36-2 = forest habitat

In the case of the two A36 green bridges and during spring it became obvious that woodland species crossed the motorway much more intensively via the bridges than across the intermediate road segments (Chi² = 15.98 and 43.37, P < 0.001; Fig. 16). The difference

was statistically significant (P < 0.05; Wilcoxon-signed-rank test). The sample size of open-habitat bird species was only small but seemed to indicate these species to prefer flying across the motorway directly. At the B33new green bridge, where the latter group of bird species was dominating, and during autumn these differences were not statistically significant.

5 Discussion

The most important function of wildlife crossing structures is to minimize the barrier effect of infrastructure by achieving adequate mobility for as many animal species as possible to preserve population size and enhance population viability (luell et al. 2003). Thus, the effectiveness of wildlife passages should be evaluated at the level of the population with effectiveness defined as how much the passageways contribute significantly to the long-term survival of populations. However, this cannot be measured over a period of a few years only because species need time to experience, learn and adjust their behaviour to these new habitat elements (Opdam 1997, Clevenger et al. 2001). For this reason this study only focused on the animals' mobility patterns around different crossing structures and how intensively these were used. As the results illustrate, with a few exceptions most of the animal species investigated used at least the larger crossing structures. But there are apparent differences when regarding either larger mammals or smaller mammals and invertebrates.

One of the most apparent findings of the two studies was that for most of the species investigated habitat attributes on the green bridges or nearby influence the use of these passages. This was obvious especially for mice, dormice and non-flying invertebrates. On most green bridges we found fewer species of these animal groups than at the sampling plots in the neighbourhood (although trap density was even higher on the bridges). The reason for this is that the bridges lack important features of the species' specific habitats like shelter or appropriate microclimate conditions (Angelstam et al. 1987, Anker 1987 for mice; Bright & Morris 1990 for dormice; De Vries et al. 1996). Thus on open-habitat green bridges species typical for forests were found only rarely or, *vice versa*, open-habitat species on shrub- and overstoreyrich bridges. This applies especially for species with very special habitat requirements, e.g. ground beetles, grasshoppers, spiders or dormice.

The same is true for the connection between the bridges and the source habitats of the animals: They often consist of inadequate habitat or are missing. However, because of their small home ranges or the short distances they can move (Montgomery 1980, Wolton & Wolton 1985; Bright & Morris 1991) for most small mammals and for invertebrates, especially stenotopic and less mobile species (Den Boer 1977, Gruttke 1993), habitat linkages are essential to find passageways at all. Further, as the case of dormice shows, even very small roads may be severe barriers. Nevertheless, on the green bridges in the Hardt forest (A36) covered with dense shrubs there were quite a number of open-habitat ground beetles and spiders also, indicating that the tree- and shrubless road verges act as corridors from the open parts of the study area into the forests. The phenomenon that via such corridors non native species may invade habitats is well known (Getz et al. 1978, Vermeulen 1994).

In this context the topology, structure and width of the crossing structures is an important factor. First, because only large green bridges and viaducts provide enough space to establish different habitats to encourage as many small mammal and invertebrate species as possible to use them as passageways. Second, because in contrast to smaller passageways they facilitate less mobile species as well as migrating species to find them. In the present studies width and age proved to promote the use of green bridges by medium sized and larger mammals as well. For these species this may be a result both of the vegetation succession and their ability to learn. Similarly, Vaere (2003) has shown that the amount of moose (*Alces alces*) using an underpass and Van Wieren & Worm (1997) that the number of red and roe deer using an overpass grows as time goes on.

Anyhow, in our studies it was striking how few ungulates used underpasses compared to predators and even the passing rates of the latter ones were low. Perhaps narrower underpasses cause stress to ungulates, as may be interpreted from the behaviour of wild boar on the smaller green bridges. On the other hand, the use of culverts and small underpasses by non-ungulate species (e.g. fox, coyote, badger, marten, weasel etc.) is well documented (Bekker and Canters 1997, Clevenger et al. 2001, Ascensão and Mira 2007). In some cases the low use may have been due to design problems also, as e.g. fences at the entrances, flooding during wet periods or the lack of structures (e.g. lines of shrubs, hedges) to guide the animals to the crossings. This conclusion seems to be supported by the result that distance to next canopy is of positive influence on green bridge use by larger mammals. And last but not least the sample periods of only four nights (videos) or five days (tracks) are very short to give a complete picture of what is happening at the passages (Malo et al. 2005).

Moreover, the results indicate that other attributes, like noise, number of gravel roads, daily presence of humans on the bridges and houses or barnes in their neighbourhood, influence large mammals' use of green bridges in a negative way too. Clevenger et al. (2001) found noise to be of negative influence on culvert use by coyotes, snowshoe hares and squirrels. Vaere (2003) and Olsson et al. (2007) report a negative impact of traffic volume on moose, red and roe deer frequentation of under- and overpasses, possibly as a consequence of traffic related noise. Whereas human disturbance is well known to influence behaviour of wild animals, up to now literature gives only little evidence of these factors influencing crossing structure use by mammals (e.g. Clevenger et al. 2001, Clevenger and Waltho 2005). In the present study all other tested variables failed to show significant effects on species' use of the different crossing structures. Possibly this was due to the varying features of the surrounding habitats, differences in the density of the populations present, specific behavioural traits of individual species or other, unknown, factors. For the same reason it is difficult to predict how a special type of crossing structure will work in a special situation.

Estimating the mitigation effect of crossing structures is rather difficult especially because of the lack of quantitative crossing data before and after road construction. In the case of the B31new this was at least roughly possible summarizing the number of medium to large mammals moving across the projected road line in 1992 (using track counts in its earth bed; Jenny et al. 1993) and the six green bridges, five wildlife and 12 small mammal underpasses in 2003-2006 (using track counts in snow, remote cameras and infrared video

observations). Whereas in 1993 the mean total of daily crossings was 680 the number of crossings in 2003-2006 amounts to only some 125 (or 20%) of that from 1992. Data from an additional investigation of the badger in the surroundings of the B31new (Herrmann et al. 1997, Hermann 2005) confirmed these results: Despite the high number of over- and underpasses the crossing rate of this species declined from 4.6 animals per kilometer and night in 1993-1997 to only 1.7 in 2003-2006. Similarly, the road without green bridges was crossed by only 5% of the ground beetles caught nearby but by about 60% via the green bridges. Following the literature on the necessary exchange between populations of only one animal per generation (Frankham et al. 2002) or one to ten animals (Mills and Allendorf 1996, Vucetich and Waite 2002) the above crossing rates seem to be a rather sufficient value.

Regarding these results the following aspects are important for planning wildlife passages to mitigate effectively the barrier effect of roads: (1) To maximize the permeability of roads for as many species as possible, planners should include in a special situation a diversity of crossing structure types of mixed size classes. (2) The location of passageways must be oriented to the occurrence of, and the use of space by, the (target) species which are to be helped. (3) Target species have to be chosen very carefully and not only regarding larger mammals; typical target species are especially those, which actively disperse but are unable to cross roads because of their barrier effect. (4) The landscape design on green bridges or under viaducts should strongly meet the habitat requirements of the target species and should be linked to the corresponding habitats outside the road area. (5) The effectiveness of passages can be increased by expanding nearby habitat and improving its quality and thereby increasing population size. (6) When installing over- or underpasses target species adapted fencing of the road is obligatory.

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