# Ecological Effects of Roads

## *A review*

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### *Abstract*

Habitat fragmentation due to transport infrastructure is receiving growing concern among ecologists and civil engineers. Much data has been gathered that gives evidence of the complex impact of infrastructure on wildlife and landscapes. Roads, railroads, and their traffic disrupt ecological processes; increase mortality in animals, lead to a degradation, loss and isolation of wildlife habitat, and cause a fragmentation of the landscape in a literal sense. Despite the quantity of empirical studies, it is still difficult to draw general conclusions or define impact thresholds that could guide evaluation work. The increasing public demand on mitigation and prevention of environmental impacts strongly requires the development of evaluation tools for civil engineers and ecologists to apply in the planning and construction of transport infrastructure. In this essay, I briefly review the scientific literature on the known ecological effects of transport infrastructure, with special focus on roads.

## Contents

## Background

Habitat fragmentation due to transport infrastructure is receiving growing concern among European countries (Prillevitz, 1997). Possible consequences to wildlife have been recognised and there is evidence of effects on both species and ecosystems at different spatial scales (Canters et al., 1997). Plenty reviews, bibliographies, symposia proceedings and other reports on the ecological effects of infrastructure illustrate the universal interest in the problem (see e.g. Van der Zande et al., 1980; Andrews, 1990; Bennett, 1991; Seiler, 1996; Spellerberg, 1998; Forman and Alexander, 1998; Trombulak and Frissell, 2000; Bernard et al., 1987; Canters et al., 1997; Pierre-LePense and Carsignol, 1999; Evink et al., 1996; Evink et al., 1998; Evink et al., 1999; Ellenberg et al., 1981; Reck and Kaule, 1993 and Forman, 1995; Jalkotzky et al., 1997; Clevenger, 1998; Glitzner et al., 1999 and Holzang et al., 2000). However, despite this bulk of literature, it becomes increasingly evident that we need an improved understanding of the effects on nature, improved methodology to assess and predict impacts, and, above all, an ecologically sound planning, to counteract fragmentation effects in the future (Treweek et al., 1993; RVV, 1996; Seiler and Eriksson, 1997; Forman, 1998).

On the following pages, I present a brief overview over how roads and railroads affect wildlife, with special reference to habitat fragmentation. I point out some major gaps in our knowledge and suggest fields for new research. My review is based on a literature study that will be published as an introductory chapter to the European State of the Art Report of the COST-341 action of the European Union on “Habitat fragmentation due to infrastructure”. I have restricted my search for literature mostly to scientific publications, but refer also to some reports and books printed by national transport authorities. At a European level, there is considerable more data available in forms of project reports and unpublished “grey” literature. Many of these sources will be summarised in the COST-341 report (for more information on COST-341 (Cooperation in the field of Scientific and Technical research) please visit: http://www.cordis.lu/cost-transport/src/cost-341.htm).

## Historic context

In Europe, roads have been constructed for more than 2000 years. The first roads were probably paths made by animals and later adopted by humans, but with the growing need for more effective communication and transport, road construction technology developed rather fast. Earliest records of simple paths adopted by humans date back to before 6000 BC near Jericho (Britannica, 2000). More elaborated road constructions were made around 4000 BC in Iraq and in England. By 2000 BC, stone paved roads became affordable as metal tools for stone carving were invented and the increased use of wheeled vehicles demanded improved roadways. The greatest systematic road builders of the ancient world were the Romans, who were very conscious of the military, economic, and administrative advantages of a good road system. Roman roads were complex in design, composed out of several layers of stone, and were often paved with cement. At the peak of the Roman Empire, nearly 85,000 km of road were in use. Twenty-nine great military roads, the *viae militares*, radiated from Rome and embraced the entire Mediterranean area. Some of these roads can still be visited today in their original shape. After the descent of the Roman Empire, most western road networks fell into centuries of disrepair.

It was but a millennium later, that the interest in an efficient infrastructure began to raise again, and new and better roads were built (Britannica, 2000). Clearly, road construction was strongly dependent on topography, soil, land cover, but also human settlements. Roads were built to support communication between human centres, but likewise they would give access to natural resources such as timber or hay. Where roads were built, new settlements, farms, fields or other human facilities were likely to follow. Thus, there grew an intimate relationship between roads and land use, which made them to an integrated part of the environmental and cultural context of the landscape (Castensson, 1991). Still many of the older local roads in Sweden carry significant cultural and ecological values (Almqvist and Syllner-Gustafsson, 1994).

Road maintenance, in medieval Sweden, was still a duty of farmers and local landowners, thus roads served primarily local interests. Governmental support to finance long-distance (national) transport routes was not implemented before the 17th century (SNA, 1992). In 1841, the first national bureau for road administration was established, surveying a total of 43,000 km of national roads (Almqvist and Syllner-Gustafsson, 1994). Until the raise of the motorised traffic in the 1920's, the Swedish national trunk road network was however mainly composed out of medieval roads and paths (Ohlmarks and Bährendtz, 1993).

It was first during the recent 70-80 years, that technical progress and modern engineering deliberated road-planers from the natural constraints of the terrain (Jönsson, 1991). Roads could be build broader, straighter and with less concern to topography and soil than in earlier times. The need of roads that could carry motorized vehicles of heavier weight and at greater speed led to a general improvement of practically all roads, especially those that serve long-distance communication. Motorways and highways are thus no longer embedded in the given context of the landscape; they do not serve local communication or give access to local resources. They are rather superimposed on the existing pattern, disrupting natural linkages and processes, causing a fragmentation of the landscape in a literal sense (Figure 1).

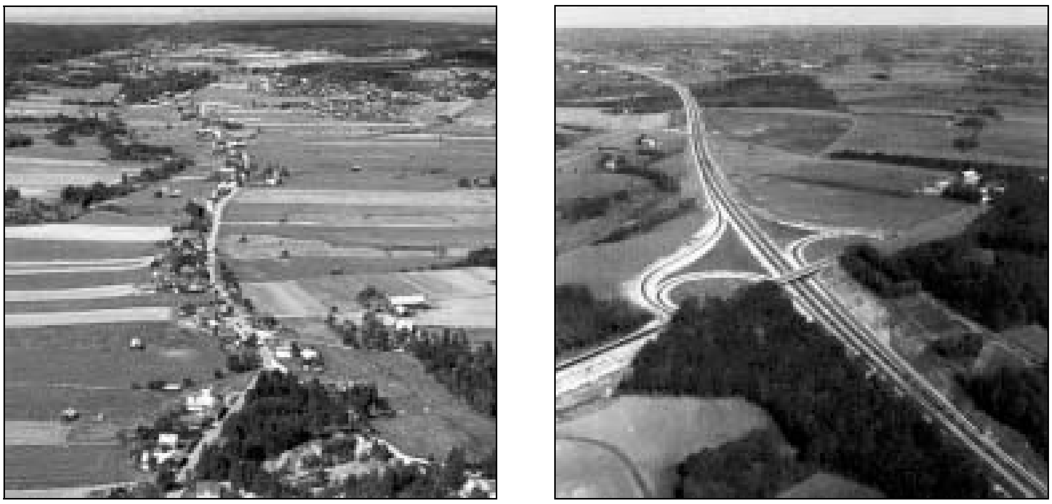

Figure 1. Roads have changed considerably during the last century: Rural roads (left) that once carried both local and regional transports have been replaced by highways that cut through the landscape and disrupt the existing pattern. (Photo: left: SNA 1992 and right: DMU 1994)

Today, there are about 420,000 km of roads in Sweden, including a variety of national, municipal, and private roads (SCB, 2000). The national trunk network comprises 23% of the total road length, but carries 70% of the overall traffic (Table 1; Figure 2). The majority of roads is still privately owned, yet partly with state subsidies and open to public transport. Some 200,000 km of roads are forest roads, built primarily to extract timber (Swedish Board of Forestry, 2000). Official statistics suggest that more than 70% of the managed forest in Sweden lies already within 500 m from the next access road. Per year, the forest road network expands with more than 1,500 km (Swedish Board of Forestry, 2000).

Table 1. Swedish Road Network in 1998 (National Road Administration, Yearbook 1999)

| **Swedish Roads & Transport** | **km** | **km/km$^2$**** | **% length** | **traffic ***** | **% traffic** |
|---|---|---|---|---|---|
| Roads trafficable in 1998 | 420,681 | 1.03 | 100 | 50.5 | 100 |
| *of which open to public* | *210,681* | *0.52* | | | |
| State-administered roads * | 97,983 | 0.24 | 23 | 35.3 | 70 |
| *national main roads (incl. motorways)* | *14,615* | *0.04* | *3* | *22.2* | *44* |
| *county roads* | *83,368* | *0.20* | *20* | *13.1* | *26* |
| Municipal roads and streets | 38,500 | 0.09 | 9 | 13.1 | 26 |
| Private roads with state subsidies | 74,198 | 0.18 | 18 | 1.5 | 3 |
| Private roads without subsidies | 210,000 | 0.51 | 50 | 0.5 | 1 |

* of which 77% is paved, ** of land surface, *** traffic: billion vehicle kilometres driven per year

With the increasing spatial demands of the road network and its physical encroachment on the land, conflicts between transport infrastructure and the natural, and cultural, heritage of the landscape have become inevitable (e.g. Nihlén, 1966; Ellenberg et al., 1981, Jedicke, 1994). Already with the construction of the first motorways, public concern about the aesthetic values of the landscape was stirred: the new bold roads would not fit into the traditional small-scaled landscapes. By 1930, a special landscape consultancy bureau was established to guide road planners in building aesthetically and culturally adapted motorways (Nihlén 1966). However, it was not before 1987 that road construction actually required approved environmental impact assessment studies (EIA) in Sweden (Pettersson & Eriksson 1995). Due to insufficient empirical data and the lack of adequate evaluation tools, the quality of the EIA work could not always fulfil the required standards or consider impacts on ecological properties in the landscape (e.g. RVV, 1996, Seiler and Eriksson, 1997). More recently, increased environmental responsibility of the transport authorities, together with the implementation of Agenda 21 into national policies and plans, have stimulated a greater engagement of road planners also in ecological-environmental concern. Authorities ask now for improved methods to evaluate the problem and to meet national and sector-level policies on conservation of biodiversity and sustainable development (EPA 1999, SNRA 1999). Mitigation and compensation concepts are to be developed that can operate across scales and be applied to strategic planning of new infrastructure, as well as to maintenance of existing links (SNRA, 1996, Canters et al., 1997, Cuperus et al., 1999). Reaching these goals is an outspoken challenge to landscape, i.e. road ecologists of this new millennium (Forman, 1998).

To understand the complex environmental impact of modern infrastructure and amend it in an ecologically sound and sustainable manner, we need a holistic landscape approach considering both cultural (historic) and natural (ecological) aspects in the landscape. We need improved empirical data that helps drawing general conclusions and build predictive models that can be used for strategic impact assessments. The following chapters shall provide a brief overview of the state-of-the art in our knowledge.

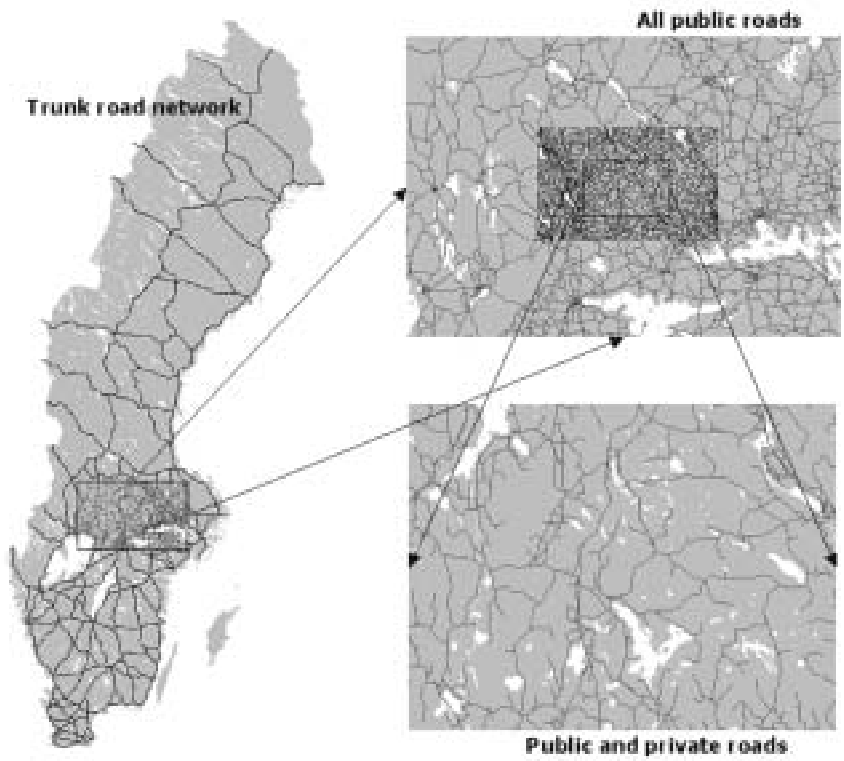


Figure 2. Hierarchical layering of the road network in Sweden. Left: trunk roads (motorways and national roads) at broad or national scale. Above: public roads (trunk roads and county roads) at intermediate or regional scale, and right below: private roads (mainly forest access roads) at small or local scale.

## Primary ecological effects

Infrastructure affects nature in both direct and indirect ways: The physical presence of roads and railroads in the landscape creates new habitat edges, alters hydrological dynamics, and disrupts natural processes and habitats. Road maintenance and traffic contaminate the surrounding environment with a variety of chemical pollutants and noise. In addition, infrastructure and traffic impose dispersal barriers to most non-flying terrestrial animals, and vehicle traffic causes the death of millions of individual animals per year. The various biotic and abiotic factors operate in a synergetic way across several scales, and cause not only an overall loss and isolation of wildlife habitat, but also splits up the landscape in a literal sense (Figure 3).

This review focuses on the primary effects of infrastructure on nature and wildlife, as these effects are usually the responsibility of the transport sector. Secondary effects, such as changes in land use, human settlement or industrial development, or resource exploitation, which may be induced by the construction of new roads or railroads, are outside the scope of this review.

Most empirical data on the effects of infrastructure on wildlife refers to primary effects that derive from a single road or railroad, are easily measurable and matter to the organisms directly and at a local scale. We can distinguish between five major categories of primary ecological effects (Figure 3.1; compare also: Van der Zande et al. (1980); Bennett (1991); Forman (1995)):

1. **Habitat loss** - Construction of roads and railroads always implies a *net loss of* wildlife habitat. The physical encroachment on the land gives rise to disturbance and barrier effects that contribute to the overall habitat fragmentation due to infrastructure.
2. **Disturbance** - Roads, railroads and traffic *disturb and pollute* the physical, chemical and biological environment and consequently alter habitat suitability for many plant and animal species for a much wider zone than the width of the road or railroad itself.
3. **Corridor** - Road verges and roadsides can however provide *refuges*, *new habitats* or serve as *movement corridors* for wildlife. These beneficial effects of infrastructure are a major challenge to planners and biologists, as management and design must be adapted to a wider landscape context.
4. **Mortality** - Traffic causes the *death* of many animals that utilise verge habitats or try to cross the road or railroad. Traffic mortality has been growing constantly over the years, but is considered as a severe threat only in few species. Collisions between vehicles and wildlife are also an important traffic safety issue.
5. **Barrier** - For most non-flying terrestrial animals, infrastructure implies *movement barriers* that restrict the animals' range, make habitats inaccessible and can finally lead to an isolation of populations. The barrier effect is the most prominent factor in the overall fragmentation caused by infrastructure.

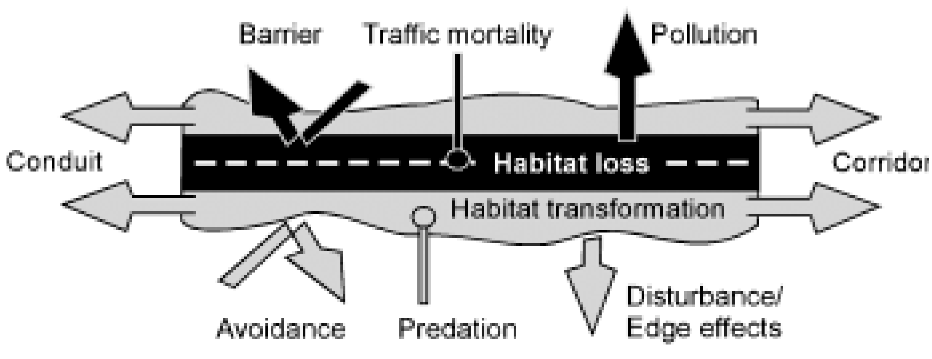


Figure 3 Schematic representation of the five primary ecological effects of infrastructure: Habitat loss and transformation, disturbance due to pollution and edge effects, barrier and avoidance, mortality due to traffic and predation, and the conduit or corridor effect. Together, the various primary effects lead to a fragmentation of habitat. Modified after Van der Zande et al. (1980).

Habitat loss, disturbance, barrier and mortality effects usually refer to single infrastructure links, yet their long-term impact on populations and ecosystem depends on the type of infrastructure, landscape, or species considered. Also the spatial scale is likely to alter the relative importance of the different primary effects (Table 2): Motorways affect wildlife in a different way than forest roads, railroads or canals. Disturbance effects spread more easily in open landscapes than in forested habitats. Also, individual roads and railroads always are part of an infrastructure network. Thus, synergetic effects with other infrastructure links or certain landscape features may aggravate or weaken the significance of the primary effects that derive from one single link. The overall fragmentation effect to the landscape caused by the combined infrastructure network may thus not be predictable from data on individual roads and railroads. Evaluating primary (ecological) effects of a planned road or railroad therefore requires studies at both local and landscape scale and must consider the single link as well as the wider infrastructure network.

Table 2 The relative importance of different primary effects in relation to the type of infrastructure and the spatial scale (opposing single infrastructure links and entire networks). The different effects have to be addressed at all scales for all species and all types of infrastructure. Yet, under certain conditions some effects should receive more attention. The order of effects in the boxes suggests the relative rank in the importance of the effects for wildlife. For instance, motorways are more likely to create dispersal barriers for wildlife than smaller roads or railroads and the barrier impact should be studied primarily at a larger scale. Habitat loss, caused by construction work, matters rather at a local scale and is more important the wider the road is. Further explanation will be given in the different subchapters.

| Infrastructure type / Scale | Primary roads | Secondary roads | Tertiary roads | Railraods |
|---|---|---|---|---|
| **Broad scale / Network level** | Barrier / Isolation<br>Mortality<br>Disturbance | Barrier / Isolation<br>Mortality | Corridor | Fragmentation<br>Corridor<br>Mortality |
| **Local scale / Single infrastructure link** | Habitat loss<br>Barrier<br>Disturbance<br>Mortality | Mortality<br>Habitat loss<br>Barrier<br>Disturbance | Corridor<br>Habitat loss | Mortality<br>Corridor<br>Disturbance<br>Habitat loss |

# 1 Habitat loss and disturbance

The construction of new roads and railroads inevitably transforms natural habitats into a sealed and highly disturbed environment (Fig. 4). Motorways may consume more than 10 ha of land per kilometre road. Narrow country roads occupy less area per kilometre, but as these roads are more frequent than motorways, their combined effect in the landscape can be considerably larger. If one includes all associated features, such as roadsides, embankments and slope cuttings, parking places, gas stations, or pedestrians walkways, the total area designated for transport is several times larger than the paved surface of the road. In most European countries, the allocation of space for new infrastructure is a superior problem for land use planning, as it necessarily conflicts with many other interests in the landscape. Not surprisingly, the land take by roads and railroads plays a central role in Environmental Impact Assessment studies in Europe, forming a general baseline for compensation and mitigation measures in modern infrastructure projects (OECD, 1994).

Figure 4 Loss of habitat due to construction and edge effects of a highway in Spain. From Rosell Pagès and Velasco Rivas (1999).

Habitat loss due to infrastructure is most significant at local scale; at broader scales, it becomes a minor issue compared to other land uses. Even in rather densely populated countries such as The Netherlands, Belgium or Germany, the total area occupied by infrastructure is generally estimated to be less than 5-7% (Jedicke, 1994). In Sweden, where transport infrastructure is sparser, roads and railroads are assumed to cover about 1.5% of the total land cover; urban areas comprise 3% of the Swedish territory (Seiler and Eriksson, 1997; Sweden Statistics 1999).

However, the total loss of habitat due to infrastructure can impossibly be evaluated from what is physically occupied. Barrier effects isolate otherwise suitable habitats and make them inaccessible for wildlife; edge effects on hydrology and microclimate and the pollution by toxins, nutrients and noise reduce the suitability of the remaining habitats. Disturbance effects spread into the surrounding landscape and contribute far more to the overall loss and degradation of natural habitat than the road body itself (Figure 5). Many attempts have been made to assess the overall width of the affected zone around infrastructure. Depending on what impacts that have been measured, the estimations range from some tens of meters (Mader, 1987a) to several hundred meters (Reichelt, 1979; Reijnen et al, 1995; Forman and Deblinger, 2000) and even kilometres (Reck and Kaule, 1993; Forman et al., 1997). Thus, despite its limited physical extent, transport infrastructure is indeed one of the more important actors in the landscape and its total influence on land use and habitat has probably been underestimated a lot. For example, Reed et al. (1996) showed that the construction of forest roads in the Rocky Mountains of Wyoming, USA, increased forest edge density up to twice as much as clear cutting practises. The overall area affected by these edges was up to three times larger than the area physically occupied by clearcuts and roads together. Forman (2000) assessed that transport infrastructure in the USA directly affects an area that is about 19 times larger than the 1% of the US land surface that is physically occupied by roads.

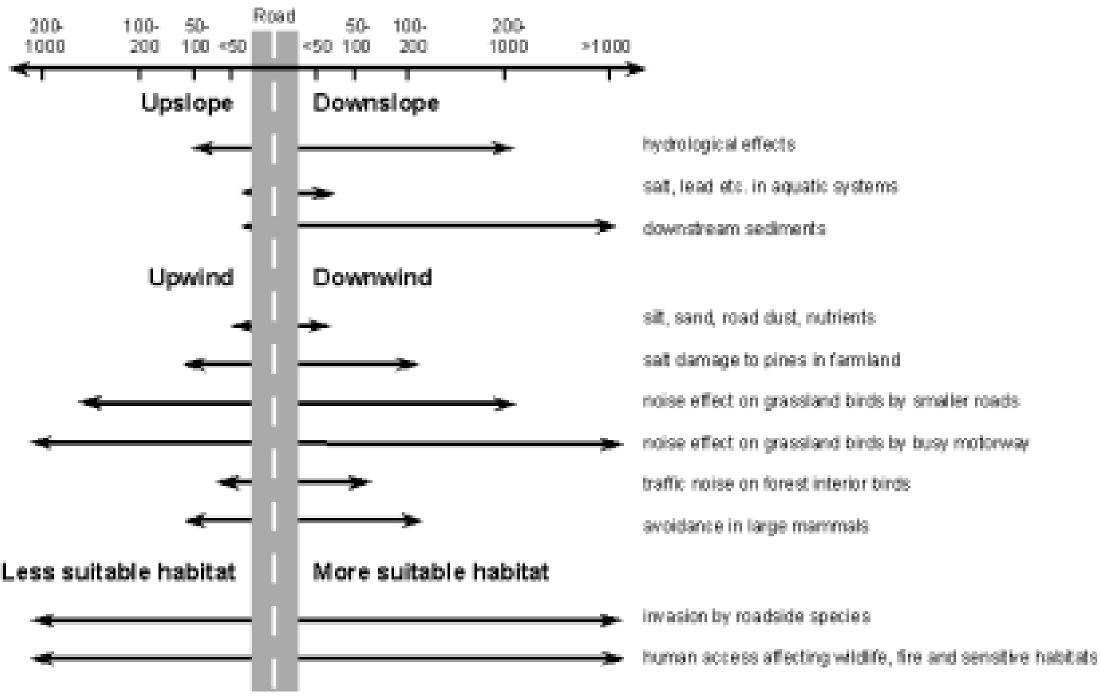


Figure 5 Disturbance effects spreading from the road into the surrounding landscape. The distance, over which disturbances affect nature depends on topography, wind direction, vegetation and the type of disturbance. The width of the affected zone is likely larger than some hundred meters on average. Redrawn after Forman et al. (1997).

How much habitat is actually affected by a new road? How much reduced is the ecological quality of the areas adjacent to roads? There is no straightforward answer to these questions. The spread of disturbances is influenced by road and traffic characteristics, landscape topography and hydrology, wind and slope and vegetation. In addition, the consequent impact on wildlife and ecosystems also depends on the sensitivity of the different species (Figure 5). To understand the pattern, we have to learn more about the different agents of disturbance.

## *1.1 Edge effects and pollution*

Road construction affects the immediate environment due to the need to clear, level, fill, and cut. Construction work changes soil density, landscape relief, surface- and ground water flows. This, in turn, can affect ecosystems, vegetation and fauna in the wider landscape. Wetlands and riparian habitats are especially sensitive to changes in hydrology as caused by road embankments (Findlay and Bourdages, 2000). Road cuttings through slopes may drain aquifers, increase the risk of soil erosion and modify disturbance regimes in riparian networks (Forman et al., 1997; Jones et al., 2000). Where roads cut through forested habitats, microclimatic conditions are strongly altered. Increased wind and light intensity, reduced air humidity and temperature disfavour forest interior species such as lichens or mosses. Effects on vegetation and fauna due to edge effects have been observed up to several tens of meters away from the road (e.g. Ellenberg et al., 1981). Mader (1987a) observed changes in plant and animal diversity occurring up to 30 m from the road edge into the adjacent forest. Ferris (1979) found that bird communities near a motorway in Maine, USA, were dominated by edge-species that otherwise comprised less than 3% of the species assemblage living farther away in the surrounding landscape.

Road maintenance and traffic aggravate edge effects on the surrounding environment by noise and pollution. Most of the pollutants accumulate in close vicinity to the road, but long distance transport (over several hundreds of meters downwind or down slope) is not a rare event (e.g. Hamilton and Harrison, 1991). For example, traffic mobilises dust from the road surface that deposits along verges and in the nearby vegetation. Epiphytic lichens and mosses in wetlands and arctic ecosystems are especially sensitive to this kind of pollution (e.g. Auerbach et al., 1997). De-icing road salt ($NaCl$, $CaCl_2$, $KCl$, $MgCl_2$) is an important environmental issue in boreal and alpine regions (Blomqvist, 1998). Road salt can cause extensive damage to vegetation, especially to coniferous forests, contaminate drinking water supplies and reduce the pH-level in soil, which increases the mobility of heavy metals (Reck and Kaule, 1993; Bauske and Goetz, 1993). Heavy metals and trace metals such as Pb, Zn, Cu, Cr, Cd, Al spread with de-icing salts or as aerosols and may accumulate in plant and animal tissues, with the consequent effects on reproduction and survival (Scanlon, 1987). Traffic exhaust contains polycyclic aromatic hydrocarbons, dioxins, ozone, and many fertilising chemicals, which in high concentrations can cause physiological distress to animals and plants (e.g. Reck and Kaule, 1993; Scanlon, 1991). Changes in plant growth and plant species diversity induced by traffic exhausts have been observed e.g. in lakes (Gjessing et al., 1984) and in heath land more than 200 m distant from the road (Angold, 1997).

### 1.2 Traffic noise and other disturbances

Traffic noise is another agent of disturbance that spreads far into the environment. Although disturbance effects by noise more difficult to measure and less understood than pollution with toxins or dust, it is considered as one of the major factors polluting natural environments in Europe (Vangent and Rietveld, 1993; Lines et al., 1994). Areas free from noise disturbance caused by traffic, industry or agriculture have become rare at European scale and tranquillity is perceived as an increasingly valuable resource (Shaw, 1996).

Traffic noise is annoying to most humans. Although it does not have immediate physical effects, long exposure to noise can induce psychological stress and eventually lead to physiological disorder (e.g. Job, 1996; Stansfeld et al., 1993; Lines et al., 1994; Job, 1996; Babisch et al., 1999). Whether wildlife is similarly stressed by noise is questionable (see Andrews, 1990), however, timid species might read traffic noise as a token for the human presence and consequently avoid noisy areas. For instance, North-American grizzly bears (*Ursus arctos*), wild rein deer (*Rangifer tarandus*), and many other cervids avoid habitats near roads or utilize these areas less frequently as could be expected from their occurrence (Klein, 1971; Rost and Bailey, 1979; Curatolo and Murphy, 1986; McLellan and Schackleton, 1988; Mace et al., 1996).

Birds seem to be especially sensitive to traffic noise, as it directly interferes with their vocal communication and thereby affects their territorial behaviour and mating success (Reijnen and Foppen, 1994). Various studies have documented reduced densities of birds breeding near trafficked roads (e.g. Veen, 1973; Räty, 1979; Van der Zande et al., 1980; Ellenberg et al., 1981; Illner, 1992; Reijnen and Foppen, 1994). Reijnen et al. (1995) observed that bird densities in open grasslands declined where the traffic noise burden exceeded 50 dbA. Birds in woodland reacted already at noise levels of 40 dbA (Figure 6). Extensive studies on willow warblers (*Phylosopus trochlius*) in The Netherlands revealed that populations close to trafficked roads suffered from lower reproductivity, lower average survival, and higher emigration rates (Foppen & Reijnen 1994). Based on the observed relationship between noise burden and bird densities, Reijnen, Veenbaas and Foppen (1995) created a simple model predicting the distance to which breeding bird populations might be affected by traffic noise. For instance, roads with a traffic volume of 10,000 vehicles per day and a traffic speed of 120 km/h, passing through an area with 70% woodland, would significantly affect bird densities at distances between 40 and 1,500 m. When applied to the entire area of The Netherlands, the model suggests that at least 17% of bird habitats in the Netherlands would be affected by traffic noise (Reijnen et al., 1995).

However, environmental factors such as the structure of road side vegetation, the type of adjacent habitat, and the relief of the landscape, will influence both noise spread and bird densities, and thus alter the amplitude of the noise impact (e.g. Reijnen et al., 1997; Kuitunen et al., 1998; Meunier et al., 1999). If roadsides provide essential breeding habitats that are rare or missing in the surrounding landscape, bird densities along roads may not necessarily be reduced, even though pollution and other disturbance effects may reduce the environmental quality of these habitats (Laursen, 1981; Warner, 1992; Meunier et al., 1999).

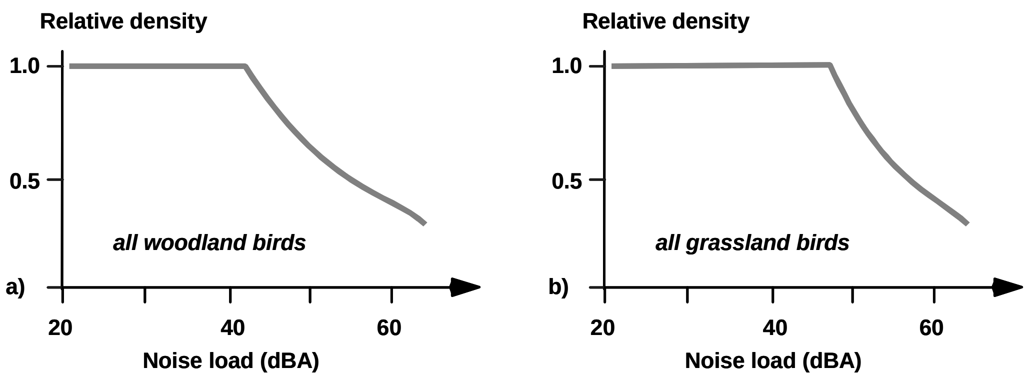


Figure 6 Schematic representation of the impact of traffic noise on breeding bird populations in The Netherlands. When the noise load exceeds a threshold of between 40 – 50 dBA, bird densities may drop significantly. The sensitivity to noise and thus the threshold is different from species to species and varies also between forest and open habitats. From Reijnen, Veenbaas and Foppen (1995).

Also artificial lighting and vehicle movement may contribute to the disturbance of wildlife near roads. For instance, white mercury vapour street lamps can affect growth regulation in plants (Spellerberg, 1998), disturb breeding and foraging behaviour in birds (Hill, 1992), and influence the behaviour of nocturnal frogs (Buchanan, 1993). Vehicle movements (probably in combination with noise) can cause stress reactions in wildlife or make animals more sensitive to any further human disturbance (Madsen, 1985). Yet, empirical studies are scarce. Compared to pollution or habitat alteration induced by changes in hydrology or microclimate, effects on the behaviour of animals may seem rather insignificant to the road planner. Many wildlife species have learned to cope with urban conditions and utilize areas that may appear much less suitable than the areas adjacent to infrastructure. Of course, in many situations, disturbances by noise, lighting or movements are of marginal importance to wildlife; unless these disturbances do not entail increased mortality or barrier effects that multiply the overall impact. Species respond very differently to the disturbance and change of habitat alongside roads. To better understand the pattern and develop tools for the assessment and evaluation of disturbance effects, we need research that specifically addresses dose-effect thresholds in wildlife.

# 2 Corridor function

Areas adjacent to infrastructure are highly disturbed environments and often even hostile for many wildlife species. Yet, they can still provide attractive resources such as shelter, food or nesting sites, and facilitate the spread of species along with the direction of the road. In heavily exploited landscapes, roadsides can provide valuable refuges for species that otherwise could not survive. Roadsides are strips of land adjacent to roads or railroads that are usually under responsibility of the transport sector and vary in width from some few meters up to several tens of meters. Roadsides are multipurpose areas and have to fulfil several technical requirements as well, such as to provide free sight for drivers, increase road safety, and screen the road from the surrounding landscape. Typically, traffic safety requires that the vegetation adjacent to roads is kept open and grassy. Farther away from the road, roadsides are often planted with bushes and shrubs for aesthetic reasons or to buffer the spread of salt and noise (Figure 7). Balancing technical and biological interests in the design and management of roadsides is an open challenge to civil engineering and ecology. It offers a great opportunity for the transport sector to increase and protect biodiversity at large scale (Mader, 1987b, Van Bohemen et al., 1991; Jedicke, 1994).

## *2.1 Roadsides as habitat for wildlife*

Numerous inventories indicate the great potential of roadsides to support a diverse plant and animal life (e.g. Hansen and Jensen, 1972; Way, 1977; Mader et al., 1983; Van der Sluijs and Van Bohemen, 1991; Sjölund et al., 1999). In his classical study, Way (1977) reported that roadsides in Great Britain supported 40 of the 200 native bird species, 20 of the 50 mammalian species, all 6 reptilian species, 5 of 6 amphibian species, as well as 25 of the 60 butterfly species occurring in the country. In the densely vegetated roadsides of agricultural Victoria, Australia, Bennett (1988) observed 78% of the native terrestrial mammalian fauna. Clearly, in areas, where much of the native vegetation has been destroyed due to agriculture, forestry or urban development, roadsides can serve as a last resort for wildlife (Loney and Hobbs, 1991). Many plant and animal species in Europe that associate with traditional (and now rare) grassland and pasture habitats, may find a refuge in the grassy roadsides along motorways and railroads, if roadside management includes frequent mowing with hay removal (e.g. Sayer and Schaefer, 1989; Melman and Verkaar, 1991; Ihse, 1995; Auestad et al., 1999). Bushes and trees that are planted along motorways to reduce disturbance of people living nearby, can provide valuable nesting sites for birds and small mammals (e.g. Adams and Geis, 1973; Laursen, 1981; Havlin, 1987; Meunier et al., 1999), and also offer food and shelter for larger species (e.g. Klein, 1971; Rost and Bailey, 1979).

Also associated technical measures along infrastructure can provide attractive habitat elements for wildlife. For instance, stonewalls and drainage pipes under motorways in Catalonia, Northeast Spain, are often populated by lizards and wall geckos (*Tarentola mauritanica*) (Rosell Pagès and Velasco Rivas, 1999). Cavities in the rocky embankments of railroads may be used as shelter and breeding sites by lizards (Reck and Kaule, 1993). Bats may find noisy but secure resting sites underneath bridges (Keeley and Tuttle, 1999).

Figure 7 Roadsides can vary considerably between different landscapes and countries. Left: Road verges along a motorway in southern Sweden consisting only of an open ditch. Toxins and salt from the road surface can easily spread onto the adjacent agricultural field. Right: Densely vegetated roadsides along a highway in Germany. Bushes and trees along roads provide nesting sites to birds and screen the road and its traffic from the surrounding landscape. Fotos: A.Seiler.

Thus, infrastructure corridors can provide valuable resources for wildlife that are rare or missing in the surrounding landscape, although they are unlikely to fully substitute the original habitat or reach a similar ecological value as comparable habitats distant from infrastructure. The composition of species in roadsides is generally skewed towards a higher proportion of generalists and pioneers that can cope with the disturbances deriving from the road and its traffic (e.g. Hansen and Jensen, 1972; Adams and Geis, 1973; Niering and Goodwin, 1974; Douglass, 1977; Mader et al., 1983; Blair, 1996). Populations living alongside roads may suffer a high mortality due to vehicle traffic and thus not be self-sustaining without the steady immigration from surrounding populations. Sink population dynamics have been observed in e.g. willow warblers living along roadsides in The Netherlands (Foppen & Reijnen 1994). It is not surprising that species, which regularly visit road corridors to forage or nest, occur frequently in road kill statistics (see chapter 3.4). In this respect, infrastructure corridors may act as an ecological trap pretending favourable habitat conditions but at the hidden cost of death. When designing and managing roadsides, it is therefore advisable to consider the risk of creating an ecological trap that may kill more species than it supports.

## 2.2 Roadsides as movement corridors for wildlife

As roadsides can provide a habitat for wildlife, they may also serve as a conduit for species moving – actively or passively – along with the direction of the road. Roadsides can support dispersal and commuting movements like “natural” corridors in the landscape (Figure 8, 9). The surface of roads (mainly small roads with little traffic) may be used as pathways by larger mammals. Vehicles and humans may serve as vectors for plants, seeds or small, less mobile animals (Schmidt, 1989; Bennett, 1991).

Figure 8 Hedgerows and woody road verges (“Knicks”) in northern Germany provide merely the only bush and tree vegetation available in the landscape. Together they create a network of green corridors on which most wildlife species in that area depend for shelter and food. Naturally, these corridors also have a strong impact on the movement of species that shy the open fields and pastures.

For instance, Wace (1977) found seeds of 259 plant species in the sludge of a car-washer in Anberra, Australia. The plants derived from various habitats, some of which occurred in areas over 100 km distant. This may offer an explanation for the high proportion of exotic and weed species that can be found along roadsides (e.g. Mader et al., 1983; Tyser and Worley, 1992; Ernst, 1998). Indeed, the spread of weeds and alien plant species along roads is considered as a severe threat to the native flora in many nature reserves (Usher, 1988; Spellerberg, 1998). In Australia, cane toads (*Bufo marinus*) are considered as pest species that often follow roads and tracks to expand their range and disperse into previously inaccessible areas (Seabrook and Dettmann, 1996). In the Netherlands, bank voles (*Clethrinomys glareolus*) have colonised the Zuid-Beveland peninsula after moving along wooded verges of rail- and motorways (Bekker and Mostert, 1998). Getz et al. (1978) documented that meadow voles (*Microtus pennsylvanicus*) dispersed over about 100 km in six years along grassy roadsides in Illinois, USA. In suburban Anchorage, Alaska, moose utilise roadsides and greenbelts to forage and find shelter – with the subsequent effect on traffic safety (Garrett and Conway, 1999). Kolb (1984) and Trewhella and Harris (1990) observed that the movement of foxes (*Vulpes vulpes*) into the Edinburgh area was strongly influenced by the presence and direction of railway lines. Badgers living in central Trondheim, Norway, are known to use riverbanks and road verges to move within the city (Kjetil Bevanger, pers. comm.). Carnivores are also known to take advantage of minor, forest roads as plain and straight pathways throughout their home ranges (e.g. Mech et al., 1988; Page, 1981; Corbett, 1989).

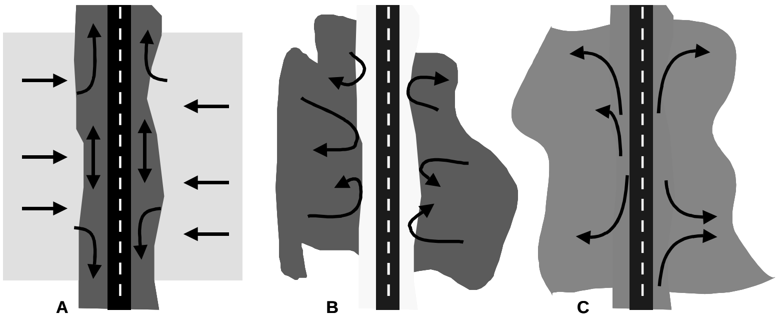


Figure 9 The corridor function of roads differs with respect to the surrounding landscape: A) In open, agricultural landscapes, richly vegetated roadsides can provide a valuable habitat for wildlife and facilitate their movements along with the roads. B) In forested landscapes, open and grassy road verges introduce new edges and can increase the road's barrier effect on forest interior species. C) Road verges may also serve as sources of – wanted and unwanted- species spreading into new habitats or re-colonising vacant areas adjacent to roads. Modified after Mader (1987b).

Thus, there are various ways in which roads and road verges can facilitate and direct animal movements or enable the spread of plants and other sessile species. It may therefore seem possible to integrate infrastructure corridors into the existing (natural) ecological network in the landscape (see Figure 8). However, there are several important characteristics that distinguish roadsides from "natural" corridors and may hamper a successful linkage between built-up and ecological infrastructure (Mader 1978b; Mader et al., 1990). For example, habitat conditions in road verges and roadsides may not be constant over longer distances as the direction of the road may turn or embankments may replace cuttings thus offering very different microclimatic and hydrological conditions. In addition, road corridors always intersect with other roads. Animals that move along with the road corridor are led towards these crossings and face a high risk of getting killed in traffic (Madsen et al., 1998; Huijser et al. (1998b, cited in Van der Grift, 1999). Also, predation pressure in roadsides may be increased compared to the surrounding habitats, as carnivores are attracted to traffic casualties scattered along road verges. Pollution and disturbances from traffic may further hinder animals from travelling along the roadsides.

Thus, the overall corridor effect of roads and roadsides is rather ambiguous. Roadsides may provide important habitats or habitat elements for wildlife, but primarily for less demanding and generalist species that can cope with disturbances and pollution from the road and are not sensitive to increased mortality due to traffic. To better understand this complexity and give practical advise to road planners, we need more empirical studies. There is no doubt, though, that an ecologically integrated management and design of infrastructure corridors will provide us with a powerful tool to govern biodiversity locally as well as at a landscape scale (e.g. Van Bohemen et al., 1991).

# 3 Fauna casualties

Road mortality is probably the most acknowledged effect of traffic on wildlife, as carcasses of dead are a common view along trafficked roads (Figure 10). For many decades, road killed animals have been of concern to biologists (e.g. Stoner 1925; Trombulak and Frissell 2000). The number of casualties appears to be constantly growing as traffic increases and infrastructure expands. In their review, Forman and Alexander (1998) concluded that: “sometime during the last three decades, roads with vehicles probably overtook hunting as the leading direct human cause of vertebrate mortality on land”.

Figure 10 Wildlife casualties – a common view along roads and railroads.

Already the bare numbers of road kills illustrate the sad story: For instance, Hodson (1966) assessed an annual road kill of about 4 million birds in the UK in 1960. In the Netherlands, Van den Tempel (1993) estimated a road kill rate of at least 2 million birds per year. In Belgium, comprehensive field inventories revealed a loss of about 4 million larger vertebrates per year due to road traffic (Rodts et al. 1998). Hansen (1982) estimated a yearly road kill of 1.5 million mammals, 3.7 million birds and more than 3.1 million amphibians in Denmark. Göransson et al. (1978) estimated an annual loss of up to 1.0 million birds and 0.5 million medium sized mammals in Sweden during the mid 1970’s. However, newer estimates based on a different sampling method suggest as much as 8.5 million bird kills on Swedish roads Svensson (1998). For the USA, assessments made by the Human Society during the 1960’s pointed at a minimum of one million animal road fatalities per day (Lalo 1987).

The quantity of road kills is impressive indeed. Not surprising, that collisions between vehicles and wildlife comprise a growing problem not only for species conservation and game management, but also for traffic safety, private and public economy (e.g. Harris and Gallagher, 1989; Hartwig, 1993; Romin and Bissonette, 1996, Putman, 1997). In most countries, traffic safety is the driving force behind mitigation efforts against fauna casualties (compare chapter 6). Although human fatalities are relatively rare in wildlife-vehicle collisions, the number of injured people is high and the total economic costs, including damages to vehicles, can be substantial. Police records in Europe (excluding Russia) suggest more than half a million ungulate-vehicle collisions per year, causing a minimum of 300 human fatalities, 30,000 injuries, and a material damage of more than US$ 1 billion (GrootBruinderink and Hazebroek, 1996).

Also from a humane point of view, there is concern about road casualties: Many animals that are hit by vehicles are not immediately killed, but die later from injuries or shock. Fehlberg (1994) stated that car drivers, who do not attempt to minimize any unnecessary suffering or pain to the animal they collided with, act against German law on animal welfare. Also hunters complain about the increasing work to hunt down injured game (e.g. Swedish Hunters Association, pers. comm.). Train drivers in northern Sweden complain about the unpleasant experiences when colliding with groups of reindeer and moose (Åhren and Larsson, 1999). Carcasses of larger mammals that decorate road verges or road surfaces are of growing annoyance to the public. Ongoing research projects, photo exhibitions and handbooks on the “flattened fauna” (e.g. Knutson, 1987, Rodts et al. 1998) further demonstrate the public awareness of the problem.

Thus, irrespective of whether road mortality is significant to the survival of a species or not, there is economical and ethical concern that demands for the construction of mitigation measures. To determine whether, when and where road casualties do require mitigation, the problem has to be studied both from an ecological perspective and the human point of view.

### *3.1 Ecological significance of road kills*

Evaluating the ecological importance of road mortality for a species must consider the species’ population size and recruitment rate. Large numbers of casualties in one species may not necessarily imply a threat to the survival of that species, but rather indicate that it is abundant and widespread. For many common wildlife species, such as rodents, rabbits, foxes, sparrows, or blackbirds, traffic mortality is generally considered as insignificant, accounting only for a small portion (less than 5%) of the total mortality (e.g. Haugen, 1944; Bergmann, 1974; Schmidley and Wilkins, 1977; Bennett, 1991; Rodts, 1998). Even in red deer (*Cervus elaphus*), roe deer or wild boar (*Sus scrofa*), traffic mortality generally accounts for less than 5% of the annual spring populations in Europe (e.g. GrootBruinderink and Hazebroek, 1996). Swedish police records on deer-vehicle collisions during the early 1990’s accounted for about 6% of the annual national harvest in roe deer and moose, respectively (Lavsund and Sandegren, 1991). However, this percentage varies considerably between areas: In some hunting districts in southern Sweden, the percentage of traffic-killed moose can be as high as 65% of the game bag (A. Seiler, unpublished). At a local scale, the losses due to traffic can thus be significant even though the numbers may appear insignificant at national scale.

In contrast to natural predation, traffic mortality is non-compensatory, and the kill rate is probably not density dependent, but may vary linearly with population size. This implies that roads would kill a constant proportion of a population and therefore can have a significant impact on rare species. In general, species that occur in small isolated populations, require large extensive areas for their home ranges, or exert long migratory movements, are especially sensitive to road mortality. The larger their home range, the more often individuals will encounter roads; the smaller their populations, the higher the relative importance of each individual. Indeed, for many endangered mammalian species around the world, traffic is considered as one of the most important sources of mortality (e.g. Harris and Gallagher, 1989).

For example, road mortality is by far the most significant source of mortality in the endangered Florida panther (*Felis concolor*), accounting for more than 50% of all known deaths (Harris and Scheck, 1991; Harris and Gallagher, 1989). The Iberian lynx (*Felis pardina*) suffers 6-10% mortality due to road traffic, which is considered as the second most important mortality factor (Rodriguez and Delibes, 1992). In Italy, traffic responded between 7% and 25% of the known annual mortality in wolf, and up to 100% of known mortality in bear between 1974 and 1984 (Boscali, 1987). About 20% of the annual badger population in The Netherlands was killed on roads, and vehicle traffic is considered as a dominant threat to the species (e.g. Van der Zee et al., 1992; Broekhuisen and Derckx, 1996). In barn owls (*Typo alba*), a 7-10% annual traffic mortality during the breeding season may suffice to depress population recruitment effectively in The Netherlands (Van den Tempel 1993). The hedgehog is one of the smaller mammals in Europe that seems to be severely affected by road traffic and may require special concern to not go extinct locally (Göransson et al., 1978; Reicholf and Esser, 1981; Huijser et al., 1998a; Rodts et al., 1998).

Much attention has been paid to amphibians, for which infrastructure is considered as one of the major factors responsible for the decline in these species worldwide (Vestjens, 1973; Blaustein and Wake, 1990; Reh and Seitz, 1990; Fahrig et al., 1995). Amphibians are especially sensitive to road mortality, as their seasonal migration from and to breeding ponds often leads them across roads. For instance, Van Gelder (1973) found that roads with a traffic volume as low as 10 vehicles per hour could cause a 30% mortality in female toads (*Bufo bufo*). Roads with more than 60 vehicles per hour comprised an almost complete barrier. Vos and Chardon (1998) calculated that breeding ponds near motorways had a significantly reduced probability to be inhabited by frogs than undisturbed ponds farther away. Sjögren-Gulve (1994) found that trafficked roads in the suburbs of Stockholm isolated amphibian populations effectively. The risk for local extinctions rose significantly as road density and traffic volume increased.

## 3.2 Factors that influence the occurrence of road kills

There are various factors that determine the risk of animal-vehicle collisions (Figure 11). The numbers of collisions generally increase with traffic intensity, animal activity and density. Temporal variations in road kills indicate different biological periods that influence the species' activity, such as the daily rhythm of foraging and resting, seasons for mating and breeding, dispersal of the young-of-the-year, or seasonal migration between winter and summer habitats (e.g. Van Gelder, 1973; Bergmann, 1974; Göransson et al., 1978; Aaris-Sorensen, 1995; GrootBruinderink and Hazebroek, 1996). Also changes in temperature, rainfall or snow cover can influence the occurrence and timing of accidents (e.g. Jaren et al., 1991; Belant, 1991; Gundersen and Andreassen, 1998).

Naturally, collisions with wildlife can only occur where a road or railroad dissects a species' habitat, but local factors can alter the relationship considerably. Road kills seems to increase with traffic intensity, but very high traffic volumes, noise and vehicle movement seem to repel many animals and mortality rates may not further increase with traffic (e.g. Oxley et al., 1974; Berthoud, 1987; Van der Zee et al. 1992; Clarke et al. 1998; see Figure 13). Clearly, also the occurrence of mitigation measures such as fences or passages affects the local risk for accidents. The clearance of roadsides and railroads from deciduous vegetation, for instance, has proven to reduce the number of moose casualties in Scandinavia with about 20% and 50%, respectively (Lavsund and Sandegren, 1991; Jaren et al., 1991). On the other hand, when roadsides provide attractive resources to wildlife, the risk for vehicle-animal collisions is likely to be increased, and should be evaluated against the positive effect of habitat improvement (e.g. Feldhamer et al., 1986, Steiof, 1996, GrootBruinderink and Hazebroek, 1996).

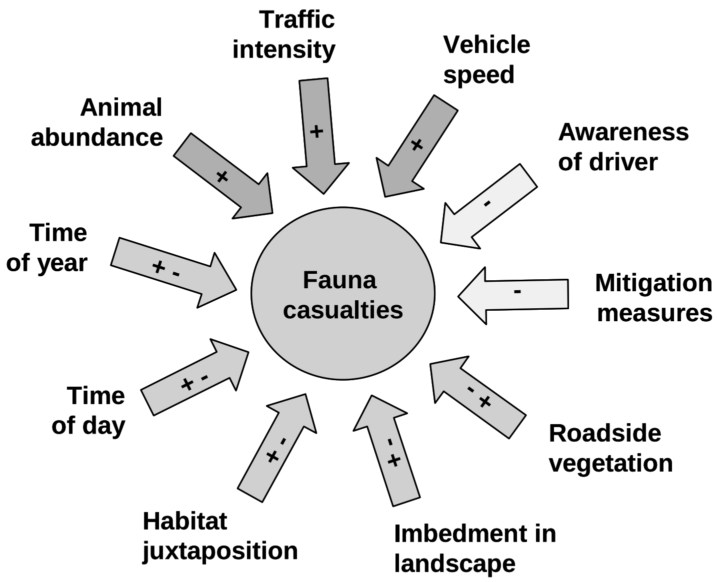


Figure 11 Factors influencing the number of road kills.

Spatial pattern in road kills clearly depend on animal population density and biology, habitat juxtaposition and landscape structure, but also to road and traffic characteristics (Bellis, 1971; Puglisi; Ashley and Robinson, 1996, Finder et al., 1999). In species with limited mobility and specific habitat requirements, such as many amphibians, it can be relatively simple to identify potential conflict areas: Most of the casualties in amphibians occur during a short period in spring, when the animals migrate from and to their breeding ponds and where roads dissect the migration routes (Van Gelder, 1973). Roads that pass close to breeding ponds, wetlands and the animals' foraging habitats, are likely to cause a much greater kill rate than roads outside the species' migratory range (about 1 km; see Vos and Chardon, 1998; Ashley and Robinson, 1996).

Other species, especially larger mammals depend less on specific habitat types and utilize the landscape at a broader scale. This combination makes it is more difficult to predict possible hotspots in collisions (Madsen et al., 1998). Still, where favourable habitat constellations coincide with infrastructure, or where roads intersect other linear structures in the landscape that may direct wildlife movements, such as hedgerows, water courses, and other (minor) roads and railroads, the risk for collisions is usually increased (e.g. Puglisi et al., 1974; Feldhamer et al., 1986; Kofler and Schulz, 1987; Putman, 1997; Gundersen et al., 1998; Lode, 2000). For example, collisions with white-tailed deer in Illinois are associated with intersections between roads and riparian corridors, and public recreational land (Finder et al., 1999). Traffic casualties in otters are most likely to occur where roads cross over watercourses (e.g. Philcox et al., 1999). Road-killed hedgehogs in The Netherlands are often found where roads intersect with railroads (Huijser et al., 1998b). Also foxes and roe deer in Denmark are more often found near intersections than elsewhere along roads (Madsen et al., 1998).

To conclude, the spatio-temporal pattern of road casualties is influenced by various factors, such as the species' biology, traffic and road characteristics, and landscape and habitat composition (Figure 11). These different factors must be understood before the local need for mitigation can be evaluated, effective measures be designed and put in place (e.g. Romin and Bissonette, 1996; Putman, 1997). GIS-based analysis of traffic kills and wildlife movements in relation to roads and landscape features may provide the necessary insight to develop predictive models for impact assessment and the localisation of mitigation measures (e.g. Gundersen et al., 1998; Finder et al., 1999).

# 4 Barrier effect

Of all primary effects of infrastructure, it is the barrier effect that contributes most to the overall fragmentation of habitat (e.g. Reck and Kaule, 1993; Forman and Alexander, 1998). Infrastructure barriers disrupt natural processes, such as ground water flow, fire spread, affect plant dispersal and inhibit animal movements (Forman et al., 1997). The barrier effect on wildlife results from a combination of disturbance and avoidance effects, physical hindrances, and traffic mortality that all reduce the number of movements across the barrier (Figure 12): Disturbances due to traffic noise, vehicle movement, pollution, and human activity may repel many species from approaching infrastructure corridors (compare 1.2). The clearance of the road corridor and the open verge creates habitat conditions that are unsuitable or hostile to many smaller species (compare 2.1). The road surface, the gutter, ditches, fences, and the embankments, may all imply physical barriers that animals cannot pass. Traffic mortality further reduces the number of individuals that successfully manage to cross the road barrier. Most infrastructure barriers do not completely block animals movements, but reduce the number of crossings quantitatively (e.g. Merriam et al. 1989). The central question is thus how many successful crossings are needed to maintain habitat connectivity.

The barrier effect is thus a non-linear function of traffic intensity, road width, roadside characteristics, the animals' behaviour and its sensitivity to disturbances. Traffic intensity and vehicle speed appear to have the strongest influence on the barrier effect on those mammals that do not experience any physical barrier or repellent habitat effect in road corridors. With increasing traffic and higher vehicle speed, mortality rates usually increase until the deterrent effect of the traffic prevents more animals from getting killed (Oxley et al., 1974; Berthoud, 1987; Kuhn, 1987; Van der Zee et al. 1992; Clarke et al. 1998). Exactly when this threshold in traffic density occurs is yet to be studied in more detail; a more general model can however already be proposed: For example, Müller and Berthoud (1994) suggested distinguishing between five categories of infrastructure / traffic intensity with respect to their barrier impact on wildlife (Figure 13):

1) Local access and service roads with very light traffic can serve as partial filters on wildlife movements. They may have limited barrier impact on invertebrates and eventually repel small mammals from crossing the open space. Larger wildlife may use these roads as corridors, if they not avoid habitat close to roads (compare 2.2).
2) Railroads and minor public roads with traffic below 1000 vehicles per day may cause incidental traffic mortality and exert a stronger barrier / avoidance effect on small species, but crossing movements will still frequently occur.
3) Intermediate link roads with up to 5,000 vehicles per day may already comprise a serious barrier to certain species. Traffic noise and vehicle movement are likely to have a major deterrent effect on small mammals and some larger mammals. Due to this repellence, the increase in the overall barrier impact is not proportional to the increase in traffic volume.
4) Arterial roads with heavy traffic between 5,000 and 10,000 vehicles per day cause a significant barrier to many terrestrial species, but due to the strong repellence by the traffic, the number of road kills is levelling out. Road kills and traffic safety are probably important issues to be solved in this category.
5) Motorways and highways with traffic above 10,000 vehicles per day impose an impermeable barrier to almost any wildlife species, as the dense traffic repels most species approaching the road and kills those that still attempt to cross.

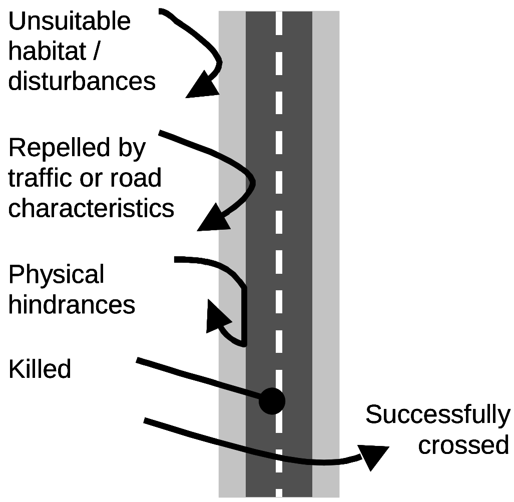


Figure 12 The barrier effect of a road or railroad results from a combination of disturbance/repellence effects, mortality and physical hindrances. Depending on the species, the number of successful crossings is but a fraction of the number of attempted movements. Some species may not experience any physical or behavioural barrier, whereas others may not try to even approach the road corridor. To effectively mitigate the barrier effect, we have to know the relative importance of the inhibiting factors.

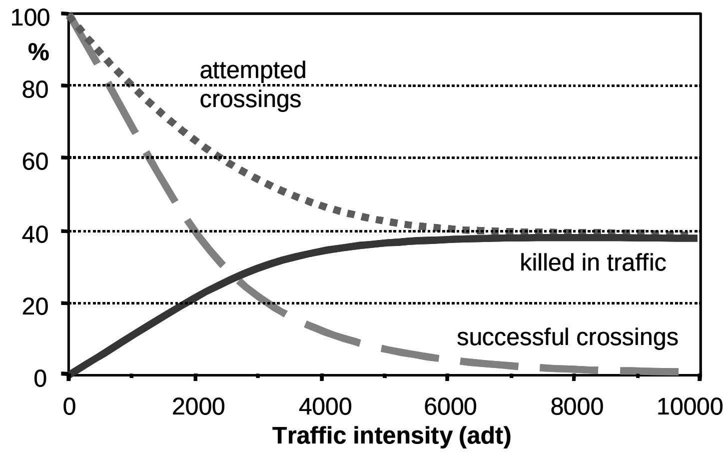


Figure 13 Theoretical model illustrating the relationship between traffic intensity and the road's barrier effect: With increasing traffic, the number of road kills increases linearly until noise and vehicle movements repel more animals from attempting to cross the road. At very high traffic volumes, the total mortality rate could eventually decrease, but the resulting barrier effect, which is reciprocal to the rate of successful crossings, will add up to 100%. Redrawn from Müller & Berthoud (1994).

## *4.1 Evidence from field studies*

Transport infrastructure inhibits the movements of practically all animals, including human pedestrians. Naturally, the significance of the different components of the barrier effect varies between species. Many invertebrates, for instance, respond significantly to differences in microclimate, substrate and openness between road surface and road verges. High temperatures, high light intensity and lack of shelter on the surface of paved roads seem repel Lycosid spiders and Carabid beetles (Mader 1988; Mader et al., 1990). Land snails may dry out or get run over while attempting to cross over a paved road (Baur and Baur, 1990). The clearance of the road corridor, the road surface and traffic intensity also impose major obstacles to the movements of small mammals, amphibians and reptiles (e.g. Joule and Cameron, 1974; Kozel and Fleharty, 1979; Mader and Pauritsch, 1981; Wilkins, 1982; Swihart and Slade, 1984; Merriam et al., 1989). Even birds can be reluctant to cross over wide and heavily trafficked roads (e.g. Van der Zande et al., 1980). Migrating fish and semi aquatic animals moving along watercourses may be inhibited by too narrow bridges or culverts (e.g. Warren and Pardew, 1998).

Much evidence for the barrier effect derives from capture-recapture experiments on small mammals. For example, Mader (1984) observed that a 6 m wide road with 250 vehicles/h completely inhibited the movement of 121 marked yellow-necked mice (*Apodemus flavicollis*) and bank voles (*Clethrionomys glareolus*)(see Figure 14). Similarly, Richardson et al. (1997) found that mice and voles were reluctant to cross paved roads wider than 20-25m although they did move equally distances along the road verge. Oxley et al. (1974) documented that white-footed mice (*Peromyscus leucopus*) would not cross over highway corridors wider than 30 m although they frequently crossed over smaller and only lightly trafficked forest roads.

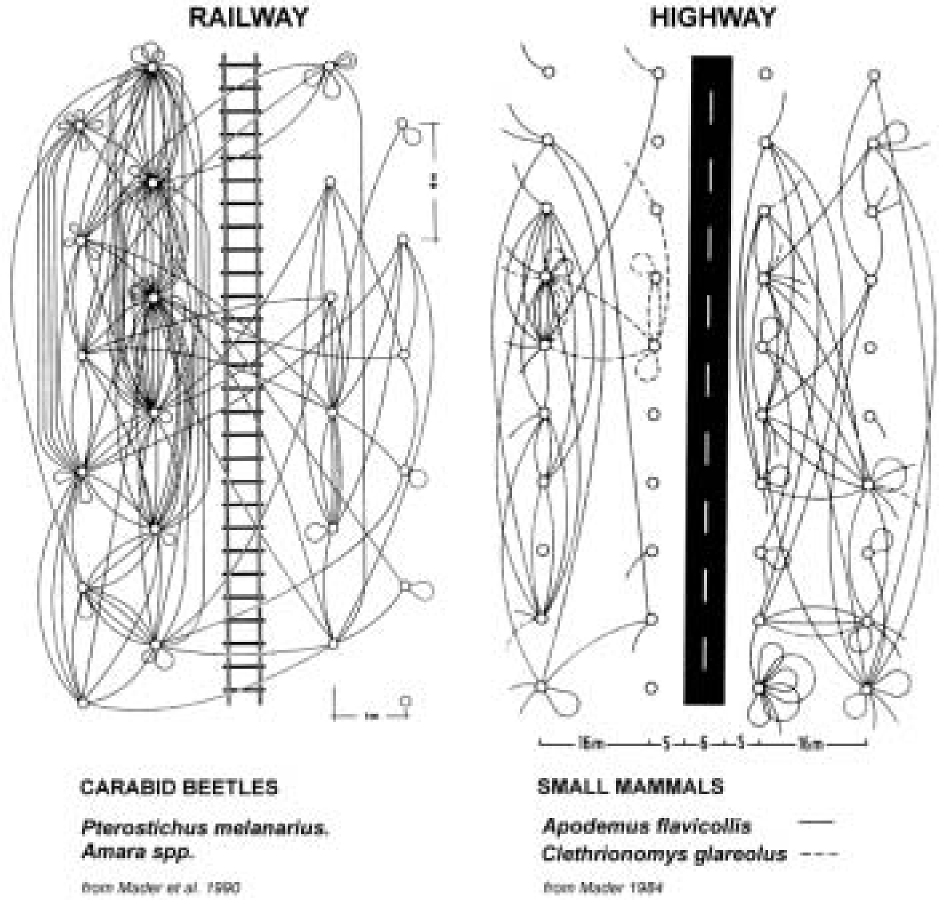


Figure 14 Mobility diagram based on capture-recapture data of carabid beetles (left) and small mammals (right) illustrating the animals' movements alongside and across a railroad and road. From Mader et al. (1990) and Mader (1984), respectively.

For larger animals, roads and railroads do hardly comprise any physical barrier, unless they are fenced or traffic intensity is too high. Most mammals, however, are sensitive to disturbances by humans. Smell, noise and vehicle movement, as well as experiences with human encounters, may repel the animals from approaching the road corridor. For example, Klein (1971) and Curatolo and Murphy (1986) observed a strong avoidance of roads in feral reindeer (but not in domestic reindeer). Rost and Bailey (1979) reported that mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*) avoided habitats closer than some hundred meters to trafficked roads. In Montana, grizzly bears avoid the vicinity of trafficked roads, but may eventually forage near roads with little or no traffic (McLellan and Shackleton 1988; Mace et al., 1996). How much this avoidance reduces the number of successful or attempted movements across roads is not clear, however. We will need more data on the actual movements of larger mammals in relation to infrastructure to judge the inhibitory effect of roads and traffic.

## 4.2 Consequences to populations

When do infrastructure barriers really become a problem for wildlife conservation? How much permeability is needed to maintain sufficient habitat connectivity? How large a barrier effect can be tolerated?

To answer these questions, we must consider the consequences at the population level. Depending on the number of successful crossings relative to the size of the population, the barrier effect can be significant to population dynamics, demographic or genetic properties. If the species does not experience a significant barrier and individuals still move frequently across the road, the dissected populations will continue to function as one unit. If the exchange of individuals is further reduced but not completely inhibited, the populations may diverge in demographic characters such as density, sex ratio, recruitment and mortality rate. Also genetic differences may emerge, as the chance for mating with individuals from the other side of the road barrier may be reduced. These changes may not necessarily be a threat to the dissected populations, but can be important for sink populations that depend on a steady immigration. In game species, demographic divergences may entail the need for an adapted population management on either side of the road barrier. If the barrier effect is even stronger, the risk for inbreeding effects and local extinctions will increase rapidly.

Evidence for effects on population genetics derives from studies on rodents and amphibians. For example, Reh and Seitz (1990) observed effects of inbreeding, reduced genetic heterozygosity, and polymorphism in small populations of the common frog (*Rana temporaria*) that were isolated by roads over many years. Merriam et al. (1989) found indications for the onset of genetic divergence in small-mammal populations separated by minor roads. Sikorski (1982) described a significant divergence in epi-genetic characters among populations of field mice inhabiting different parks in the city of Warsaw. Bakowski and Kozakiewicz (1988) noted that bank voles were highly reluctant to cross over a forest road, yet they did not observe any difference in sex ratio, density or body size between the populations on either side of the road. However, Sikorski and Bernshtein (1984) detected differences in non-metrical cranial traits between two vole populations separated by a forest road similar to the one studied by Bakowski and Kozakiewicz (1988).

However, populations dissected by one single barrier may not automatically suffer from inbreeding depression, unless they are critically small or do not have contact with other surrounding populations farther away in the landscape. To evaluate the consequences of a new road barrier, we must therefore consider the combined isolation effects of all surrounding infrastructure and other natural and artificial barriers. The denser the infrastructure network and the more intense its traffic, the more likely it is to cause a significant isolation of populations. The smaller and more isolated a population, the greater is its sensitivity for inbreeding effects, genetic drift and stochastic hazardous events that eventually may lead to its extinction (Soulé, 1987). By definition, populations of rare and endemic species are more sensitive to barrier effects and isolation than populations of abundant and widespread species. Species with large area requirements and wide individual home ranges will more frequently need to cross over road barriers than smaller and less mobile species.

Again, it is the combination of population size, mobility, and the individuals' area requirements that makes a species sensitive to the barrier impact of infrastructure (e.g. Verkaar and Bekker, 1991). Choosing between alternative routes for a new road may thus help to prevent dissecting local populations of small species, but does not reduce the barrier effect on larger, wide roaming species. In most cases, it will need technical measures, such as fauna passages or ecoducts, to mitigate barrier impacts and re-establish habitat connectivity across infrastructure barriers.

# 5 Fragmentation

The previous discussions show, that the total impact of roads and railroads on wildlife can impossibly be evaluated without considering a broader landscape context. Roads and railroads are always part in a network, where synergetic effects with other infrastructure links may occur, and cause additional habitat loss and isolation. The overall impact of the combined infrastructure network on wildlife may thus not be predictable with data from single infrastructure links. Studies on the effects of fragmentation must address larger areas and cover longer time periods than studies that address primary effects of a single road or railroad.

The process of habitat fragmentation and its effect on wildlife has been studied extensively in forestry and agriculture (e.g. Harris, 1984). Fragmentation means a splitting of contiguous areas into smaller and increasingly dispersed fragments. With increasing degree of fragmentation, the individual fragments may become too small and too isolated from each other to support the species that depend on the fragmented habitat (Figure 15). Fragmentation reduces the amount of habitat available to wildlife in the landscape and thereby diminishes population sizes and the number of species that can live in the landscape. Empirical studies on habitat fragmentation due to e.g. forestry practises suggest that a habitat loss of more than 80% in the landscape may entail sudden extinctions (e.g. Andrén, 1994). Already when 60% of the habitat is depleted from the landscape, habitat remnants may become too isolated to be used (O'Neill et al., 1992). In landscapes where the degree of fragmentation is near these thresholds, any additional isolation, as caused by infrastructure barrier, for example, may increase the risk for local extinctions unproportionally. In contrast to fragmentation caused by agriculture or forestry, it is not primarily the direct loss of habitat that characterises the fragmentation impact caused by infrastructure, but the increased isolation due to barrier effects. Of course, pollution and edge effects also reduce the amount of undisturbed habitat left within the road network (Figure 15), but the overall loss of habitat is likely of subordinate importance.

Evaluating the degree of fragmentation due to infrastructure in an area is not a simple task. The significance of fragmentation is highly species specific and depends also on the amplitude of barrier and disturbance effects, the amount and juxtaposition of habitats within the landscape, and the size of the unfragmented areas between infrastructure links (i.e. the density of infrastructure). Forman et al. (1997) suggested the use of road density as a simple but straight forward measure of fragmentation. This measure could be improved by adding information on traffic density, speed, road width or road design. However, road density is likely to correlate with the overall intensity of land use. It may thus be difficult to distinguish the sole effects of infrastructure from the impact of urbanisation, agriculture, recreation, hunting or forestry.

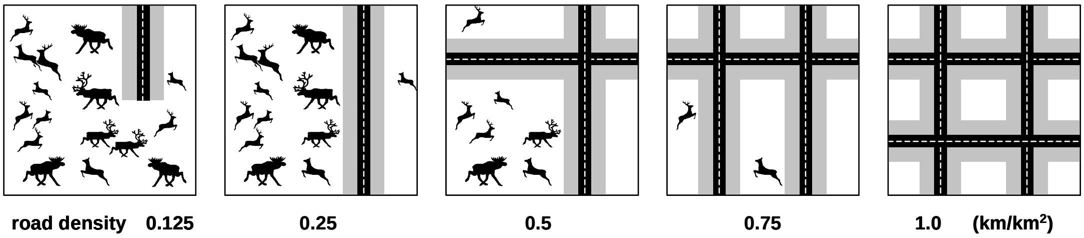


Figure 15 Illustration of the process of habitat fragmentation due to infrastructure: Roads cause a loss and degradation of habitat due to disturbance effects (grey roadside corridors) and isolation. With increasing road density, areas of undisturbed habitat (white) are reduced in size and become inaccessible. Remnant fragments of suitable habitat may eventually become too small and too isolated to prevent local populations from going extinct. The critical threshold in road density is species specific, but will also depend on landscape and infrastructure characteristics.

Several studies have described critical thresholds in road density for the occurrence of wildlife species in the landscape. For example, Mladenoff et al. (1999) observed that wolves in Minnesota, USA, did not establish pack territories in areas where the densities of roads exceeded 0.45 km/km$^2$. In regions with road densities above 0.6 km/km$^2$, wolves and mountain lions did not sustain viable populations (Thiel, 1985; Van Dyke et al., 1986). Also other large mammals in the USA, such as elk, moose and grizzly bear, appear to decrease in numbers as road densities increase (e.g. Holbrook and Vaughan, 1985; Mech et al., 1988; Forman et al., 1997). Lyon (1983) used field observations and road density models to predict the potential habitat available to the North American elk (*Cervus canadensis*). His models suggested that a road density of 1.2 to 1.9 km/km$^2$ reduced the available elk habitat below 50% of the potential in the landscape.

The observed fragmentation effect may however not be associated with the direct impact of roads and traffic, but rather with the increased access to wildlife areas that roads (especially forest roads) offer to hunters and poachers (e.g. Holbrook and Vaughan, 1985; Gratson and Whitman, 2000). In areas, where roads are absent or closed for public transport, the relationship between road density and wildlife habitat is likely to be different. Large unroaded and undisturbed (inaccessible) habitats make an essential requisite for wildlife conservation worldwide (Harris and Gallagher, 1989; Forman, 1995). In Europe, areas remote from roads or with only low road density, low traffic volumes, and high proportion of natural vegetation are considered as core areas in the ecological network (e.g. Jongman, 1994; Bennett, 1997). With the steady increase in road density and traffic, these core areas are becoming critically rare in Europe. For example, Lassen (1990) documented that the size of low traffic core areas (defined as areas larger than 100 km$^2$ and without roads carrying more than 1000 vehicles per day) has been reduced by about 18 % between 1977 and 1987 in former West Germany, comprising less than 20% of the total area of the country. How much unroaded habitat is needed and how large unroaded landscape fragments should be for a given species is task for future research.

Clearly, the best option to counteract the fragmentation process is the reclamation of nature areas for wildlife by the removal of roads or a permanent or temporary road closure. Road closure helps to reduce motorised access to wildlife habitat and enlarges undisturbed core areas, yet the physical barrier and its edge effects still remain. The physical removal of roads is the ultimate solution. In some countries, such as on federal land in the United States, attempts are made to integrate road removal as a part of the Grizzly bear conservation program (see Evink et al., 1999, Wildlands CPR, 2001). As bears are sensitive to disturbances associated to roads and human activities (e.g. Mace et al., 1996; McLellan et al. 1999), bear habitat has been reduced significantly with the expanding network of forest and public roads. To ensure the survival of grizzlies in the core areas of their distribution, it has been suggested to establish unroaded secure habitats of at least 70% of the size of an average female home range. In regions designated to grizzly bear conservation where road densities are higher than what is required for the secure habitats, roads should consequently be removed.

In Europe, temporary closure of (local) roads is sometimes applied for the protection of seasonally migrating amphibians (Dehlinger, 1994). Speed limitations on local transit roads can also offer a simple tool to change traffic flows in the road network and reduce disturbance and mortality in wildlife areas. In situations where roads cannot be removed or closed, or where traffic cannot be reduced, technical measures such as faunapassages and ecoducts may be necessary to mitigate fragmentation and reconnect wildlife habitats (e.g. DWW, 1995).

# 6 Concluding remarks

On the previous pages, I briefly reviewed some of the major literature on the ecological effects of infrastructure. There is a growing concern about habitat fragmentation caused by roads and railroads all around the world; and the increasing demand for mitigation and prevention makes clear that there is still much for us to understand until we can assess and evaluate the potential impact in an efficient and practical way. There is considerable amount of research done already, yet most of the studies are descriptive, dealing with problems of individual roads or railroads, but without providing answers to general questions that may be asked in the planning (and construction) of infrastructure.

For instance, how much habitat is actually lost due to construction and disturbance effects of infrastructure? How wide is the effected zone along roads and how does the width change with traffic intensity and type of surrounding habitat? How can transport infrastructure be integrated in the “ecological” infrastructure in the landscape without causing an increase in the risk for animal-vehicle collisions? Where and when are mitigation measures against road mortality in wildlife necessary or advisable (because affordable)? How much infrastructure is too much infrastructure in areas designated for wildlife? What are the ecological thresholds that we must not surpass and how can we make best use of the potential in a road or railroad project to improve the current situation?

Finding answers to these questions is an outspoken challenge to landscape ecologists, field biologists and civil engineers (e.g. Forman, 1998; Cuperus et al., 1999). To develop operative tools and guidelines for the planning of infrastructure and bring them into action, we need research that focuses on ecological processes and pattern, uses experiments and simulation to identify critical impact thresholds. Empirical studies are necessary to provide the basic data for defining evaluation criteria and indices. Computer simulations and spatial modelling will be helpful in evaluating alternative scenarios. Remotely sensed landscape data, GIS-techniques, and simulation models provide promising tools for future large-scale research, but they must rely on empirical field studies at local scales. Clearly, we need a better understanding of the large-scale long-term fragmentation impact on the landscape, yet the solution to the problems will rather be found at a local scale. Richard T.T. Forman, a pioneer in landscape and road ecology at Harvard University put it simply: We must learn to "think globally, plan regionally but act locally" (*sensu* Forman, 1995).

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