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Amphibian road kills: a global perspective

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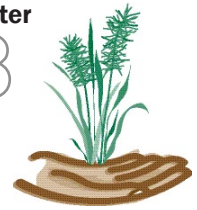
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Amphibian road kills: a global perspective

Abstract

Transportation infrastructure is a major factor determining land use forms. As global changes in this factor are the most important for biodiversity, roads fundamentally influence wildlife. The effect of roads on wildlife has been categorized in several ways resulting in six to ten categories with road kill as an obvious and important component, and amphibians are greatly affected by this factor. As this animal group has been documented to decline from multiple threats worldwide, the study and mitigation of their deaths on roads has become an important conservation priority. It was also detected as a single cause of decline, and data have accumulated on related population fluctuations, isolation, decline, and extinction in several countries. Genetics studies greatly improve our insight into these processes, e.g., by repeatedly proving significantly low heterozygosity in populations of several species living near roads. Amphibian road kills have been long documented and described due to their spectacular nature, but the overall effect of transportation infrastructure on amphibians was often underestimated due to contrasting research results. The speed of transport and the duration and timing of the surveys in which information was collected turned out to be decisive factors, causing differences of 5.5-16 times the number of road-killed amphibians recorded, mainly in connection with the low visibility and retention time of amphibians on roads. In light of such amphibian-related differences, the often cited national road kill estimates may well be considerably higher in practice, as well. Amphibian road mortality studies have been conducted almost exclusively in developed countries, mostly in Europe and North America, and under temperate zone conditions. In general, all terrestrial and semi-aquatic amphibian species can suffer from road kills where they have populations near roads. However, different amphibian species are threatened to a different extent by traffic because of their specific life history characteristics. Besides amphibian-specific factors (amphibian movement types, length and direction of movement, velocity, temporal movement pattern, behavioural changes on roads), the spatio-temporal pattern of amphibian road kill is also influenced by habitat and transportation characteristics (especially aquatic habitats and vegetation, road density, traffic intensity, vehicle speed, position and structure of roads, and awareness of drivers, respectively) and weather conditions (precipitation, temperature, wind). The effect of these factors must be understood before the need for mitigation can be evaluated and measures designed and built. Many mitigation measures have been built since the first amphibian tunnels were created in 1969 near Zürich, Switzerland, and a high diversity of technical solutions successfully reduced amphibian road kills under different conditions.

New research results have shown that amphibian tunnels can also be permeable for reptiles, such as snakes and small mammals. However, the lack of maintenance and construction deficiencies are common problems, which lower the efficiency of these measures worldwide. Road kills also have socio-ecological importance. Successful road-kill related projects have the potential to improve the understanding of decision-makers regarding road-related problems, also leading to their support of more complex conservation projects, including, for example, habitat restoration or compensatory developments near roads. Using the media to educate the general public about conservation efforts to reduce road kill, such as setting up frog fences in the USA and toad saving campaigns in Europe, clearly helps to realise this aim by influencing support provided by various authorities.



AMPHIBIAN ROAD KILLS: A GLOBAL PERSPECTIVE

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Abstract: Transportation infrastructure is a major factor determining land use forms. As global changes in this factor are the most important for biodiversity, roads fundamentally influence wildlife. The effect of roads on wildlife has been categorized in several ways resulting in six to ten categories with road kill as an obvious and important component, and amphibians are greatly affected by this factor. As this animal group has been documented to decline from multiple threats worldwide, the study and mitigation of their deaths on roads has become an important conservation priority. It was also detected as a single cause of decline, and data have accumulated on related population fluctuations, isolation, decline, and extinction in several countries. Genetics studies greatly improve our insight into these processes, e.g., by repeatedly proving significantly low heterozygosity in populations of several species living near roads.

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Amphibian road mortality studies have been conducted almost exclusively in developed countries, mostly in Europe and North America, and under temperate zone conditions. In general, all terrestrial and semi-aquatic amphibian species can suffer from road kills where they have populations near roads. However, different amphibian species are threatened to a different extent by traffic because of their specific life history characteristics. Besides amphibian-specific factors (amphibian movement types, length and direction of movement, velocity, temporal movement pattern, behavioural changes on roads), the spatio-temporal pattern of amphibian road kill is also influenced by habitat and transportation characteristics (especially aquatic habitats and vegetation, road density, traffic intensity, vehicle speed, position and structure of roads, and awareness of drivers, respectively) and weather conditions (precipitation, temperature, wind). The effect of these factors must be understood before the need for mitigation can be evaluated and measures designed and built.

Many mitigation measures have been built since the first amphibian tunnels were created in 1969 near Zürich, Switzerland, and a high diversity of technical solutions successfully reduced amphibian road kills under different conditions. New research results have shown that amphibian tunnels can also be permeable for reptiles, such as snakes and small mammals. However, the lack of maintenance and construction deficiencies are common problems, which lower the efficiency of these measures worldwide.

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Introduction

Effect of roads on wildlife

Transportation infrastructure is a major factor determining land use forms. As global changes in this factor are the most important for biodiversity (Sala et al. 2001), roads fundamentally influence wildlife. The effect of roads on wildlife is categorized in several ways according to the background, approach, and aim of the investigators. Trombulak and Frissel (2000), for example, put road effects into seven categories (increased mortality from road construction, increased mortality from collision with vehicles, modification of animal behavior, alteration of the physical environment, alteration of the chemical environment, spread of exotic species, increased alteration, and use of habitats by humans); and Jackson (2000), into ten (direct loss of habitat, degradation of habitat quality, habitat fragmentation, road avoidance, increased human exploitation, road mortality leading to loss of populations, disruption of social structure, reduced access to vital habitats, population fragmentation and isolation, disruption of processes that maintain regional populations). Andrews (1990) divided them into six (habitat loss and modification with accompanying effects on populations, intrusion of the edge effect into the core of natural areas, subdivision and isolation of populations by roads acting as a barrier, source of disturbance to wildlife, increased road-kills, increased human access with undesirable impacts on undisturbed areas); Seiler (2001, 2003), into five (habitat loss, disturbance, corridor, mortality, barrier); Scocciati (2001) regarding animals, into eight (loss of habitats, increasing harm to the habitat and fragmentation of the territory, increased "edge effect," restricted movement of individuals in the territory, growing genetic isolation of

the populations residing on each side of the road, higher mortality rate, with consequent numerical impoverishment of the populations living on each side of the road, increased human access to natural habitats, greater likelihood of invasion by alien species, with consequent risks of increased predation and competition); and Rudolph (2000), focusing on amphibians and reptiles, into six categories (habitat loss, habitat degradation, habitat fragmentation, increased mortality due to direct vehicular mortality, increased mortality due to increased vulnerability to harvest, alteration of behavior). As demonstrated by the lists above, the effect of roads on wildlife has been categorized in several ways, but road kill is an obvious and important component, and amphibians are an animal group that is greatly affected by this factor.

Conservation status of amphibians

Amphibians, which are threatened more than most other animal groups (Abramovitz 1996, IUCN, Conservation International and NatureServe 2004), suffer from multiple threats leading to a worldwide decline documented in all continents (Blaustein and Wake 1990; Griffiths and Beebee 1992; Houlihan et al. 2000). Some of the factors in this process, such as habitat destruction or pollution, are long known and studied; others have been recognized only relatively recently. Potential threats were grouped into several categories by different authors. For example, Collins and Storer (2003) distinguished six (alien species, over-exploitation, land use change, global change including UV-radiation and climate change, contaminants, emerging infectious diseases), while Waldman and Tocher (1998) listed nine (UV-B radiation, climate change, acid rain, pesticides and fertilizers, habitat disappearance or destruction, fragmentation, demographical causes, genetic causes, diseases) groups. In most cases, however, the combination of several factors leads to the decline of a species (see, e.g., Hatch and Blaustein 2000), and different species react differently (see, e.g., Hamer et al. 2004).

Besides a wide-scale decline, several amphibian species became extinct at the end of the 20th century, such as *Bufo perigrinus* in South America (Crump et al. 1992, Pounds and Crump, 1994), *Rheobatrachus silus* and *R. vitellinus* in Australia (Tyler 1991, Griffiths and Beebee 1992). This event is an even greater cause for concern as this animal group is less known than other vertebrates, which is well demonstrated by the unprecedented ratio of new species (even new families) described in the last 20 years. The number of known amphibian species changed by nearly 20 percent from 4,003 to 4,780 between 1985 and 1995 (Hanken 1999); it became higher than that of mammals by the millenium (Glaw and Köhler 1998) reaching 5,743 by 2004 (IUCN, Conservation International and NatureServe 2004). New species were not only found in less studied continents, but also in Europe and North America, where a new *Batrachoseps* species was discovered 50 km from San Francisco (Hanken 1999). As a result, there is a fair chance, that some amphibian species become extinct even before they are described.

Effect of roads on amphibians

The effect of roads and, to a lesser extent, rail traffic on amphibians has been long known due to its spectacular nature. What is more, amphibians, because they are predominantly surface water-bound organisms, are among the most affected taxa by this factor. Besides the overall loss and alteration of habitats, creation of edges and their consequences, which all animal groups suffer, they are also greatly influenced by pollution, such as lead accumulation in tadpoles developing near roads (Birdsall et al. 1986), road kill, and the related barrier effect. Amphibian road mortality was first described by Savage (1935), who reported 49 *Rana temporaria* road kill near London. Besides common species, which often encounter transportation infrastructure, rare taxa, such as *Ambystoma macrodactylum croceum* in California, are also threatened by roads (Robinson 1986). However, the overall effect of transportation infrastructure on amphibians was often underestimated even as late as the 1980s in spite of, e.g., several earlier studies demonstrating high mortality rates on roads (van Gelder 1973; Kuhn 1987).

Aim of work

Because amphibians have been documented to decline from multiple threats world-wide and transportation infrastructure plays a role in this process, the study and mitigation of amphibian road kills has also become an important conservation priority. The aim of this study is to summarize the available knowledge on amphibian road kills at a global scale.

Amphibian Road Kill

Significance of amphibian road kill

Though the phenomenon was recognized as early as the 1930s (Savage 1935), evidence of the ecological consequences of amphibian road kill accumulated only at the end of the 20th century (for an overview, see table 1). Road mortality was detected as a single cause of decline in the Austrian Alps (Landmann et al. 1999), and data accumulated on road kills and related population fluctuations, isolation, unequal sex ratio, decline, and extinction (e.g., Bressi 1999, Cooke 1995, Fahrig et al. 1995, Reh 1989, Ryser 1988, Sjögren-Gulve 1994, Vos and Chardon 1998, Vos et al. 2001). The length of paved road within 1 km was found to be negatively associated with salamander diversity and also with the presence of *Ambystoma tigrinum tigrinum* (Porej et al. 2004), and the chorus index of frog and toad relative density was also negatively correlated with traffic intensity, i.e., the frog and toad density decreased with increasing traffic intensity (Fahrig et al. 1995).

Table 1. Effect of road kills on amphibians (for more information, see the text above)

Effect	Country	References
determination of distribution areas	Netherlands	Vos et al. 2001
extremely unequal sex ratio	Hungary	Csapó et al. 1989
genetical isolation, low heterozigocy	United Kingdom France Germany Netherlands	Hitchings and Beebee 1997 Lesbarrés et al. 2003 Reh 1989 Vos et al. 2001
low density in the vicinity of sections with high traffic	Canada Switzerland Netherlands	Fahrig et al. 1995 Ryser 1988 Vos et al. 2001
single cause of decline	Austria	Landmann et al. 1999
local extinction	Italy United Kingdom Sweden Switzerland	Bressi 1999 Cooke 1995 Sjögren-Gulve 1994 Holzgang et al. 2000

Genetic studies greatly improved our insight into these processes. Lesbarrés et al. (2003) studied small (less than 40 adult frogs or 20 egg clutches) *Rana dalmatina* populations along the A11 highway in France and at control sites. Heterozygosity was significantly lower in populations near the highway, indicating the negative influence of roads by road kills during breeding migration and juvenile dispersal. Similarly, Vos and Chardon (1998) detected negative correlation between *Rana arvalis* populations and roads within 250 meters. Furthermore, the density of roads within 750 m of the breeding sites was also negatively associated with the probability that the pond would be occupied. What is more, in the Netherlands the genetic structure of *Rana arvalis* populations correlated better with the position of roads and railways than with geographical distances (Vos et al. 2001). As a consequence of these findings, today traffic mortality is also listed as a significant factor causing amphibian decline (Seburn and Seburn 2000).

In contrast to natural predation, traffic mortality is non-compensatory, and the kill rate is independent of density. This implies that traffic will kill a constant proportion of a population and, therefore, affect rare species most significantly. In general, species that occur in small, isolated populations, and those which require large, extensive areas for their home ranges, or have long migratory movements, are especially sensitive to road mortality (Seiler 2003). Moreover, road kills also have a sociological significance as they can be used for education purposes, e.g., on amphibian decline, more easily than more sophisticated and sometimes even contradictory processes.

Importance of methodology: relative frequency of amphibian road kill and its relation to survey speed and timing

The method of collecting information on road kills seems to be easy and obvious. However, though both long-term and (if coincided with mass amphibian migration or dispersal) short-term studies show the relative importance of amphibian road kill among vertebrates, a lot of contradictory results have been published due to differences in sampling protocols, especially in the duration and timing of the surveys, period of the day in which information was collected, and speed of driving/cycling/walking.

To analyze these differences at a global level, ten studies from Canada, Czech Republic, Hungary, Poland, Slovenia, UK, and the USA (figure 1.), with different sampling protocols were selected for comparison (Ashley and Robinson 1996, Bartosewicz 1997, Clevenger et al. 2003, Denac 2003, Fenyves 1989, Holisová and Obrtel 1986, Kline and Swan 1998, Lodé 2000, Slater, 2002, Wolk 1978). Figure 2 shows the relative frequency of vertebrates among road-killed animals. As demonstrated by figure 2, the relative frequency of amphibians varied between 4.9 and 92.1 percent in the individual studies. The comparative analysis of the sampling protocols emphasized the determining power of driving/cycling/walking speed in this respect. The five studies plotted on the left side of the graph detecting considerably more amphibians were made by walking/cycling or motorcycling while the other five by driving a car. Besides the comparison of different studies, this difference was also noted in the same survey. In Wales Slater (2002) recorded 5.5 times more road killed animals surveying on foot than driving by car even if it was relatively slow, less than 40 km per hour.



Figure 1. Distribution of road kill survey localities compared in the present study (• = locality).

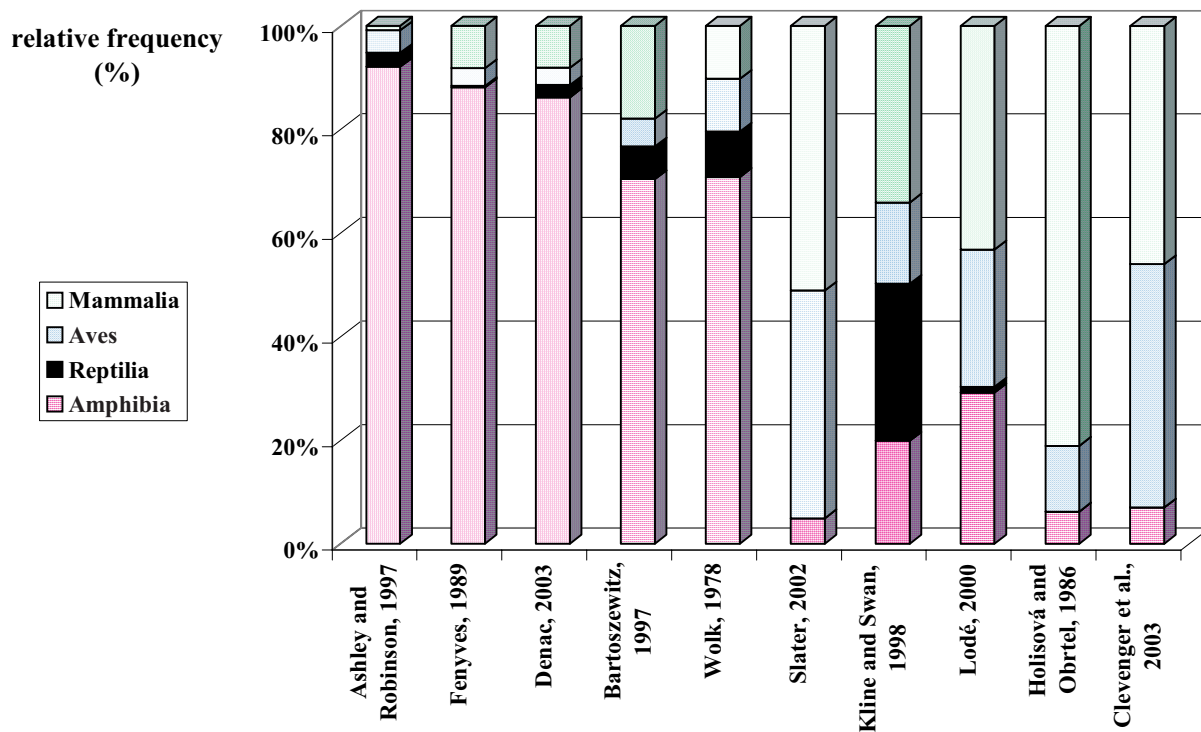


Figure 2. Relative frequency of vertebrate road kill in ten European and North American studies.

In other studies, walking surveys also recorded taxa, which were otherwise overlooked, such as *Triturus* in France, which turned out to be commonly noted on roads in the Rhone-Alpes region only during more detailed walking surveys (Grossi et al. 2001) or *Notophthalmus viridescens* efts, which were found every 1.4 m along a stretch of a Virginia road (Mitchell 2000). Difficulties in the detectability of newts due to their size and shape and the consequent underestimation of newt migration was also noted by Denac (2003) and Evans (1989).

Besides speed, timing within the year and the part of the day selected to collect samples are also key elements in determining road kill results. Slater (2002) recorded a 4.8 percent amphibian road kill in a year long survey in Wales when driving in the morning. However, an observation within the same study recorded 178 *Bufo bufo* (50%) corpses removed from the road surface from a short section near Llandrindod Wells Lake on the same circuit within an hour after dawn

on a single morning during migration, proving that the actual relative frequency of amphibian road kills is much higher. During a regular, 10 a.m. survey no evidence of road kill would have been found there. The fact that this single event included ten times more amphibians than the annual total amphibian mortality recorded over a year for a 68 km circuit driven by less than 40 km per hour twice a week, because the remains of very degraded amphibian corpses are visible only on close inspection, show the difficulty of such estimations.

Similar evidence exist in other studies in America as well as in Europe. Kline and Swan (1998) found that only 15 of at least 63 *Scaphiopus couchi* corpses (< 23.8%) remained on the road surface until the time of regular morning surveys between 8:30 a.m. and 12:00 noon, while Hels and Buchwald (2001) calculated a 7- to 67-percent retention rate for members of a six species amphibian community. Besides scavengers, people occasionally also remove amphibians from the road for their legs (Ashley and Robinson 1996).

The underestimation of amphibian road kill originates both from low retention time on roads as compared with other vertebrate classes and from small size, especially for newts and juveniles. Short retention time partly originates from the lack of hair, feathers and scales (Hels and Buchwald 2001). Taking into consideration all factors Slater (2002) estimated a 12-16 times greater vertebrate kill rate on roads than what could be found by a single daily census. This figure is nearly identical with that was suggested for bird road kill in Sweden by Svensson (1998).

In the past twenty years various national estimates have been made for road casualties. Lalo (1987) estimated that one million vertebrates are killed on U.S. roads every day, while Caletrio et al. (1996) calculated an annual 10 million vertebrate road kill rate for Spain. Ehmann and Cogger (1985) estimated an annual amphibian and reptile mortality of five and a half million individuals for Australia. In light of the primarily amphibian-related data described above, these often-cited figures may well be considerably higher in practice.

A determining network characteristic: global road density

As the distribution of road kill surveys in figure 1 suggests, amphibian road kill studies are mostly limited to developed countries, first of all to Europe and North America. However, roads occupy an increasing area in most countries, which urges further studies in this field. There are striking differences, however, in the extent to which individual countries and continents are affected by the transportation network due to its density and the traffic intensity on them as there are three orders of magnitude of difference in road density between different countries in the world (fig. 1). The quality and width of roads also greatly differ among individual countries, and not only according to their economical development. The density of motorways and highways alone is 0.47 km/km² in Belgium, which is at least twice as dense as the total road density of many African, South American, and Asian countries, but the primary and secondary road network of the Netherlands, for example, is also nearly 12 times denser than the Swedish network (Farral et al. 2003). Smaller countries and some islands usually have a denser road network than large, mainland states. The ratio of paved sections to the total paved and unpaved road network also differs. Usually it is over 50 percent in Europe and under that ratio in Africa, South- and Central-America, and Asia, which is also an important factor for determining road kill through affecting driving speed.

Characterization of amphibian road kills

In general, road traffic poses a severe threat to amphibians due to their slow capacity of movement; their inability to notice the danger from cars in time and to make successful attempts to avoid them; their tendency to become immobilized in moments of danger, which causes them to remain on the road longer; limited dispersal rate; and thus, ability to recolonize areas, and complex life cycle of many species, which involves periodic migrations between different habitats (Scoccianti 2001). As amphibian road mortality studies were made nearly exclusively under temperate zone conditions, the results presented here (e.g., seasonality) primarily refer to those conditions.

Species composition: In general, all terrestrial and semi-aquatic amphibian species can suffer from road kills where they have populations near roads. However, some species are more common victims. According to a national survey in the Czech Republic, although 14 species were recorded killed on roads, 82 percent of the populations affected by road kills were of either *Bufo bufo* or *Rana temporaria* (Mikátová and Mojmir, 2002), two abundant species with long breeding migration routes (for a comparison of average migration radius of seven European species, see figure 4.) and large size, which makes it easier for humans to detect the corpses. Similar species-related differences exist not only at the population, but also at the individual level. *Bufo bufo* and *Triturus helveticus* represented 56.7 percent and 28.4 percent of road-killed amphibians, respectively, in a 33-week survey along the A83 motorway in France while *Rana dalmatina* and *Alytes obstetricans* corpses were only recorded in low numbers (Lodé 2000).

The species composition of road kills, however, also reflects the local species pool, resulting in different species compositions and relative frequency in different regions. This phenomenon was also statistically proved using G test to check the similarity (homogeneity) of amphibian road kill data collected over seven years from five protected regions in Hungary. The distribution of the sampling localities can be seen in figure 5, where the color change from green to dark brown symbolizes an elevation change of nearly 1,000 m. As expected, the species composition of road kill was significantly different from the hilly or lowland areas in the Körös - Maros National Park, which is a lowland area in the southeastern part of the country.

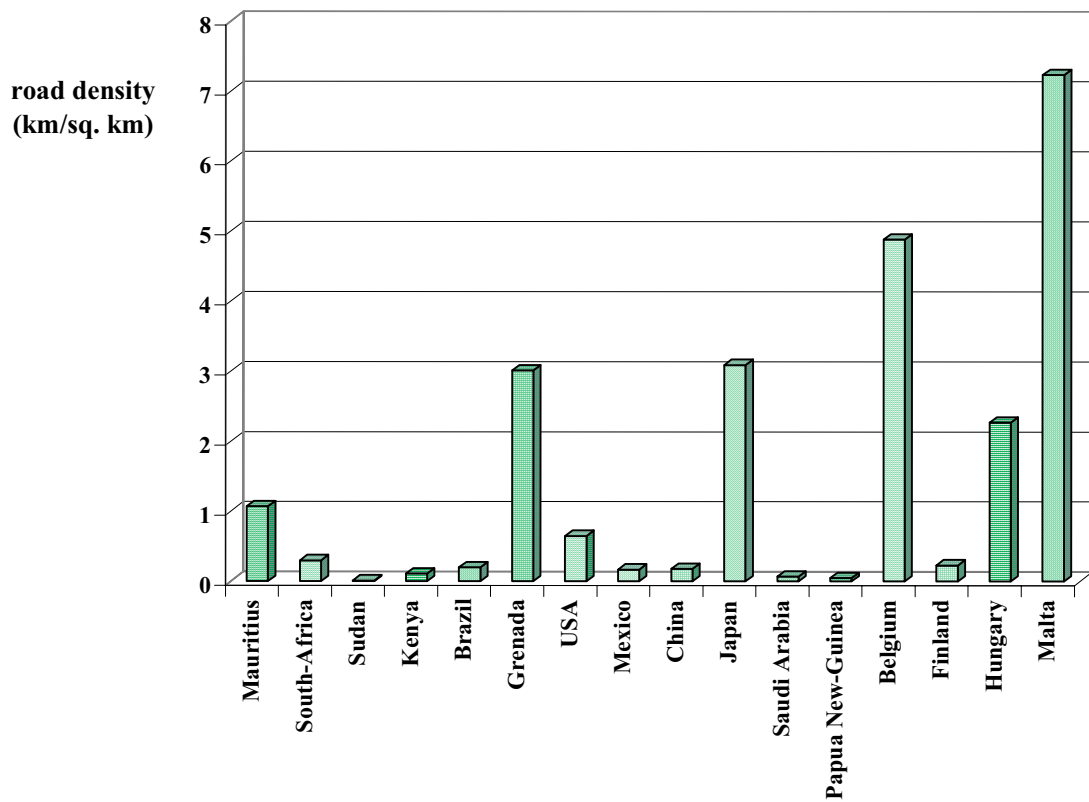


Figure 3. Density of national road networks. (Source: IRF World Road Statistics 2003)

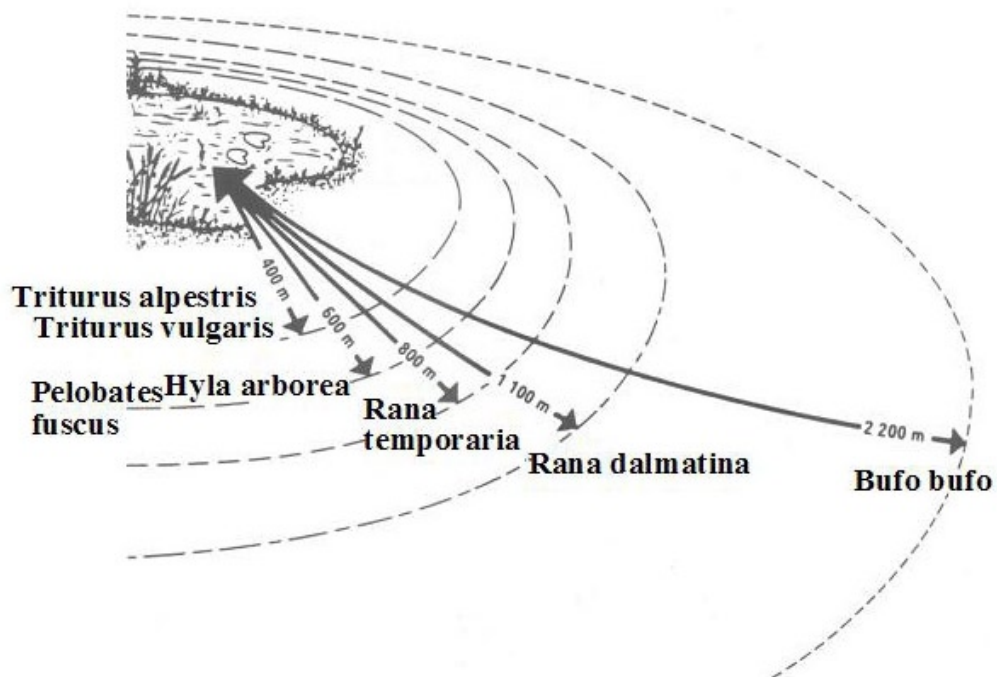


Figure 4. Migration radius of seven European amphibian species (after Blab 1986).

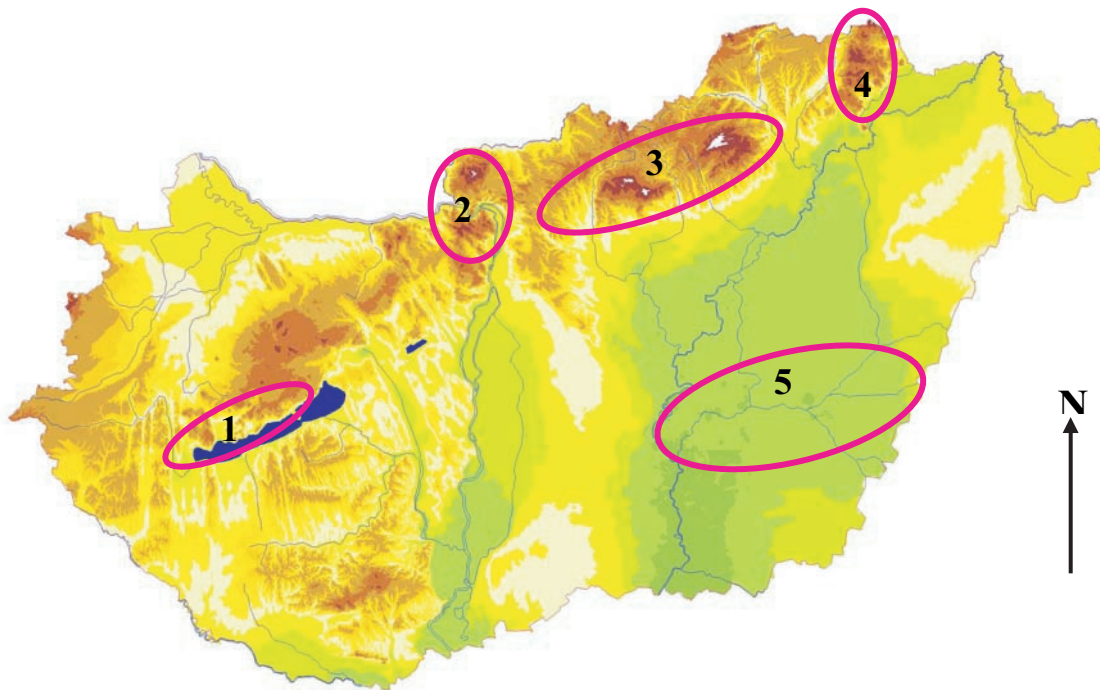


Figure 5. Localities of the national amphibian road kill surveys. (1= Balaton Uplands National Park, 2= Danube - Ipoly National Park, 3= Bükk National Park - Mátra Landscape Protection Area - Kelet-Cserhát Landscape Protection Area, 4= Zemplén Landscape Protection Area, 5= Körös - Maros National Park)

Usually more than one amphibian population is present at the same breeding site, and the migration periods of the populations partially overlap. As a result, usually individuals of different species are affected by roads, and they also often cross roads at the same section. For example, Aresco (2003), Frank et al. (1991), and Kelemen (2000, 2001) recorded ten; Grossi et al. (2001), up to nine; Kárpáti (1988), nine; and Denac (2003), at least eight species at the road sections studied. Often, there is also a spatially different migration pattern of the individual species, and they cross the road at slightly different spots within the the same section (Grossi et al. 2001; Proess 2003).

Seasonality and annual changes

Under temperate zone conditions the highest peaks are usually recorded during spring (breeding migration to, where overwintering sites overlap with summer habitats, and also from the breeding sites). This pattern has been shown by several authors, e.g., Rettig (1996), who found 73.4 percent of all amphibian road casualties in March during a whole year survey. Juvenile dispersal, however, if recorded, can produce even higher peaks during summer (see, e.g., Ashley and Robinson 1996). Where the habitat is more homogenous, e.g., when roads cross wetlands, amphibian mortality remains high throughout the year. In either case, if tadpoles metamorphose successfully, juvenile dispersal occurs in summer. In autumn, there is also a longer migration period with smaller peaks than in spring. In other climate zones the actual weather pattern, e.g., the time of monsoons, summer rains in deserts, etc., determines the activity periods of amphibians and, thus, the presence of amphibians on roads (Kline and Swan 1998).

There are major fluctuations in the number of amphibians crossing the road each year, which can reach an order of magnitude difference between years (Marsh 2001). To achieve reliable counts and accurately pinpoint the main crossing points, where mitigation measures should be built, and still produce results within a reliable amount of time, the detailed monitoring of amphibian road kill for at least three years was suggested by Grossi et al. (2001).

Sex-related differences

Male and female amphibians spend different periods of time in different habitats, and there can also be marked differences in the migration radius as well as the period of migration of the two sexes. Regosin et al. (2003) found that a higher ratio of *Rana sylvatica* males winter near (65 m) their breeding ponds than farther from the pond, which also means that females of this species (at least at the site studied) had a longer migration radius. Kuhn (1994) noted that a large number of females die at the breeding sites, which lowers the number of amphibians migrating out of the breeding area, and consequently a lower number crossing the road. Similar to individual number changes, the sex ratio of migrating amphibians can also change. Such a shift was described by Griffiths et al. (1986): from 6.5:1 to 2.1:1 males to females in four years with *Bufo bufo*. Other species (*Triturus vulgaris*, *Triturus helveticus*, *Rana temporaria*) migrating at the same site in Wales, however, did not show a similar phenomenon.

Site of road kills

The proximity of natural and artificial water bodies increases the probability of road kills. Scoccianti (2001) found 80 percent of main amphibian crossing sites near artificial water bodies. Road kills often happen along sections with contrasting habitats including wetlands on either side of the road (Csapó et al. 1989). Another crucial habitat type is forests, where the majority of amphibians might cross as opposed to open areas, as with *Notophthalmus viridescens* (Mitchell 2000). Because of construction considerations, roads are often situated along the edge of geographic features that provide different habitats for amphibians, e.g., as winter hibernation sites, breeding sites, or summer habitats. As a result, a seasonal migration pattern is likely to occur in such sections that run, for example, between foothills of mountains and floodplain, or along large lakes and reservoirs (Rybacki 1995). In other cases, roads cut the same habitat, e.g., wetlands into smaller fragments (Dodd et al. 2004) causing road-kill problems to be present as long as the animals are active (Puky 2003).

Factors determining amphibian road kills

The spatio-temporal pattern of amphibian road kill is influenced by various factors. They can be grouped into major units as amphibian-specific factors, habitat and transportation characteristics, and weather (table 2). Due to the length of this paper, the overview of only three less frequently discussed factors (temporal movement pattern, habitat characteristics, awareness of drivers) are given here, but the effect of all these factors must be understood before the need for mitigation can be evaluated and measures be designed and built.

Table 2. Factors determining amphibian road kill

Major unit	Individual factor
amphibian specific factors	amphibian movement types length and direction of movement velocity temporal movement pattern behavioural changes on roads
main habitat characteristics	vegetation available aquatic habitats
transportation characteristics	road density traffic intensity vehicle speed position and structure of roads awareness of drivers
weather conditions	precipitation temperature wind annual changes of weather conditions

Temporal movement pattern

In temperate zone conditions most amphibians move across roads during the night (e.g., Ashley and Robinson 1996). In general, they migrate from dusk on, but the exact timing and daily peaks vary between species of the same community (Hels and Buchwald 2001). During the peak of migration amphibians also move during the day. Under cooler climates, however, this phenomenon can become regular, as it was described for *Rana pipiens* by Linck (2000). At Baker Park Reserve, Minnesota, this species starts spring migration in mid-morning, after basking while the night air temperature is below freezing. The autumn migration at that locality, however, occurs during the night as well. Species which move diurnally are at greater risk than nocturnal species due to the greater traffic by day (Hels and Buchwald 2001).

Habitat characteristics

The effects of two factors are important to stress here. Amphibian movement is often associated with water, e.g., streams as demonstrated by Beshkov and Jameson (1980) on *Bombina variagata*. On the other hand, Ashley and Robinson (1996) found that *Rana pipiens* road kill was significantly associated with roadside vegetation. In some studies both factors were revealed as important. Mitchell (2000), for example, found that road-killed *Notophthalmus viridescens* efts were distributed more or less equally on the road stretch next to a wetland and a wooded road section, further indicating the importance of both habitat characteristics.

Awareness of drivers

There are several experiments with contrasting results on the effect of informing drivers through road signs and the media and asking them to slow down. Flashing road construction signs operated during peak (diurnal) migration hours received positive reactions by drivers in Minnesota (Linck 2000). However, road signs in Wales at migratory amphibian crossings encouraged some drivers to deliberately kill toads with their cars (Slater 1994). Although referring to marsupials and not amphibians, the speed of vehicles was not reduced by use of signs in Australia (Coulson 1982).

Mitigation Measures: Summarizing History, Design, and Problems

Amphibian mortality can be reduced by several ways. Avoidance is the best solution if an important breeding site should be protected. Compensatory measures, such as creating new aquatic habitats, are becoming more common, and in the construction phase the translocation of amphibians was also used in several cases, such as at the Wilmslow and Handforth Bypass of the A34 road in Cheshire, England. After construction, the temporary closing of road sections is the best solution; however, it is rarely a realistic option, similar to the removal or translocation of the road itself. However, mitigation measures are the most widely used solutions to lower the effect of transportation infrastructure on amphibians. Frog rescues have been organized and temporary protective measures introduced by many national park authorities, non-governmental organizations, and private people in Europe and North America (see, for example, Ballasina 1989, Kárpáti 1988, Langton 1989a, Puky et al. 1990, Schád et al. 1999, Wisniewski 2001). Amphibians may use wildlife bridges if adequate fencing is provided, but in most cases amphibian tunnels and fences are set up to protect anurans, newts, and salamanders.

The first amphibian tunnel was built in 1969 near Zürich in Switzerland (Ryser and Grossenbacher 1989). In North America an amphibian tunnel was first constructed in 1987 near Amherst, Massachusetts (Jackson and Tynning 1989), while in the Oceanian region one was constructed in 1995 near Auckland, New Zealand (Close 1995). In the past 40 years, tunnels of different design and fences of different material were successfully used to help amphibians cross roads (for an overview on its development in Central-Europe, see Puky 2003).

Besides the success of many different designs and the improvement of tunnel parameters, such as material and size over the years (see, e.g., Langton 1989b, Puky 2003, Ryser and Grossenbacher 1989), the limitations of these constructions also became obvious. In Hungary, for example, less than half of the amphibian mitigation measures work properly (figure 6), which is an unacceptably low percentage. In general, most problems originate from lack of maintenance and construction deficiencies (see figs. 7 and 8.). To avoid such problems, several guidelines exist, which can be used in the planning and construction phase as well as during the operation of roads and railroads (Luell et al. 2003; for amphibian-specific recommendations, see Puky 2003).

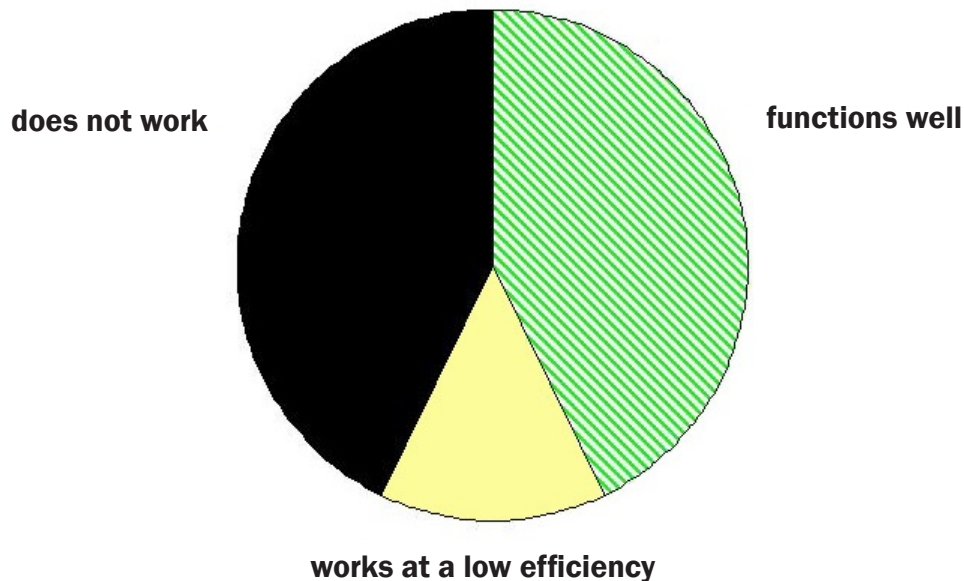


Figure 6. Efficiency of amphibian mitigation measures in Hungary (modified after Puky and Vogel 2004).

In the light of data collected at the tunnel systems at Fertőboz and Mosonszentmiklós in 2004 (for more detailed description, see Puky 2003), the functioning of amphibian tunnels is also important for other fauna elements of the local ecosystems, namely reptiles and small mammals, as they also cross under roads using these passages (Puky et al. 2005).

Socio-Ecological Importance of Road Kills

Importance of road kills for non-road oriented studies

Road kills can also provide valuable information for non-road related projects, too. They can serve as an important data source in mapping projects, especially when time and personnel are limited, to obtain a rapid overview of a large (e.g. 10 km x 10 km) sampling unit (Puky 2001). There is also the possibility of using them in molecular analyses similarly to mammals (Doyon et al. 2003) or other research projects with a similar need of samples, which would be especially important when conservation regulations make it difficult to get licences for such studies.



Figure 7. Main causes of malfunctioning amphibian mitigation measures I.: lack of maintenance (Henley-on-Thames, England).



Figure 8. Main causes of malfunctioning amphibian mitigation measures II.: construction problems (tunnel entrance over the ground), besides the fence is lacking (near Auckland, New Zealand). (Photo courtesy: Dr. Phil J. Bishop)

A main challenge and opportunity: education

Successful road-kill-related projects have the potential to improve the understanding of road-related problems, leading to the launching of more complex conservation projects, including, for example, habitat restoration or compensatory developments near roads. As stressed by many, there is still a lot to do in this respect world wide. Even if regulations have been made in many countries, authorities are often negligent with regard to amphibian conservation and conservation in general along roads (see Caletrio et al. 1996 remarks for Spain). Influencing that group, however, is far from being the only task at which road-related education activities should aim. If mitigation measures are built at the local road level, it is important to inform local people as well as the general public on the aim, benefits, and functioning of the mitigation measures in order to build up social support. Convincing local people and NGOs about supporting their local wildlife tunnel, for example, may even reduce the construction cost of permanent mitigation measures, as happened in Lab Hollow, New York State (pers. comm. Kurt Weiskotten, NYSDOT), and it also protects against vandalism in the region, which also clearly improves the efficiency of toad tunnels. Using the media to inform the general public on conservation efforts on roads to reduce road kill, such as the setting up of frog fences in the USA (Hoffman 2003) and toad saving campaigns in Europe, is also important. Educating these groups effectively, however, requires different strategies as summarised in table 3.

Table 3. Important target-specific aspects of road-related environmental education

Target group	Important information and communication forms in road-related education
Children	personal experience (in the field or with live animals) and involvement interesting stories (e.g. on the life of amphibians) realising their own abilities, and that they can have a positive influence
General public	general overview (also on e.g. protected species) interesting stories (e.g. on the life of amphibians) important relationships
Local people	general overview (also on e.g. protected species) values of local habitats why and how the project is done how they can benefit and get involved and help (contact addresses)
Decision-makers	concise text easily understandable message list of actions

The support of well-known (and positive) personalities, such as Dr. Jane Goodall, may also be a key element of a long-term education strategy. Her general support and talk in front of a large audience (fig. 9), increased, for example, the recognition of the Toad Action Group (DAPTF Hungary) by ministry officials and helped gain more attention to road-related environmental projects. In another example, as figure 10 demonstrates, a minister, children, and frogs can participate in such project activities with the hope of bringing a brighter future for road-crossing amphibians. Besides informing and educating many motorists, news articles and television/radio programs reporting on road-related environmental education activities clearly help to get support from different authorities, when they realize that such conservation efforts are not only a legal obligation, but also an important objective for the communities in which they live and especially for the children around them. Partly due to such developments, positive changes can also be recognized in the approach of decision-makers, such as road builders, towards wildlife mitigation measures. At the beginning of the 1990s debates in Hungary often dealt with the necessity of such constructions and if they should be

built at all. By the 2000s, it has shifted toward discussions on the number and dimensions of tunnels, how many, and what size should be made to protect amphibians – which is, even if there remains much left to do, still a great step forward.



Figure 9. Dr. Jane Goodall gives a talk in Hungary organized by the Toad Action Group, an international award winning NGO founded in 1986. (Photo courtesy of Norbert Erdei)



Figure 10. The Hungarian Minister for the Environment and Water Management participates in a frog saving project in March 2005. (Photo courtesy of Szabolcs Jónás, Toad Action Group)

Final Remarks

The importance of amphibian road kills was recognised at the end of the 20th century. Its relative frequency greatly depends on the speed and timing of the survey. The comparison of earlier studies indicates that the number of road-killed amphibians is often considerably higher than was previously estimated. Mitigation measures can be an effective way of lowering amphibian road kills, but they often fail to work due to construction problems or lack of maintenance. As figure 11 demonstrates, the ratio of amphibian studies among road studies is lower than what the conservation status of the group and the importance of this factor would need. Also, more studies in new geographic areas as well as the monitoring of existing mitigation measures are needed. In the future, a new, comprehensive strategy needs to be applied using the available knowledge and experience to make new, effective mitigation measures and increase the efficiency of the existing ones both on old and new roads. Education has an important role in this process. As a result, new projects should be at least as much based on conservation-minded planning, building, and maintenance as on using more financial resources.

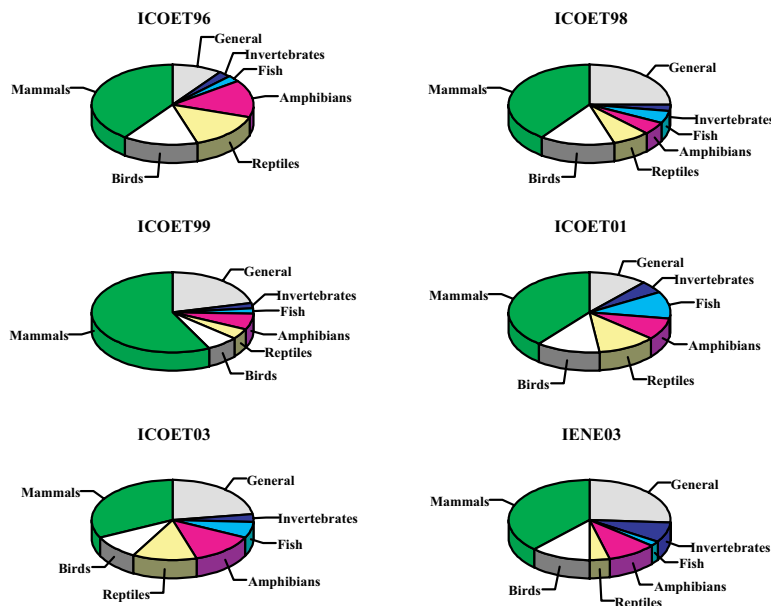


Figure 11. Relative frequency of papers dealing with different animal groups presented at road ecology conferences between 1996 and 2003.

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References

- Andrews, A. (1990): Fragmentation of habitat by roads and utility corridors: a review. *Australian Zoologist* 26: 130-141.
- Aresco, M. J. (2003): Highway mortality of turtles and other herpetofauna at Lake Jackson, Florida, USA, and the efficacy of a temporary fence/culvert system to reduce roadkills. In Irwin, C. L., Garrett P. and McDermott, K. P. (eds): *2003 Proceedings of the International Conference on Ecology and Transportation*, The Center for Transportation and the Environment, Raleigh, North Carolina (24-29 August, 2003, Lake Placid, New York). pp. 433-449.
- Ashley, P. E. and Robinson, J. T. (1996): Road mortality of amphibians, reptiles and other wildlife on the Long Point causeway, Lake Erie, Ontario. *Canadian Field Naturalist* 110(3): 403-412.
- Ballasina, D. (1989): Toads on Roads in Belgium. In Langton, T. E. S. (ed): *Amphibians and Roads*. ACO Polimer Products Ltd., London. 83-86.
- Bartoszewicz, M. (1997): Śmiertelność kregowców na szosie graniczącej z rezerwatem przyrody Słonsk (Mortality of vertebrates on the highway bordering the Słonsk Reserve, Western Poland). *Parki Narodowe i Rezerваты Przyrody, Białowieża* 16(4): 59-69.
- Beshkov, V. A. and D. L. Jameson. (1980): Movement and abundance of the yellow-bellied toad *Bombina variegata*. *Herpetologica* 36: 365-370.
- Birdsall, C. W., Grue., C. E. and Anderson, A. (1986): Lead concentration in bullfrog *Rana catesbiana* and green frog *Rana clamitans* tadpoles inhabiting highway drainages. *Environmental Pollution Series A Ecological and Biological* 40: 233-248.
- Blab, J. (1986): Biologie, Ökologie und Schutz von Amphibien (Biology, ecology and protection of amphibians). Schriftenreihe für Landschaftspflege und Naturschutz. Heft 18. Kilda Verlag, Bonn. pp. 150.
- Bressi, N. (1999): Habitat fragmentation, metapopulation dynamics and declining amphibian populations: a field study of green frogs, *Rana (Pelophylax) synklepton esculenta* Linné 1758. In Miaud, C. és Guyétant, R. (ed): *Current studies in herpetology*. Le Bourget du Lac (SEH). 71-78.
- Caletrio, J., Fernandez, J. M., Lopez, J. and Roviralta, F. (1996): Spanish national inventory on road mortality of vertebrates. *Global Biodiversity* 5: 15-18.
- Clevenger, A. P., Chruszcz, B. and Gunson, K. (2003): Spatial patterns and factors influencing small vertebrate fauna road-kill aggregations. *Biological Conservation* 109: 15-26.
- Close, I. (1995): Conservation briefs: frog tunnel. *Forest and Bird* 277: 6.
- Collins, J. P. and Storfer, A. (2003): Global amphibian declines: sorting the hypotheses. *Diversity and Distributions* 9: 89-98.
- Cooke, S. A. (1995): Road mortality of common toads (*Bufo bufo*) near a breeding site, 1974-1994. *Amphibia - Reptilia* 87-90.
- Coulson, G., 1982. Road-kills: wheels v wildlife. *Wildlife Aust.* 22: 26-28.
- Crump, M. L., Hensley, F. R. and Clark, K. L. (1992): Apparent decline of the golden toad: underground or extinct. *Copeia* 1992: 413-420.
- Denac, K. (2003): Mortaliteteta vretencarjev na cestah Ljubljanskega barja (Mortality of vertebrates on the roads of Ljubljana moor, Slovenia). BSc. thesis. University of Ljubljana. pp. 62.
- Dodd, K. C. Jr., Barachivich, W. J. and Smith, L. L. (2004): Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily travelled highway in Florida. *Biological Conservation* 118: 619-631.
- Doyon, C., Trudeau, V. L., Hilbert, B. M., Howes, L. A. and Moon, T. W. (2003): mRNA analysis in flattened fauna: obtaining gene-sequence information from road-kill and game-hunting samples. *Canadian Journal of Zoology* 81: 692-698.
- Ehmann, H. and Cogger, H. (1985): Australia's endangered herpetofauna: a review of criteria and policies. In Grigg, G., Shine, R. and Ehmann, H. (eds): *Biology of Australian frogs and reptiles*. Surrey Beatty & Sons and Royal Zoological Society of New South Wales, Sydney, Australia. pp. 435-447.
- Evans, G. M. (1989): Observations on *Bufo bufo* and *Triturus cristatus* road fatalities at Yarlet in Stafford. *Herpetile* 14: 139-142.
- Fahrig, L., Pedlar, J. H., Pope, S. E. Taylor, P. D. and Wegner, J. F. (1995): Effect of road mortality on amphibian density. *Biological Conservation* 73: 177-182.
- Farral, H., Bouwma, I. M. and Fry, G. (2003): European nature and transportation infrastructure. Trocmé, M., Cahill, S., de Vries, H. J. G., Farral, H., Folkson, L., Fry, G., Hicks, C. and Peymen, J. (eds): *Habitat fragmentation due to transportation infrastructure*. The European review Office for Official Publications of the European Communities, Luxemburg. 51-71.
- Fenyves, L. (1989): Gerinces állatok pusztulása az utakon. *Madártani Tájékoztató* 1-2: 54-55.
- Frank, T., Pellinger, A. and Selyem, J. (1991): Kétéltű- (Amphibia) és hüllő- (Reptilia) védelem a Fertő-tó mentén (1987-1990) (Amphibian (Amphibia) and reptile (Reptilia) protection along Lake Fertő/Neusiedlersee (1987-1990). A Magyar Madártani és Természetvédelmi Egyesület III. Tudományos Ülése. MME, Szombathely. 330-337.
- Grossi, J. L., Coffre, H. and Marciau, R. (2001): Conservation strategy for amphibians in the Rhone-Alpes region. Tools in preserving biodiversity in nemoral and boreonemoral biomes of Europe, Naconex. pp. 76-79.
- Hanken, J. (1999): 4780 and counting. *Natural History* 7-8: 82.
- Hels, T. and Buchwald, E. (2001): The effect of road kills on amphibian populations. *Biological Conservation* 99: 331-340.

- Hoffman, N. (2003): Frog fence along Vermont Rt 2 in Sandbar Wildlife Management Area. Collaboration between Vermont Agency of Transportation and Vermont Agency of Natural Resources. In Irwin, L. C., Garrett, P. and McDermott, K. P. (eds): *2003 Proceedings of the International Conference on Ecology and Transportation*, The Center for Transportation and the Environment, Raleigh, North Carolina (24-29 August, 2003, Lake Placid, New York). pp. 431-432.
- Holisová, V. and Obrtel, R. (1986): Vertebrate casualties on a Moravian road. *Acta scientiarum naturalium Academiae scientiarum bohemoslovacae*, Brno. 20(9): 1-44.
- Holzgang, O., Zumbach, S. and Bornhauser-Sieber, U. (2000): Effects on populations. In COST 341. *Habitat Fragmentation due to Transportation Infrastructure*. Swiss State of the Art Report. pp. 53-54.
- IUCN, Conservation International and NatureServe (2004): *Global Amphibian Assessment*. <www.globalamphibians.org>. Accessed on 15 October 2004.
- Iuell, B., Bekker, G. J., Cuperus, R., Dufek, J., Fry, G., Hicks, C., Hlaváč, V., Keller, V. B., Rosell, C., Sangwine, T., Torslov, N. and Wandall, B. le Maire (eds) (2003): *Wildlife and traffic: A European handbook for identifying conflicts and designing solutions*. KNNV Publishers.
- Jackson, S. D. (2000): Overview of transportation impacts on wildlife movement and populations. In Messmer, T. A. and West, B. (eds): *Wildlife and highways: seeking solutions to an ecological and a socio-economic dilemma*. The Wildlife Society, Nashville. pp. 7-20.
- Jackson, S. D. and Tynning, T. F. (1989): Effectiveness of drift fences and tunnels for moving spotted salamanders *Ambystoma maculatum* under roads. In Langton, T. E. S. (ed): *Amphibians and Roads*. ACO Polymer Products, Shefford, Bedfordshire, UK. 101-113.
- Kárpáti, L. (1988): Massensterben der Herpetofauna (Amphibien und Reptilien) infolge des Kraftverkehrs. Möglichkeiten und Ergebnisse des Schutzes am Südufer des Neusiedlersees (Mass mortality of the herpetofauna (Amphibians and reptiles) due to road kill. Conservation opportunities and tasks along the southern shore of Lake Fertő/Neusiedlersee). BFB Bericht.
- Kelemen, T. (2000): A második békamentés Balogunyom határában (Second frog rescue at Balogunyom). *Cinege* 5: 8-9.
- Kelemen, T. (2001): A harmadik békamentés Balogunyom határában (Third frog rescue at Balogunyom). *Cinege* 5: 10-11.
- Kline, N. C. and Swan, D. E. (1998): Quantifying wildlife road mortality in Saguaro National Park. In Evink, G. L., Garrett, P. Zeigler, D. & Berry, J. (eds): *Proceedings of the International Conference on Wildlife Ecology and Transportation (ICOWET)*. Florida Department of Transportation (9-12 February, 1998, Fort Myers, Florida). 23-31.
- Kuhn, J. (1987): Strassentod der Erdkröte (*Bufo bufo* L.): Verlustquoten und Verkehrsaufkommen. Verhalten auf der Strasse. *Beih. Veröff. Naturschutz Landschaftspflege Baden-Württemberg*. 41: 175-186.
- Lalo, J. (1987): The problem of roadkill. *American Forests* (September – October): 50-52.
- Landmann, A., Böhm, C. and Fischler, D. (1999): Bestandssituation und Gefährdung des Grasfrosches (*Rana temporaria*) in Talboden der Ostalpen: Beziehungen zwischen der Grosse von Laichpopulationen und dem Landschaftscharakter (Current status and threats to grass frogs in river valleys of the Austrian Alps: relationship between the spawning populations and landscape structure). *Zeitschrift für Ökologie und Naturschutz* 8(1-2): 71-79.
- Langton, T. E. S. (1989a): Reasons for preventing amphibian mortality on roads. In Langton, T. E. S. (ed): *Amphibians and Roads*. ACO Polymer Products, Shefford, Bedfordshire, UK. 75-80.
- Langton, T. E. S. (1989b): Tunnels and temperature: results from a study of a drift fence and tunnel system for amphibians at Henley-on-Thames, Buckinghamshire, England. In Langton, T. E. S. (ed): *Amphibians and Roads*. ACO Polymer Products, Shefford, Bedfordshire, UK. 145-152.
- Lesbarrés, D., Pagano, A. and Lodé, T. (2003): Inbreeding and road effect zone in a Ranidae: the case of the agile frog, *Rana dalmatina* Bonaparte, 1840. *Comptes Rendus Biologies* 326: S68-S72.
- Linck, M. H. (2000): Reduction in road mortality in a northern leopard frog population. *Journal of the Iowa Academy of Sciences* 107(3): 209-211.
- Lodé, T. (2000): Effect of a motorway on mortality and isolation of wildlife populations. *Ambio*. 29: 165-168.
- Mikátová, B. and Mojžíř, V., 2002. "Ochrana obojzivelniku. Metodika Českého svazu ochránců přírody c. 1.". Cesky Svaz Ochránců Přírody and Ekocentrum, Brno.
- Mitchell, J. C. (2000): Mass mortality of red-spotted newts (*Notophthalmus viridescens* Rafinesque) on a central Virginia road. *Banisteria* 15: 45-47.
- Pounds, J. A. and Crump, M. L. (1994): Amphibian declines and climate disturbance: the case of the golden toad and the harlequin frog. *Conservation Biology* 8: 72-85.
- Proess, R. (2003): Die Amphibienwanderung im oberen Abschnitt der StraBe Bridel-Steinsel (Luxemburg) (Amphibian migration in the upper section of the Bridel - Steinsel road (Luxemburg). *Bull. Soc. Nat. Luxemb.* 103: 93-100.
- Puky, M. (2001): Herpetological methods: I. On the use of the road transect method in surveying amphibians with examples from different zoogeographical regions of Hungary. *Opuscula Zoologica. Budapest* 33: 75-81.
- Puky, M. (2003): Amphibian mitigation measures in Central-Europe. In Irwin, L. C., Garrett, P. and McDermott, K. P. (eds): *2003 Proceedings of the International Conference on Ecology and Transportation*, The Center for Transportation and the Environment, Raleigh, North Carolina (24-29 August, 2003, Lake Placid, New York). pp. 413-429.
- Puky, M., Bakó, B. and Krolopp, A. (1990): A barna varangy vándorlási sajátosságainak vizsgálata (Migration characteristics of the common toad). *Állattani Közlemények*. LXXVI.: 99-104.
- Puky, M., Farkas, J. and Tóth, M. (2005): Amphibian and reptile road kills: importance, frequency, mitigation measures. Fifth World Congress of Herpetology, Abstracts (Stellenbosch, South-Africa. 19-24, June, 2005). 83.
- Puky, M. and Vogel, Zs. (2004): Amphibian mitigation measures on Hungarian roads: design, efficiency, problems and possible improvement, need for a co-ordinated European environmental education strategy. In: *Proceedings of the IENE Conference on Habitat fragmentation due to transportation infrastructure*. Infra Eco Network Europe, Brussels (13-15 November, 2003, Brussels). CD-ROM. 1-13.

- Reh, W. (1989): Investigations into the influences of roads on the genetic structure of populations of the common frog *Rana temporaria*. In Langton, T. E. S. (ed): Amphibians and Roads. ACO Polymer Products, Shefford, Bedfordshire, UK. 101-113.
- Rudolph, D. C. (2000): An overview of the impact of roads on amphibians and reptiles. In Messmer, T. A. and West, B. (eds): Wildlife and highways: seeking solutions to an ecological and a socio-economic dilemma. The Wildlife Society, Nashville. pp. 31-41.
- Rybacki, M. (1995): Zagrozenie plazów na drogach Pieninskiego Parku Narodowego (Threats of amphibians on roads of the Pieniny National Park). Pieniny - Przyroda i Człowiek. 4: 85-97.
- Ryser, J. (1988): Amphibien und Verkehr. Teil 2. KARCH, Bern.
- Ryser, J. and Grossenbacher, K. (1989): A survey of amphibian preservation at roads in Switzerland. In Langton, T. E. S. (ed): Amphibians and Roads. ACO Polimer Products Ltd., London. 7-13.
- Sala, O. E., Chapin III, F. S. and Huber-Sannwald, E. (2001): Potential biodiversity change: global pattern and biome comparisons. In Chapin III, F. S., Sala, O. E. and Huber-Sannwald, E. (eds): Global biodiversity in a changing environment. Scenarios for the 21st century. Ecological studies Vol 152. Springer, New York, Berlin, Heidelberg. pp. 351-367.
- Savage, R. M. (1935): The influence of external factors on the spawning date and migration of the common frog, *Rana temporaria*. Proceedings of the Zoological Society, London. 2: 49-98.
- Schád, P., Puky, M. and Kiss, I. (1999): A Naplás-tó Természetvédelmi Területen élő kétélűek vonulási sajátosságai (Breeding migration characteristics of amphibians at Lake Naplás Nature Conservation Area). Természetvédelmi Közlemények. 8:161-172.
- Scocciati, C. (2001): Amphibia: aspetti di ecologia della conservazione (Amphibia: Aspects of Conservation Ecology). WWF Italia, Sezione Toscana. pp. 428.
- Seburn, D. and Seburn, C. (2000): Conservation priorities for the amphibians and reptiles of Canada. WWF Canada and CARCON, Toronto, Delta.
- Seiler, A. (2001): Ecological effects of roads. A review. Department of Conservation Biology, SLU, Uppsala.
- Seiler, A. (2003): Effects of infrastructure on nature. In Trocmé, M., Cahill, S., de Vries, H. J. G., Farral, H., Folkesson, L., Fry, G., Hicks, C. and Peymen, J. (eds): Habitat fragmentation due to transportation infrastructure. The European review Office for Official Publications of the European Communities, Luxemburg. 31-50.
- Sjögren-Gulve, P. (1994): Distribution and extinction pattern within a northern metapopulation of the pool frog, *Rana lessonae*. Ecology. 75: 1357-1367.
- Slater, F. M. (1994): Wildlife road casualties. British Wildlife. 5: 214-222.
- Slater, F. M. (2002): An assessment of wildlife road casualties – the potential discrepancy between numbers counted and numbers killed. Web Ecology. 3: 33-42.
- Trombulak, S. C. and Frissel, C. A. (2000): Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology. 14: 18-30.
- Tyler, M. (1991): Declining amphibian populations: a global phenomenon? An Australian perspective. Alytes. 9:43-50.
- van Gelder, J. J. (1973): A qualitative approach to the mortality resulting from traffic in a population of *Bufo bufo*. Oecologia. 13: 93-95.
- Vos, C. C. and Chardon, J. P. (1998): Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. Journal of Applied Ecology. 35: 44-56.
- Vos, C. C., Antonisse-De-Jong, A. G., Goedhart, P. W., and Smulders, J. M. (2001): Genetic similarity as a measure for connectivity between fragmented populations of the moor frog (*Rana arvalis*). Heredity 86(5): 598-608.
- Waldman, B. and Tocher, M. (1998): Behavioural ecology, genetic diversity, and declining amphibian populations. In Caro, T. (ed): Behavioural ecology and conservation biology. Oxford University Press, New York. pp. 394-443.
- Wisniewski, A. (2001): Zapora typu "King Frog" chroniaca male zwierzeta w obszarach graniczacych z siecia dróg ("King Frog" type barrier protecting small animals in areas along road systems). Planpol-1, Starachowice, Poland. pp. 16.
- Wolk, K. (1978): Zabijanie zwierzat przez pojazdy samochodowe w Rezerwacie Krajobrazowym Puszczy Bialowieskiej (Road-killed animals in the Bialowieza Nature Reserve). Chronmy Przyrode Ojczyzna. 34: 20-29.