The toll of the automobile: Wildlife and roads in Sweden

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Abstract

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Animal-vehicle collisions are a common phenomenon worldwide, causing injury or death to millions of animals and hundreds of human passengers each year. Collision numbers can be significant to species conservation, wildlife management, traffic safety, as well as from an economic and political point of view, and should thus be evaluated from these different perspectives. In this thesis, I assess, evaluate, analyse and predict animal-vehicle collisions with respect to their extent, their effect on populations, and their broad and fine scale distribution. A questionnaire with Swedish drivers indicated that nationwide road traffic in 1992 may caused an annual loss in harvest of common game species of 7% to 97% and of 1% to 12% of estimated populations. Road mortality did not appear as an existential threat to most species, although in badgers (*Meles meles*), traffic probably is the largest single cause of death. A slow population growth rate coupled with a high proportion of adult badger road-kills is responsible for their sensitivity to road mortality. Provided that road mortality is additive, we predicted that losses due to nationwide traffic might already exceed birth rates and limit badger population growth. In roe deer (*Capreolus capreolus*) and moose (*Alces alces*), road mortality is of minor importance to the population. Broad-scale trends and patterns in collision numbers correlate with harvest and traffic volumes, thus providing a simple means to monitor the toll of road traffic. To predict local collision risks with these species, information on animal abundance and landscape composition, on road traffic parameters, and on the spatial coincidence of roads and landscape elements is needed. However, vehicle speed appeared as one of the most important factors determining collision risks with moose, underlining the influence of human factors on collision risks. Successful counteraction therefore requires an interdisciplinary approach that addresses both the animal and the driver in their shared environment.

Key words: animal-vehicle collisions, fences, impact assessment, infrastructure, mitigation, road planning, traffic mortality, traffic safety.

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In the still of the night or day
There's a thumping sound on the highway
What looked like a river was a road
With headlights for eyes and bumpers for toes
Bozo cruises at full speed ahead
Mr Todd is seconds from dead
Blinded by a flash from heaven
Smashed by heavy metal from hell

Adapted from Arapaho, 1.2 Mile from Eden

Contents

Appendix

Paper I-IV

This thesis is based on the following papers, which are referred to by their Roman numerals.

I. Seiler, A., Helldin, J-O. & Seiler, Ch. Road mortality in Swedish mammals – Results of a drivers' questionnaire. *Wildlife Biology, in press.*

II. Seiler, A., Helldin, J-O. & Eckersten, T. Road mortality in Swedish Badgers (*Meles meles*): Effects on population. *Manuscript*.

III. Seiler, A. Trends and spatial patterns in ungulate-vehicle collisions in Sweden. *Wildlife Biology, in press.*

IV. Seiler, A. Spatial models to predict moose-vehicle collision in Sweden. *submitted to J. Appl. Ecol.*

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Introduction

The impact of transport infrastructure on wildlife receives growing concern worldwide (e.g., Bernard et al. 1987, Canters et al. 1997, Evink et al. 1999, Trocmé et al. 2003). Possible consequences to wildlife have been recognised and there is evidence of direct and indirect effects at both species and ecosystem level (Forman et al. 2003). The physical presence of roads, railways, and canals in the landscape dissects habitats, disrupts natural processes, alters microclimate and groundwater flow, but also introduces new and potentially valuable habitats. Maintenance and operational activities contaminate the surrounding environment with a variety of chemical pollutants and noise. In addition, infrastructure and traffic impose movement barriers to most terrestrial animals and cause the death of billions of animals each year. These various biotic and abiotic effects operate in a synergetic way, locally as well as at a broader scale, leading to a fragmentation of wildlife habitat in a broad sense (Seiler 2003).

Numerous field reports, conference proceedings, reviews, and handbooks have been published on this topic so far (Bernard et al. 1987, Reck & Kaule 1993, Canters et al. 1997, Rosell Pagès & Velasco Rivas 1999, Forman et al. 2003, Trocmé et al. 2003). Nevertheless, there is still need to improve our understanding of the complex pressure of transport infrastructure on wildlife populations and the environment. Authorities urgently ask for adequate methods to predict, evaluate, and counteract adverse effects, and implement this knowledge into the planning and maintenance of transport infrastructure in order to meet sector-level policies on sustainable development and conservation of biodiversity (Eriksson & Skoog 1996, Westermark 1996, Iuell et al. 2003). Mitigation concepts are needed that operate at both strategic and project planning level and can affect the underlying causes as well as the resulting effects and consequences to populations and society (Pettersson & Eriksson 1995, Canters et al. 1997, Cuperus et al. 1999). In many cases, dose-effect relationships need to be quantified and potential thresholds identified, before adequate mitigation can be chosen and eventually implemented. Existing ecological knowledge must be combined with economical and social sciences to achieve a holistic approach that allows the whole range of ecological factors operating across the landscape to be integrated within the planning process (Seiler & Eriksson 1997, Damard 2003). This does not apply solely to the planning of transport infrastructure, but likewise to all exploitation and management of natural resources.

A recent tool to describe, analyse, and manage human impacts on the environment and its consequences to environmental quality is the so called DPSIR framework (Luiten 1999, Anonymous 1999). It helps to distinguish causal linkages between driving forces (D) such as policy or economy, their pressure (P) to environmental state (S) and the impact (I) on wildlife and society that initiates a response (R) in policy or legislation affecting the 'driving forces' or providing direct feed-back to the sources of 'pressure' (Figure 1). The DPSIR approach has found ample appliance in environmental monitoring and management in Sweden (e.g., Anonymous 1999, Segnestam & Persson 2002). However, the problem still remains to define adequate indicators that help to quantify pressures and impacts.

No such indicators have yet been implemented to tackle habitat fragmentation caused by transport infrastructure or measure the overall ecological impact of roads and railways on wildlife; proposals have been made however (e.g., Westermark 1996, Damard et al. 2003).

It is within this context that the present thesis and its four papers should be viewed. In this thesis, I have chosen to focus on the problem of animal-vehicle collisions, although this issue is only one among several, and certainly not even the most important pressure of transport infrastructure on wildlife. However, it is easily monitored and can be evaluated in a quantitative way as required for the development of indicators. It is also intimately linked with other direct effects of infrastructure such as barrier and disturbance effects, and it relates to both animals (road mortality) and humans (traffic safety) (e.g., Seiler 2003).

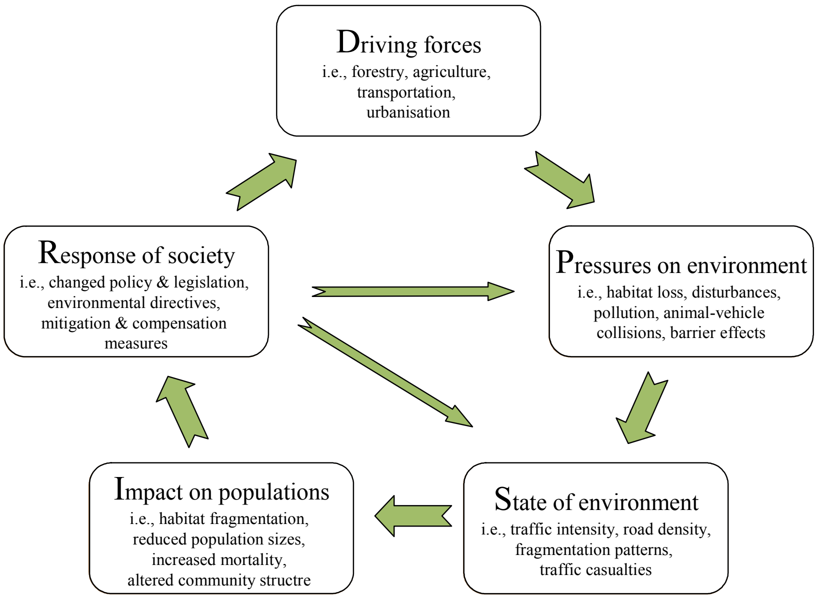

Figure 1. Schematic representation of the causal links within the DPSIR framework.

In the following, I first discuss the extent of animal-vehicle collisions and present new estimates of the number of road-killed mammals in Sweden. This knowledge is crucial for the evaluation of mitigation needs. Evaluating animal-vehicle collisions can and must be done from different perspectives including ecological, economical, ethical, and political viewpoints. I discuss these different perspectives, with special emphasis on ecological aspects, and conclude that for the most part economic and traffic safety concerns will be more stringent and conservative. If the problem is considered significant and counteractive measures are required, for whatever reason, more effort is needed to analyse what factors determine the spatial and temporal distribution of animal-vehicle collisions. I present analyses of trends and spatial patterns in ungulate-vehicle collisions, at both broad and local scales. Finally, I discuss two major mitigation options and their efficacy in reducing the likelihood of collisions with moose.

These steps are represented by the papers included in this thesis:

I. In paper I, we present new estimates of the magnitude of road mortality in some medium-sized and large mammals in Sweden, based on the results of a drivers' questionnaire. In the questionnaire, we asked drivers to estimate the total mileage they had driven and the number of collisions with wild mammals larger than mice with which they were personally involved as drivers during a period they were free to choose, but for which they were confident that they could remember any incident. By summarizing the driven mileage and the number of collisions reported by all respondents, we calculated a frequency of collisions that could be extrapolated to a national level. Although the sample size was limited (705 replies with 343 collisions), and the reported number uncertain, the estimates were surprisingly concordant with independent statistics on, e.g., police reported ungulate-vehicle collisions and earlier road-kill studies. For most species included in our survey, the level of road mortality did not appear as a threat to the nationwide survival of the species. In badgers (*Meles meles*), however, estimated road-kill was considerably larger than previously assumed. In addition, the ratio of road-killed to hunted animals appears to increase in several species, suggesting that the relative importance of road traffic has risen during the past decades. Our results further suggest that drivers' questionnaires can be a practical and inexpensive way of monitoring animal-vehicle collisions at broad scale.

II. In paper II, we evaluated the significance of road mortality to a selected species, the badger, and estimated the critical level of road mortality that a badger population can sustain without decline. Nationwide road kill estimates for badger (paper I) were significantly higher than previously assumed and road traffic is probably the largest single cause of death in this species. We used life table analysis and matrix population models to assess a stable age-structure and population growth. Demographic parameters among road-killed badgers were estimated from literature and from 76 carcasses that we collected from public roads. Our population models suggested that losses due to road traffic account for 12-13% of the post-breeding population, which is close to the maximum sustainable loss. Assuming the number of road-killed badgers is proportional to traffic intensity, we predict that between 1978 and 2049 nationwide road traffic will kill more badgers than the population can sustain without declining. In other words, this critical threshold may already be passed in areas of low badger density and high traffic loads. We recommend showing greater concern for this species when planning and maintaining roads in such areas.

III. In paper III, I investigated the influence of traffic and population density on trends and spatial patterns in ungulate-vehicle collisions. Naturally, for a given species, collision numbers should be a function of the abundance of vehicles and animals, although this relationship may not necessarily be linear. I could show that during the past 30 years in Sweden, changes in collision numbers were strongly related to changes in annual game bags and traffic intensity. With increased resolution, however, other environmental factors such as land cover, road density, and the presence of mitigation measures gained significance over the density of ungulates and vehicles. Spatial patterns were studied at the level of individual hunting areas (N=311), moose management districts (N=95), and counties (N=22), whereas trends in ungulate-vehicle collisions (UVC) were studied at national, county, and district level covering periods of 30, 16, and 12 years, respectively. Thus, prediction and evaluation of ungulate-vehicle collisions are scale-dependent, whereas large-scale relationships do not necessarily apply at local scales. To develop spatially explicit models, improved knowledge about passage design, fence location, and occurrence of UVC in time and space is needed.

IV. In paper IV, I developed logistic regression models to predict the risk for vehicle collisions with moose (*Alces alces*) on public roads based on remotely sensed landscape data, road and traffic statistics, moose harvest as an index of population densities, and collision statistics from 1990 to 1999. I quantified environmental data from 2000 accident and 2000 non-accident control sites in south-central Sweden (mainly the county of Östergötland) and tested the predictions on 2600 one-km road sections classified as either accident or non-accident roads in the county of Örebro. Traffic volume, vehicle speed, and the occurrence of exclusion fences appeared as the dominant road-traffic factors determining collision risks, identifying 72.7% of all accident sites. Within a given road category, however, the amount of and distance to forest cover, density of intersections between forest edges, private roads and the main accident road, and moose abundance indexed by harvest statistics significantly distinguished between accident and control sites. In combination, road-traffic and landscape parameters produced an overall concordance in 83.6% of the predicted sites and identified 76.4% of all test road sections correctly. The risk of moose-vehicle collisions in Sweden can thus be predicted from remotely sensed landscape data in combination with road traffic data. Combining road fences with designated wildlife passages, increased roadside clearance, and reduced vehicle speed may provide the most effective mitigation measures against collisions with moose.

A natural continuation of these studies will be the analysis of spatio-temporal patterns in collisions. How does season, weather, or daylight influence effects of habitat, topography, and latitude on the occurrence of collisions? Traffic flow, animal abundance, and animal activity fluctuate at diurnal and seasonal intervals, as do records of animal-vehicle collisions (e.g., Lavsund & Sandegren 1991, Groot-Bruinderink & Hazebroek 1996, Gundersen & Andreassen 1998). It is possible that the patterns studied in paper III and IV will become even clearer if their actual timing is considered.

The extent of animal-vehicle collisions

The ‘toll of the automobile’ (*sensu* Stoner 1925) is certainly the most widely acknowledged effect of transport infrastructure on wildlife. Since the appearance of the automobile, road and railway kills of wildlife have been of public concern (Stoner 1925, Dickerson 1939, Haugen 1944, McClure 1951, Hodson & Snow 1965, Way 1970, Jonkers & De Vries 1977, Hansen 1982, Lalo 1987, Van den Tempel 1993, Caletrio et al. 1996, Rodts et al. 1998, Huijser 2000, Forman et al. 2003). Road-killed fauna includes a widespread variety of terrestrial animal species, regardless of whether it has a backbone, wings, or legs. Smashed and flattened animals alongside roads or railways have become part of the common experience of humans around the world, and are probably seen by many more people than their living conspecifics (e.g., Knutson 1987). The numbers of casualties appear to be steadily growing as traffic increases and infrastructure networks expand. In their review, Forman & 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’.

The pure numbers of road kills may illustrate the extent of the problem. National road-kill estimates range from some hundred thousand to some hundred million casualties each year (Table 1). Fortunately, only a small fraction of all animal-related traffic accidents cause human injury or death (Seiler & Folkeson 2003). For the involved animals, however, collisions with vehicles are usually fatal. For example, approximately 92% of all moose and 98% of all roe deer involved in police-reported vehicle collisions in Sweden ultimately died as a consequence of an accident (Almkvist et al. 1980). In smaller, slower species, this percentage is likely much higher (Table 1).

Unfortunately, most national road-kill estimates are not related to road density, traffic work (driven mileage), or animal density. In addition, most estimates are extrapolations of rather limited data (but see Caletrio et al. 1996, Rodts et al. 1998) obtained by field inventories, drivers’ interviews, or expert estimates. Due to differences in quality and uncertainties in these numbers, a quantitative comparison among countries is likely not feasible.

In many countries, statistics on vehicle collisions with large ungulates (UVC) provide the most detailed and extensive road kill estimates, because accidents with these species often involve material damage and considerable risk of human injury. In the United States, it was estimated that more than a half million collisions with deer (*Odocoileus* spp.) occurred in 1991 (Romin & Bissonette 1996). Within Europe (excluding Russia), approximately 500,000 UVC are recorded each year, with Sweden contributing the greatest number of UVC per year, followed by Austria and Germany (Groot-Bruinderink & Hazebroek 1996). The conflict between ungulates and vehicles in Sweden was highlighted already during the late 1960’s (Anonymous 1971), when UVC accounted for 19% of all police reported road accidents. In recent years, this percentage has exceeded 60% and UVC records amounted to over 5,000 moose, 25,000 roe deer (*Capreolus capreolus*), 2,000 reindeer (*Rangifer tarandus*), and approximately 1,000 other ungulates each year (paper III, Lavsund & Sandegren 1991). This increase coincided with a doubling in traffic volume since 1970, but more important for trends and large-scale spatial patterns in UVC was the increased abundance of moose and roe deer (paper III).

Table 1. *Estimates of annual nationwide road kills in wildlife, as obtained from field inventories or drivers enquiries.*

Species	Road kills *	Country	Year/Period	Reference
vertebrates	365	USA	1960's	Humane Society 1960, in Lalo 1987
	100	ES	1990's	Caletrio et al. 1996
	6.5	FI	2002	Manneri 2002
	4.0	BE	1994	Rodts et al. 1998
birds	8.5	SE	1998	Svensson 1998
	5.0	BL	1983	Mankinov & Todorov 1983
	4.0	UK	1966	Hodson 1966
	3.7	DK	1981	Hansen 1982
	2.5	UK	1965	Hodson & Snow 1965
	2.0	NL	1993	Tempel 1993
	1.0	SE	1970's	Göransson et al. 1978
	0.6	NL	1977	Jonkers & De Vries 1977
birds & mammals	2.0	CAN	1970's	Oxley & fenton 1976
large & medium sized mammals	1.5	DK	1980	Hansen 1982
	0.5	SE	1970's	Göransson et al. 1979
	0.2	NL	1977	Jonkers & De Vries 1978
amphibians	5.0	AUS	1983	Ehmann & Cogger 1983, in Bennett 1991
	3.0	DK	1982	Hansen 1982
ungulates	0.5	USA **	1991	Romin & Bissonette 1996
	0.5	EU	1995	Groot-Bruinderink & Hazebroek 1996
	0.004	F	1990's	SETRA 1998
	0.002	ES	1992	Fernandez 1993

** in millions per year, nationwide*
*** only deer (Odocoileus spp.)*

However, official accident statistics systematically underestimate the true number of ungulate-vehicle collisions, because not all collisions are detected by the driver, reported to the police, or registered by the Swedish National Road Administration (SNRA) (Almkvist et al. 1980). Studies during the 1970's suggested that about 25% of all UVC with human injury involved and approximately 60% of all other UVC were not filed by SNRA. Collisions with moose on highways seemed more likely to be recorded than collisions with roe deer on county roads. However, this pattern was not conclusive and the authors recommended assuming a standard proportional loss of 60% (Almkvist et al. 1980). Thus, the true number of UVC occurring in Sweden may be at least twice the size as suggested by official statistics (paper I).

In Sweden, little is known about vehicle collisions with other species than ungulates. Early studies on wildlife road casualties date back to the 1960's (Bengtsson 1962) and 1970's (Bolund 1974, Göransson et al. 1978). Initial national road kill estimates ranged from 550,000 to 20 million wild animals per year (Bolund 1974). More accurate estimates were obtained by Göransson et al. (1978) who conducted intensive inventories along roads in south-central Sweden. They suggested nationwide mortalities may reach a minimum of 1.0 million birds and 0.5 million medium-sized mammals (excluding small mammals and ungulates) annually. For most species, road mortality was considered being within tolerable limits, accounting for less than 5% of the assumed population size. Since this study, however, traffic intensity has increased by approximately 50%, the length of motorways has doubled (Anonymous 2000), and numbers of UVC increased fourteen-fold (paper III). It is, therefore, reasonable to believe that road mortality has also increased in other species. A recent estimate on avian road-kills, for example, suggested as many as 8.5 million birds casualties on Swedish roads in 1995 (Svensson 1998). This is eight times greater than suggested by Göransson et al. (1978).

Road kill questionnaire

We obtained updated information on animal-vehicle collisions in Sweden (paper I). During 2000 and 2001, we sent out a questionnaire to Swedish car drivers, asking them to estimate the number of animals per driven mileage they had collided with during a specified time. A total of 705 drivers' reports could be evaluated, covering 243.6 million travelled km from 1960 to 2000. The reports suggested a total loss of between 7,000-13,500 moose, 43,500-59,000 roe deer, 63,500-81,500 hares (*Lepus* spp.), 22,000-33,000 badgers, and 6,500-12,500 foxes (*Vulpes vulpes*) during the mean reference year 1992 (paper I, Table 3). Among these game species, the extrapolated nationwide road-kill ranged between 7% and 97% of the average annual harvest, and between 1% and 12% of the assessed total populations in 1992. The frequency of road-kills appeared to have increased over the past 40 years, probably because of changes in traffic volume and population sizes (harvest) (Figure 2). However, in badgers and hares, the ratio of estimated road-kill to the annual harvest increased two-fold, which suggests an increase in the relative importance of road mortality. If the relationship between road-kill frequency and traffic volume is constant, and density of animals the similar to 1992, then road traffic in 2002, for example, may kill up to 15,000 moose, 64,500 roe deer and 36,500 badgers.

Of course, the uncertainty in these estimates is large and there is also risk for bias in the reported accidents, but the results are concordant with independent estimates on animal-vehicle collisions and well in line with official UVC statistics if adjusted for the 60% unregistered accidents (paper I). Our study suggested that driver interviews can be a cost-efficient source of information on road kills at least for larger wildlife. Provided that road networks are extensive, traffic volumes quantified, and data on animal-vehicle collisions can be obtained in a standardized way, our study suggested that driver interviews can be a cost-efficient source of information on road kills at least for larger wildlife. Crucial to such assessment is, however, control of the large bias that can be expected due to differences in drivers remember collisions with wildlife, are reliable in their identification of the species, and are willing to report the true number of incidents. We recommend therefore to use standardized and shortened reference periods (for example one year), and exact estimates of the driven mileages. Such data could be obtained for example during the annual safety inspections on motor vehicles made by the Swedish Motor Vehicle Inspection Company (Svensk Bilprovning AB).

In extension to our data, we agree with several other researchers (Jahn 1959, McCaffery 1973, Göransson & Karlsson 1979, Hicks 1993, Loughry & McDonough 1996) who recommended using road-kill indices for the monitoring populaitons of large and medium sized mammals that eventually might be superior to harvest statistics.

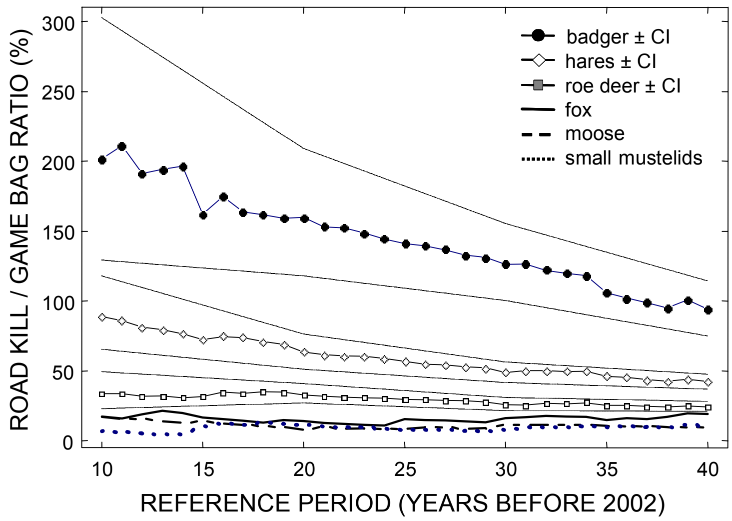

Figure 2. Change in the ratio between estimated road kill in Sweden (with 95% confidence limits) and annual harvest in relation to the length of reference periods covering the past 40 years (1960 – 2000). In badgers (*Meles meles*) and hares (*Lepus* spp.), the ratio increased two-fold as the maximum number of reference years was limited from 40 to 10 years (paper I, Figure 1).

Although this thesis deals exclusively with animal-vehicle collisions on roads, one should also bear in mind that railway traffic also kills a hitherto unknown but certainly large number of animals each year (Seiler & Folkeson 2003). Radio-telemetry studies on over 400 moose from 4 regions in Sweden suggest that trains may account for up to half of all traffic related mortality in moose populations (K. Wallin & G. Cederlund, unpubl. data). Thus far, Swedish rail authorities have not granted permission to conduct inventories of train-animal collisions, but since the year 2000, train engineer reports on animal-related issues are filed by the Swedish Rail Administration. Preliminary analyses of these first statistics suggest that trains may kill at least 1,000 roe deer and 900 moose each year (my wife, pers.

comments). In the northern rail district, approximately 5 moose are killed annually per 100 km railway, with peak rates during winter (Johansson & Larsson 1999). For comparison, car traffic on public roads in northern Sweden causes less than 3 moose casualties per 100 km and year (SNRA, database). However, it is unknown to what degree official reports represent the true number of animal kills and whether this relationship applies to species other than moose and roe deer.

Evaluation of animal-vehicle collisions

The amount of road mortality is staggering indeed, but is this toll really significant and always worthy the costs of mitigation? Evaluating the importance of animal-vehicle collisions is a complex task and must involve ecological, economical, social, and technical perspectives and consider both regional and local scales (Figure 3). For example, animal-vehicle collisions may be insignificant for the conservation of larger herbivores, but may still conflict with harvest management goals or even be unacceptable for traffic safety reasons. On the other hand, collisions with smaller species such as amphibians may be substantial to the survival of local populations but receive lesser public concern than accidents with ungulates. National estimates of road mortality in wildlife may appear negligible, but the local impact may be considerable.

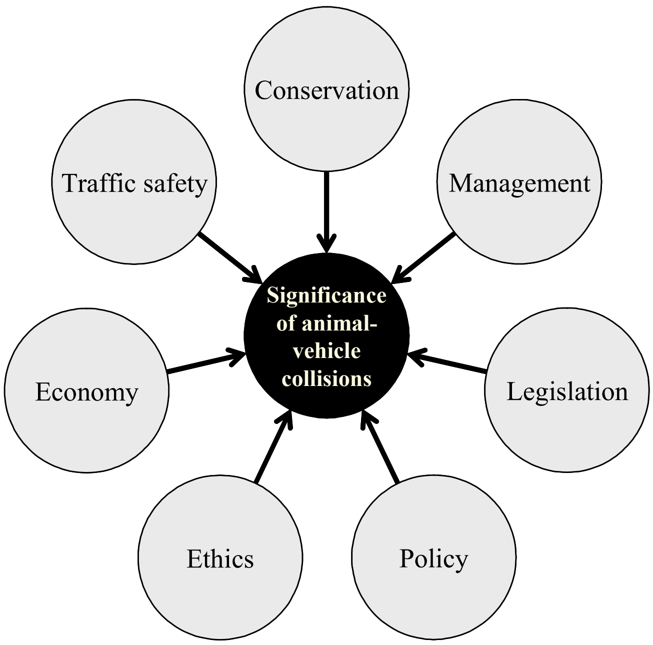

Figure 3. Different perspectives from which animal-vehicle collisions can be evaluated.

How great a loss can a species cope with? How great an impact are we willing to accept? There are no simple rules or thresholds defined thus far that could guide decision-making, but in many cases, it is probably a political issue rather than a biological problem, to determine whether the extent of animal-vehicle collisions is critical and counteraction necessary or not.

Human perspective

Political, ethical, and legal aspects

From an animal welfare point of view, any collision between wild animals and motor vehicles is troublesome because it causes unnecessary and partially avoidable suffering and damage to the animal involved (e.g., Sainsbury et al. 1995, Fehlberg 1994). Smaller animals probably suffer less as they die immediately upon impact, but the larger the animal, the greater is the proportion of wounded survivors. In Sweden, for example, Almkvist et al. (1980) documented that about 25% of all roe deer but 64% of all moose involved in police reported vehicle collisions were not killed immediately but died later or had to be tracked down and shot because of their injuries. The true proportion of injured ungulates is certainly much higher, because collisions that are not perceived as serious by the driver (although the animal may suffer internal injury) may not be reported to the police.

The risk to collide with wild animals on roads or railways worries many people in Sweden (e.g., Johansson & Larsson 1999). Many respondents to our road kill enquiry (paper I), for example, expressed concern for animals they injured but were not killed. Especially collisions with large mammals can be traumatic to the driver (if not hazardous). The European public is generally more concerned about killing and injuring wildlife than about habitat destruction or air pollution (Kirby 1997). Nonetheless, there is better legal protection for the physical environment than for the welfare of organisms living within. Animal protection laws at a European level, as well as in Sweden (Animal Welfare Act, 1988:534), make it an offence to cause unnecessary suffering in captive or domestic but not in free-living animals. Only Norway and Finland provide legal protection for the welfare of wild animals (Norwegian Animal Welfare Act (Code: 750.000, 16.06.95), Finnish Act on Animal Protection (247/1996)). Sainsbury et al. (1993) illustrated this inconsistency in a large number of cases across the European Community, where the welfare of wildlife had been compromised due to human activities, including collisions with vehicles and hunting activities. The authors developed a methodology for the assessment of wildlife welfare (Kirkwood et al. 1994) and suggested it to be integrated in environmental impact assessment (EIA). However, resistance to include welfare of wildlife under legal protection is strong, as it may have considerable consequences to e.g., hunting and fishing practises and recreational land use.

In European policies and directives, the issue of animal-vehicle collisions is instead considered as part of the ecological problem of habitat fragmentation caused by transport infrastructure (e.g., OECD 1994, Trocmé et al. 2003). The European Strategic Environmental Impact Assessment (SEA) Directive

(2001/42/EC) enforces the integration of ecological aspects in future planning and programming of infrastructure. Recently, a new 'Code of Practice for the Incorporation of Landscape and Biodiversity in the Planning of Linear Transport Infrastructure' has been developed by the European Council for endorsement in 2003 that includes recommendations for integration of the Pan-European Biological and Landscape Diversity Strategy in environmental impact assessment (Damard et al. 2003). Habitat fragmentation issues (including road mortality) are also considered in the new environmental goals for the transport sector in Sweden (Eriksson & Skoog 1996, Westermark 1996, Seiler & Eriksson 1997). However, these policies consider the survival of a species and the maintenance of biodiversity, rather than the welfare of individual animals.

Traffic safety and economical concern

In most countries, traffic safety and economy are the driving forces behind mitigation efforts against animal-vehicle collisions (e.g., Hartwig 1991, Romin & Bissonette 1996, Putman 1997, Trocmé et al. 2003). This occurs even though the total socio-economic costs are systematically underestimated, central statistics are often incomplete, and the usual assessment methods inadequate (Borer & Fry 2003). In most European countries, animal-vehicle collisions are believed to make up only a small proportion of the total number of traffic accidents. In The Netherlands, for example, only 0.3% (29 out of 11,124) reported accidents involving personal injury or death were due to animals (Borer & Fry 2003). This contrasts the situation in Sweden where about 8% of all road accidents that involved human injuries or deaths and more than 60% of all police reported road accidents were due to collisions with ungulates (paper III). Of course, there is a direct relationship between the seriousness of collisions with animals and the size of the animals involved. The larger the species, the greater is the risk for material damage and human injury. Indeed, moose are among the most dangerous animals in Sweden, on average about 12 humans are killed and more than 600 are injured in collisions with ungulates annually, most of which (78%) included moose. Its tall shoulder height and heavy body weight can result in collisions where the whole body mass of the animal strikes directly against the windshield pillars and the front roof of the vehicle. Such accidents can cause severe head and neck injuries to front seat passengers (Björnstig et al. 1986).

The SNRA calculates an average direct cost of between 7,400 and 20,000 € per moose-vehicle collision, but only between 1,400 and 2,800 € per collision with roe deer or reindeer, depending on the speed of the vehicle and the severity of the human injury (Seiler & Folkeson 2003). Annually, the direct cost of ungulate-vehicle collisions in Sweden probably exceeds 100 million € (paper III), while in Norway, annual costs for about 1,200 recorded moose-vehicle collisions sum up to 11-17 million €. An average moose accident has been evaluated to 9,100 or 14,400 €, depending on whether only the material damage to the vehicle or also the cost to moose management is included (Stikbakke & Gaasemyr 1997). At the European level (excluding Russia), vehicle collisions with ungulates have been estimated to exceed half a million incidents each year, including 300 human fatalities and 30,000 injuries, producing a total cost of more than 1 billion € (Groot-Bruinderink & Hazebroek 1996).

Such economic estimations usually include costs for material damage, and human injuries and fatalities, but rarely account for "external" costs such as loss of meat or hunting opportunities, call-out costs for veterinarians, gamekeepers and police to deal with injured or dead animals, costs for ambulances and any subsequent human medical costs, or societal costs of traffic delays. Understanding the external costs of animal-vehicle collisions is crucial when assessing the monetary value of mitigation measures - and the funds that should be made available for further research or mitigation measures (Borer & Fry 2003). Estimations made thus far are unsatisfactory and hardly applicable in road planning. With increasing internalization of external costs in the transport sector and increasing constraints on public spending, there is a strong need to improve economic models and methods for evaluating nature and wildlife (e.g., Cedermark & von Koch 2000).

Ecological perspective

Species conservation and population management

Despite the huge numbers of road-kills occurring each year, road traffic likely has not yet had a significant effect on survival or management of most small and common wildlife species. In rodents, rabbits (*Oryctolagus cuniculus*), foxes, and many song birds that often dominate road-kill statistics, traffic usually contributes less than 5% to the overall (direct) mortality (Haugen 1944, Vestjens 1973, Adams & Geis 1973, Bergmann 1974, Oxley et al. 1974, Schmidley & Wilkins 1977, Göransson et al. 1978, Caletrio et al. 1996). Instead, high numbers of road kills may instead indicate that species are abundant and widespread. Road kill statistics may even be more reliable than hunting statistics in reflecting large scale trends in game species (paper III).

Also in most game species, road mortality is not considered a conservation problem (Groot-Bruinderink & Hazebroek 1996). Still, traffic losses should be considered in harvest goals and should reduce maximum sustainable yield to a hunter, if management strategies aim to balance game populations against environmental, social, and economic constraints. Moose population dynamics, for example, are mainly regulated through hunting (Cederlund & Markgren 1987, Sylvén et al. 1987, Sylvén 2003). Road kills in moose account for approximately 10% of the annual harvest or 3-5% of the total population (paper I, III). This loss is considered ecologically sustainable and economically acceptable, at least at a national level (Lavsund & Sandegren 1991). However, since road kills in Sweden are usually not included in ordinary moose licenses of an area, the planned harvest does not compensate for traffic losses and in certain hunting districts, more moose are eventually killed by vehicles than shot by hunters (paper III, see also Schwartz & Bartley 1991, Child 1998). In Norway, for comparison, traffic mortality is considered in moose management plans, which aim to keep the ratio of traffic losses to harvest below 4% at a national and 10% at a municipal level (Stikbakke & Gaasemyr 1997).

Nevertheless, there is evidence for a significant effect of road mortality on certain wildlife populations including some rare species (e.g., Forman et al. 2003).

For instance, traffic is especially dangerous to herpetofauna (Blaustein & Wake 1990, Hels & Buchwald 2001). Road density has a proven negative effect on survival and recruitment of amphibian populations and the risk for local extinctions increases with proximity of breeding ponds to well-travelled roads (Sjögren-Gulve 1994, Fahrig et al. 1995, Vos & Chardon 1998). Traffic losses can be significant to population recruitment in several large mammals such as Florida panther (*Felis concolor*) (Harris & Scheck 1991, Foster & Humphrey 1995) and Florida Key deer (*Odocoileus virginianus clavium*) (e.g., Calvo & Silvy 1996), Iberian lynx (*Felis pardina*) (Rodriguez & Delibes 1992), as well as European badger in The Netherlands (Van der Zee et al. 1992, Wiertz 1993). Other well-known examples of species heavily affected by road traffic include hedgehog (*Erinaceus europaeus*) (Reichholf & Esser 1981, Holsbreek et al. 1999, Huijser 2000), otter (*Lutra lutra*) (Madsen 1990, Philcox et al. 1999), barn owl (*Typo alba*) (Newton et al. 1997) and several other birds of prey (Van der Zande et al. 1980, Van den Tempel 1993).

Many questions arise concerning animal-vehicle collisions. For example, what distinguishes species that are vulnerable to road traffic from those that are not? When does road mortality become a threat to the survival of a species or its management? Finally, how great a loss of individuals should be tolerated politically or ecologically?

To evaluate the significance of road mortality (like any other mortality factor) from an ecological standpoint, it should be studied in the context of population demography, considering sex- and age-specific mortality and fecundity rates. As a rule of thumb, the larger the percentage of road kills on all deaths, the more likely traffic is a 'key factor', unless road mortality is compensated for by increased survival or fecundity of the remaining individuals, or mainly affects the already 'doomed surplus' (Southwood & Henderson 2000). However, most mortality factors, including traffic, are neither completely compensatory nor completely additive. Therefore, the percentage of road kills may eventually produce a misleading picture. Similar to the assessment of a maximum sustainable harvest in game or fish (Robinson & Bodmer 1999, Sutherland 2001), estimation of an ecologically 'sustainable' level of road mortality should relate to population growth rather than to the size of the population or the proportional kill. A 'sustainable' loss takes the interest in population growth and does not affect the population capital, i.e., the population size. The higher the growth rate, the larger a loss can be sustained without changes in population density. If population growth rate is already close to stationary, however, even a small uncompensated increase in mortality can be significant and provoke a decline of the population (e.g., Caughley 1994).

Thus, species that are sensitive to road mortality are typically slow reproducing (low growth rate) and long-lived, whereas species that are most exposed to road traffic are wide-ranging or migratory animals with little or no habitat specialisation (Verkaar & Bekker 1991, Forman et al. 2003). These behaviours and life history traits are typical for many medium to large carnivores, and include the European badger (Neal & Cheeseman 1996).

Effect on badger population dynamics

Badgers are common throughout Europe (Griffiths & Thomas 1993), and can adapt to a variety of environments, such as arid subtropics (Pigozzi 1991, Rodriguez & Delibes 1992) or cold boreal habitats (Lindström 1989). They are opportunistic in their search for food, and collect rather than hunt their prey, which, at least in low-productive habitats, links them to agricultural areas and human settlements, and inevitably, roads. Badgers can range over large areas, especially in low density habitats (Seiler et al. 1995, Rodriguez et al. 1996), and are hardly cautious when crossing roads, possibly because they have few natural enemies and a limited visual sense (Neal & Cheeseman 1996). In addition, badgers are slow reproducing, exhibit delayed implantation, and live in social clans where subordinate females may not be allowed to reproduce (e.g., Neal & Cheeseman 1996). With their small litter sizes, late maturation, and low adult mortality, badgers resemble more of a large carnivore than the medium-sized opportunist they are considered (e.g., Anderson & Trewhella 1985). Badger population dynamics are atypically 'slow' (Heppell et al. 2000) compared to ecologically similar species such as red fox, raccoon (*Procyon lotor*), or raccoon dog (*Nyctereutes procyonoides*).

Not surprisingly, road traffic is a major source of mortality in badgers across Europe (Griffiths & Thomas 1993), and in The Netherlands, road traffic is held responsible for a nationwide decline during the 1980's (Van der Zee et al. 1992). Reported badger road casualties in The Netherlands during the early 1990's accounted for 10-16% of the summer population, but the total loss, including unreported accidents and death of juveniles that lost their mother on a road, probably exceeded 25% (Bekker & Canters 1997), which is more than 50% of the annual reproduction (Lankester et al. 1991). In the United Kingdom, local declines in badger populations have been attributed to increasing traffic (Clarke et al. 1998), where road casualties probably amount to over 50,000 individuals annually or 20% of the total British population (Harris et al. 1991, Neal & Cheeseman 1996). Also in Denmark (Aaris-Sörensen 1995), Spain (Revilla et al. 2001) and Sweden (paper I), road traffic is a major source of mortality, killing between 10-20% of badger populations annually.

We evaluated the effect of road mortality on badger population dynamics in Sweden by estimating a maximum road-kill that the Swedish population can sustain without declining provided that road mortality is entirely additive (paper II). We simulated population dynamics in an age-specific model based on published estimates on fecundity and mortality (Ahnlund 1980). The model suggested an almost stationary growth rate in the Swedish badger population. Harvest statistics over the past two decades seem to support this finding (Swedish Association for Hunting and Wildlife Management). To measure the effect of road mortality on population growth rate and estimate the total number of road kills, we simulated population dynamics under roadless conditions, assuming that no badgers would be hit by cars keeping all other mortality factors constant. For this calculation, we needed information on the contribution of road traffic to the overall mortality in badgers and data on age and sex ratios among road kills. Estimates of road mortality derived from two independent mark and recapture studies suggesting that between 36% and 50% of all deaths might be due to road traffic. A sample of 76 road-killed badgers collected from public roads during 2001 and literature data (Ahnlund 1980) indicated a strong bias in age structure towards adults (Figure 4), but no difference in sex ratio or fecundity was found between the road-killed and modelled (living) populations. Through reducing mortality rates with the age-specific contribution of road traffic, we observed that population growth would increase by 18-22% from the base-line population model. The results suggested a 'maximum sustainable' loss of 12-13% of the living population, a proportion that is close to the nationwide road-kill estimated from driver' interviews in paper I. Although badgers are numerous in Sweden, and traffic intensity is low compared to other European countries, the present level of road mortality in badgers may thus be substantial. Even though some compensation of road mortality will occur, we conclude that nationwide road traffic is probably close to the limit that the Swedish badger population can sustain without declining. Especially in poorer habitats, such as the boreal coniferous forest, population growth may already be limited by road mortality, whereas in areas with traffic loads above average, road traffic probably surpasses hunting as the leading cause of death in badgers. Bear in mind, however, that there is reason to assume substantial regional variations related to habitat quality and traffic intensity. For the protection of badgers, we recommend increased efforts on counteracting measures such as fences and 'badger tunnels' (e.g., Bekker & Canters 1997) to reduce badger road mortality in the most critical areas.

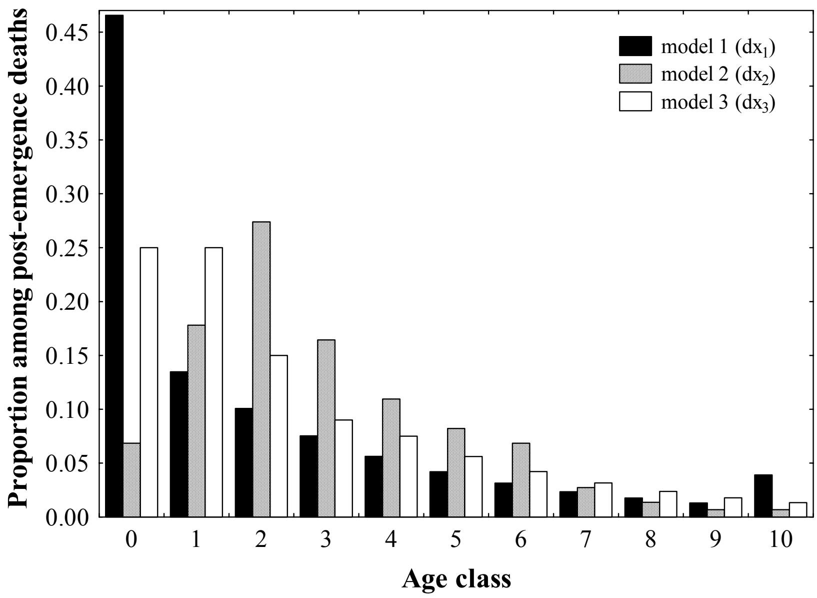

Figure 4. Proportions of badgers dying during age x as obtained from model 1 assuming age independent road mortality (dx_1) and from samples of road-kills from model 2 (dx_2) and model 3 (dx_3; Ahnlund 1980a). All age distributions are significantly different from each other, but the road-killed samples were biased towards a higher proportion of adults and fewer juveniles than expected from the base-line model (compare to paper II).

An important assumption in our model, however, is that the effect of road mortality is entirely additive and not compensated by increased survival or fecundity of the remaining individuals. In the real world, of course, compensation occurs to a certain degree. For example, badger hunting in Sweden is not regulated through hunting quota or aiming at a certain quantitative harvest goal. Badger hunting is a sport rather than a harvest or management tool. Thus, annual harvest is probably linked to badger abundance and thereby indirectly influenced by road mortality, i.e., the more badgers that are killed by cars, the fewer can be trapped by hunters. If this applies, road and hunting mortalities are compensatory and the critical level of road mortality will be higher than suggested by our model. In its extreme, if all hunting would be prohibited, road traffic could kill about twice as many badgers as we assume are killed at present.

On the other hand, collections of road-kills not always provide a representative sample of the living population (see also Jahn 1959, Hodson & Snow 1965, Dixon et al. 1996, paper II). Males or dispersing subadults may be more active and thus more often encounter roads than females or stationary individuals. Young and inexperienced animals may be less cautious with traffic, and old and weak animals slower in their reactions to approaching vehicles than prime-aged individuals. We observed that the sex ratio among road-killed badgers was skewed towards a higher proportion of females in spring and males in autumn/winter. This probably reflects differences in activity and mobility associated with nursing and mating behaviour (e.g., Jefferies 1975, Anderson & Trewhella 1985, Van Apeldoorn 1997). In addition, the proportion of adult badgers among road kills was significantly higher than expected from the modelled living population. If these individuals were primarily subdominants or dispersers, their chances of survival as well as their fecundity might be smaller than compared to other adults. In dense populations, the loss of these individuals would have only little effect on population growth. Under poorer conditions and in small, low-density populations, however, their relative contribution to population recruitment is pronounced. Also, female mortality in spring is of particular importance to badger populations because at this time of year, cubs are still dependent on their mother and most adult females are already pregnant. Thus, the loss of a single adult female in spring thus can strike three generations in one blow.

Thus, there is reason to believe that road mortality in badgers is partly compensatory; however, the effect probably varies with habitat quality and population density. In boreal (poor) environments and close to the northern edge of their distributional range, badgers may be relatively more sensitive to road traffic than their conspecifics from dense populations and richer habitats in southern Sweden. Due to the large regional variation in badger density, increased traffic probably first affects the distributional range of badgers (in marginal habitats) before reducing their density in southern (optimal) habitats.

Evaluation in practise

Evaluating the significance of animal-vehicle collisions should be included in environmental impact assessment for roads and railroads (Seiler & Eriksson 1997). Similar to other aspects in EIA studies, evaluation of animal-vehicle collisions requires a clear perspective: What may seem unimportant from one point of view may appear significant if seen from another angle. In most species, collisions with vehicles are a political or ethical issue rather than an ecological problem. The number of collisions may be small and unimportant with respect to species conservation, but significant from a traffic safety point of view. Likewise, collisions may be unknown to and disregarded by the public but of significant ecological importance. For use in EIA, I propose a simple chain of reasoning that ranks the different perspectives along a gradient of increasing amount of collisions and assists in finding adequate counteractive measures (Figure 4).

The foremost question to be asked is whether the number of collisions can be significant to the conservation of a species. In red-listed and endangered species (Gärdenfors 2000), any road mortality can be a substantial problem even if it is a rare event. According to the new environmental law in Sweden, counteraction or at least compensation is obligatory if there is reason to assume a significant impact on these species. Without the involvement of endangered or rare species, however, there is no legal demand on mitigation, although the impact may still be significant to the management of wildlife populations. In situations where road mortality exceeds other sources of mortality, traffic and not hunting probably acts as the main regulating factor for a population. In order to determine whether road mortality is significant to the conservation or management of a species, the following questions should be answered:

Conservation:

- Is the proportion of road-kills large in relation to other sources of mortality?
- Is road mortality additive?
- Do traffic losses approximate population recruitment?
- Is the realized growth rate of the population close to stationary?
- Does road mortality affect individuals that would otherwise enjoy a rather high chance of survival?
- How much reduction in road mortality is needed to reach a level with that the population can sustain?

Management:

- Are road-kills considered in the annual harvest?
- How large are traffic losses compared to the average harvest?
- Can harvest goals be adjusted to compensate for traffic losses?

If road mortality is neither a conservation nor a management problem, then there may still be traffic safety aspects that will limit the acceptable level of collision numbers. In addition, there may be economic profit from mitigation efforts in terms of improved traffic flow, reduced train delays, and reduced human injury or damage to private property. Internalization of the external costs of animal-vehicle collisions probably encourages increased mitigation efforts. However, even if there is no economic gain in reducing animal-vehicle collisions, there may still be limitations to the number of accidents assigned by environmental policies or from an animal welfare point of view. In practise, it may also be of goodwill to a landowner or public opinion that local mitigation measures are recommendable.

Today, transport infrastructure is to be an integrated part of our life and this includes the physical as well as the social environment. It is ultimately a question of what we want with nature in our environmental goals and visions, rather than to finding the maximum load that the environment can still contend with.

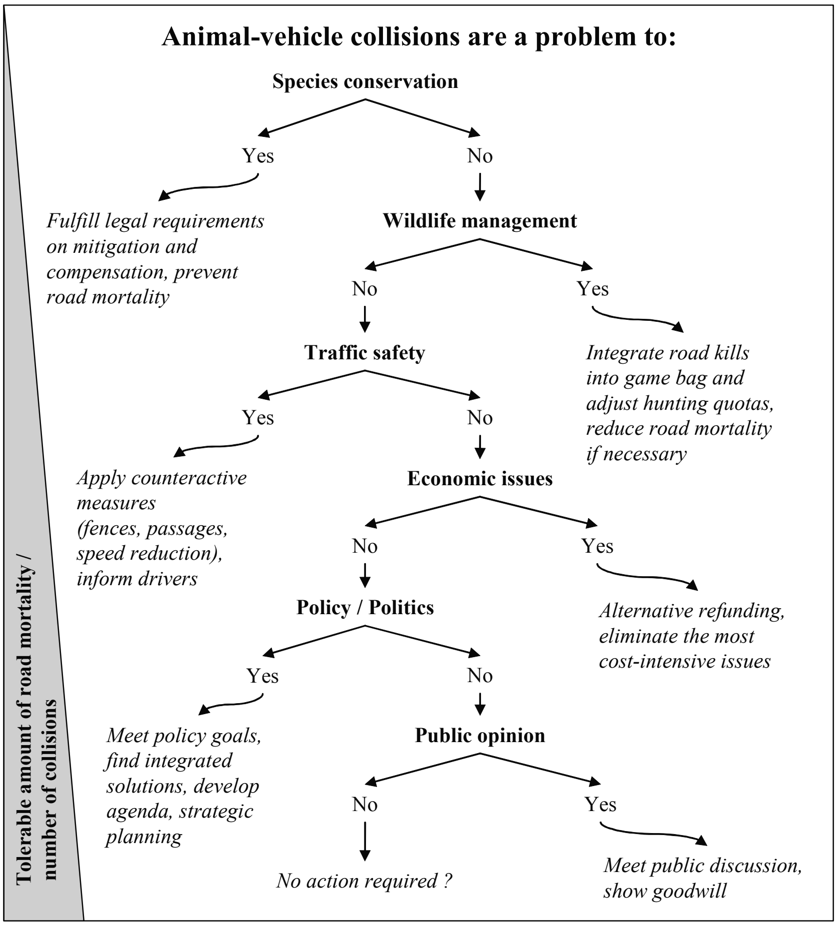

Figure 4. Flow chart illustrating possible steps in the evaluation of animal-vehicle collisions. If, under a given situation, animal-vehicle collisions are not a problem to the conservation or management of a species, there may very well be traffic safety or economic reasons that encourage counteraction. Also environmental policies, including protection of biological diversity, or animal welfare considerations, may set a limit to the maximum acceptable number of collisions.

Factors and patterns in animal-vehicle collisions

If the amount of animal-vehicle collisions is considered significant at any of the proposed levels (Figure 4), more knowledge is needed about the why, where and when of the accidents to develop adequate counteractive measures. This can be approached from different perspectives: From the viewpoint of the wildlife manager or ecologist, one may ask why the animal enters the road corridor and what its odds are to cross the road barrier successfully. One may study differences in road mortality and collision risks between species and attempt to identify those that are most exposed and sensitive. As a car driver, one may be most interested in identifying where and when the risk to collide with an animal is greatest. One may want to learn how collisions can be avoided, how animals react on the road or can be alerted or scared off as we approach. From a governmental standpoint, however, it may be more important to understand why certain road sections embed a greater risk of animal-vehicle collisions than others do. Road planners may need to develop tools that can help to predict the probability of "black spots" irrespective of the number of animals and vehicles that pass. Since roads are supposed to last for decades, if not longer, one may need to grasp the wider picture and study patterns that are long-term and of a broad scale, instead of attempting to answer the most detailed and local issues.

Factors responsible for the occurrence of animal-vehicle collisions can be summarized under three major categories: a) the animal, its ecology and behaviour, b) the traffic, its density and velocity, and c) the environment including the road as well as the surrounding landscape (Table 2). The interplay of these factors creates a complex pattern in the spatial and temporal distribution of animal-vehicle collisions that must be understood before effective counteraction can be designed and employed (e.g., Putman 1997, Forman et al. 2003). Spatial patterns may relate to local variations in animal abundance and activity, habitat distribution, landscape topography, and road and traffic characteristics (e.g., Feldhamer et al. 1986, Berthoud 1987, Groot-Bruinderink & Hazebroek 1996, Hubbard et al. 2000, Nielsen et al. 2003, Clevenger et al. 2003). Temporal patterns may reflect seasonal and diurnal variations in traffic volume, weather and light conditions, and animal activity associated with e.g., foraging, mating or breeding behaviour (e.g., Davies et al. 1987, Kofler & Schulz 1987, Reh & Seitz 1990, Jaren et al. 1991, Neal & Cheeseman 1996, Gundersen et al. 1998).

I studied trends and spatial patterns in vehicle collisions with ungulates mainly from a traffic safety and road planning perspective. More specifically, I analyzed the effect of animal abundance and traffic intensity on collision risks in order to develop predictive models. At broad scales, harvest statistics served as an index of animal abundance and provided the most powerful predictor of collision numbers. Locally, however, environmental factors, such as habitat distribution or road features, more reliably predicted the risk for accidents. Answering the where and when of animal-vehicle collisions seems, therefore, to be a matter of scale.

Table 2. *Factors responsible for the occurrence and patterns of animal-vehicle collisions.*

Animal factors	Traffic factors	Environmental factors
Individual behavior	***Vehicle/Driver***	***Road corridor***
- sex, age, status	- vehicle speed	- corridor width
- dispersal, mating, foraging movements	- road surface	- road side habitat
	- visibility	- fences, gullies
- explorative, defensive, aggressive behaviour	- reaction time	- bridges, tunnels
		- road lighting
Species ecology	***Traffic***	***Landscape***
- abundance	- density	- topography
- solitary / group-living	- continuous / clumped	- linear features
- habitat utilisation	- velocity	- adjacent habitat
- areal needs	- diurnal / seasonal pattern	- landscape composition
- migratory movements		- microclimate
- nocturnal / diurnal		

Animal abundance

In theory, the number of animal-vehicle collisions should be a function of the density and activity of animals and vehicles. Various studies have confirmed that broad-scaled patterns in distribution of animal-vehicle collisions reflect variations in animal abundance and, to a lesser degree, traffic volume (e.g., Carbaugh et al. 1975, Kofler & Schulz 1987, Oosenbrug et al. 1991). McCaffery (1973), for example, observed significant correlations between numbers of collisions with white-tailed deer and antlered buck harvest in 28 of 29 management areas in Wisconsin, USA. Puglisi et al. (1974) reported positive relationships between county deer population estimates and collision numbers among 15 counties in Pennsylvania. Similarly, I found strong correlations between densities of ungulate-vehicle collisions and average annual harvests among 22 Swedish counties as well as among moose hunting districts within counties (paper III). The significant change in ungulate-vehicle collisions that occurred in Sweden over the past 3 decades could also be attributed to increasing ungulate densities (Figure 5; paper III). Harvest statistics, as an index to ungulate abundance, were the primary correlate with collision numbers at national level, whereas the steadily increasing traffic explained a significant part of the residual variation and kept collision numbers at a high level while population sizes declined.

The strong relationship between animal-vehicle collisions and harvest data may suggest that trends and patterns in accident numbers could be predicted from harvest statistics. However, this conclusion applies only at broad scales and only to species in which harvest directly reflects population density and stands for a major part of the total mortality. Several authors have criticized the use of harvest data as an index of population density, especially since other estimation methods such as hunter observations or pellet counts more accurately reflect population patterns at finer scales (e.g., Ericsson & Wallin 1999, Solberg & Saether 1999, but see Fuller 1991). In species such as the moose, in which hunting is regulated through licences and in which management goals aim at balancing harvest against environmental, social, and economic constraints, game bag statistics may not relate to population density at all (e.g., Sylvén 2003). In addition, hunting licenses for moose in Sweden are usually based on previous years' harvest and population estimates. The attempt to balance moose densities can delay harvest-based population indices with one or two years compared to the actual development of the population (e.g., Cederlund & Markgren 1987). Indeed, I observed a time lag of 2 years between annual moose harvests and moose-vehicle collisions at a national level, but no time lag in the relationship for roe deer, in which hunting is not license-based (paper III).

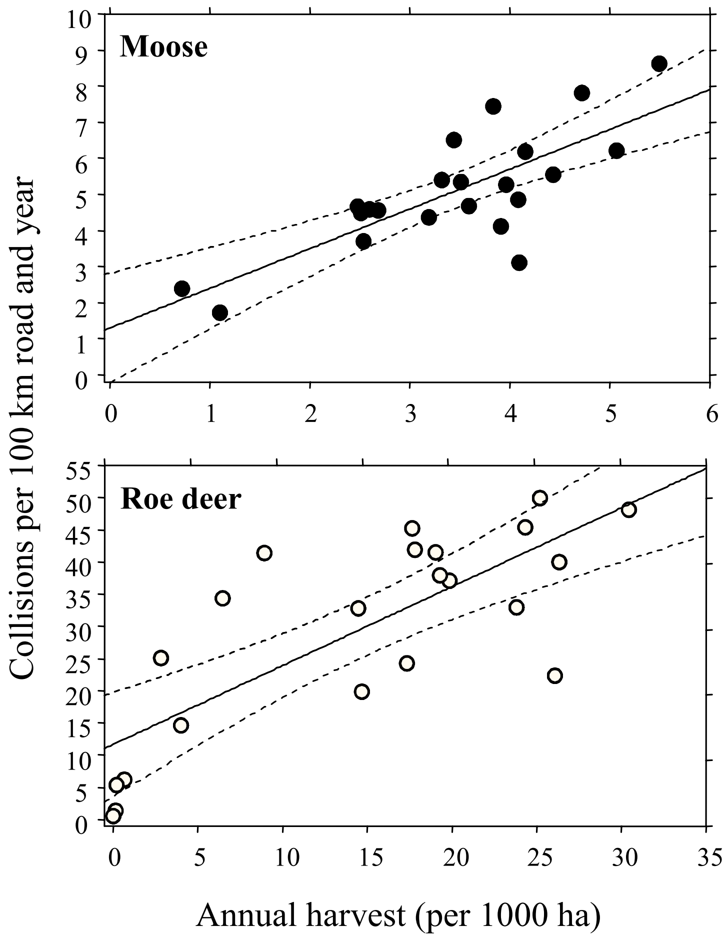

Figure 5. Relationship between the average frequencies of police-reported ungulate-vehicle collisions and average annual harvest in moose and roe deer among Swedish counties during 1985 to 1999. In moose: $R^2=0.598$, $F(1,20)=29.787$, $p<0.0001$; in roe deer: $R^2=0.568$, $F(1,20)=26.297$ $p<0.0001$.

Furthermore, measures of animal density usually refer to comparatively large areas, encompassing many individuals' home ranges or even management units. At a local scale though, they will fail to produce an adequate picture of the abundance of individuals. Animal-vehicle collisions are spatially and temporally aggregated (e.g., Bashore et al. 1985, Hartwig 1993, Finder et al. 1999, Hubbard et al. 2000, Madsen et al. 2002). This implies that patterns observed at a broad scale may not apply at a finer scale (O'Neill et al. 1986, paper III), which is partially due partly to an emerging influence of local factors, partially to an increased variance and error, and partially to a scale-dependency in the parameters studied. Consequently, different criteria need to be studied to understand the pattern at different scales. For local risk assessment, measures of animal movement and activity will thus be more appropriate than any density measure. In part, these can be derived from knowledge about the species' habitat utilisation and distribution of preferred habitat in the landscape (paper III).

Traffic intensity

The second category of factors influencing numbers and likelihood of animal-vehicle collisions is related to traffic density and vehicle speed. Increasing traffic has been held responsible for the growing number of animal-vehicle collisions worldwide (e.g., Forman & Alexander 1998). Trend analyses and comparisons of field inventories made during different decades seem to support this idea (e.g., Jonkers & De Vries 1977, Hansen 1982, Van den Tempel 1993, Newton et al. 1997, paper I). I observed that the increase in traffic intensity in Sweden over the past 30 years explained well the deviation between trends in ungulate harvest and ungulate-vehicle collisions (paper III). Also in other species (Figure 2), the increase in the ratio of collisions to harvest may partially be attributed to increasing traffic.

However, the effect of traffic on animal-vehicle collisions is not necessarily linear and can be confounded by population dynamics, animal behaviour, spatial and temporal factors, as well as the scale of observation (e.g., Groot-Bruinderink & Hazebroek 1996). For example, studies on amphibians (Van Gelder 1973, Kuhn 1987), small mammals and birds (Oxley et al. 1974), carnivores (Clarke et al. 1998, Rosell Pagès & Velasco Rivas 1999), and ungulates (Skölving 1987, Berthoud 1987, paper IV) showed a higher density of collisions on intermediate roads than on major highways or on local access roads. Similarly, I found the highest frequencies of moose-vehicle collisions in Sweden on unfenced roads with a speed limit of 90 km/h and a traffic volume of between 4,000-6,000 vehicles per average day (paper IV). Significantly fewer collisions occurred on minor county roads with reduced speed limits and on unfenced highways with traffic denser than 8,000 vehicles per day and a speed limit of 100 km/h (Figure 6).

These observations suggest that at low traffic volumes, animals may not waver to enter a roadway but only few may collide with vehicles while attempting to cross. With increased traffic, more animals will be killed while trying to cross a road. On very busy roads, however, approaching animals will more likely be repelled by traffic noise or vehicle movement, which leaves fewer to be run over and reduces the fraction of successful individuals. This interaction between mortality risk and repellence produces a barrier effect that increases exponentially with traffic volume (Figure 7). Busy highways and large motorways should therefore be considered as an insurmountable barrier to most terrestrial vertebrates. For practical use in road planning, traffic levels above 10,000 vehicles per day have been proposed as a critical level for considering roads as an effective barrier (e.g., Reck & Kaule 1993, Müller & Berthoud 1997, Rosell Pagès & Velasco Rivas 1999).

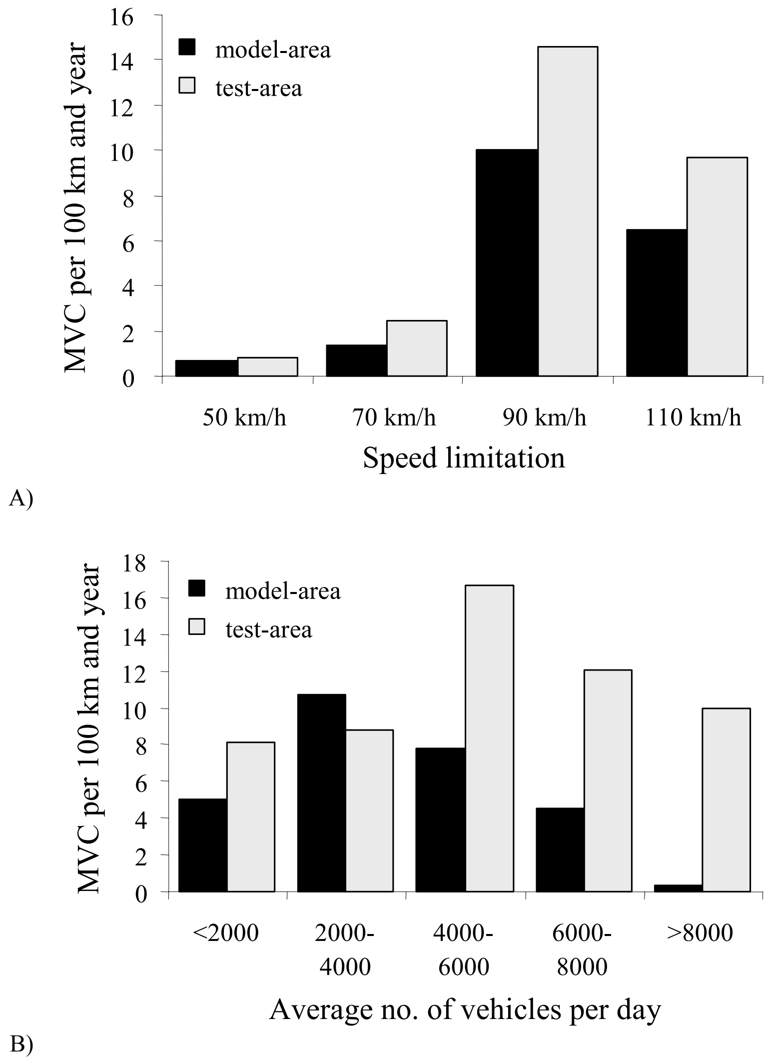

Figure 6. Average annual numbers of moose-vehicle collisions (MVC) per 100 km unfenced public road during 1990 to 1999 for different road categories in the model-area (N = 2185 MVC) and the test-area (N = 1655 MVC) in south-central Sweden. A) MVC densities on roads with different speed limitations. B) MVC densities on roads with varying traffic load (number of vehicles per average day). For more details, see paper IV.

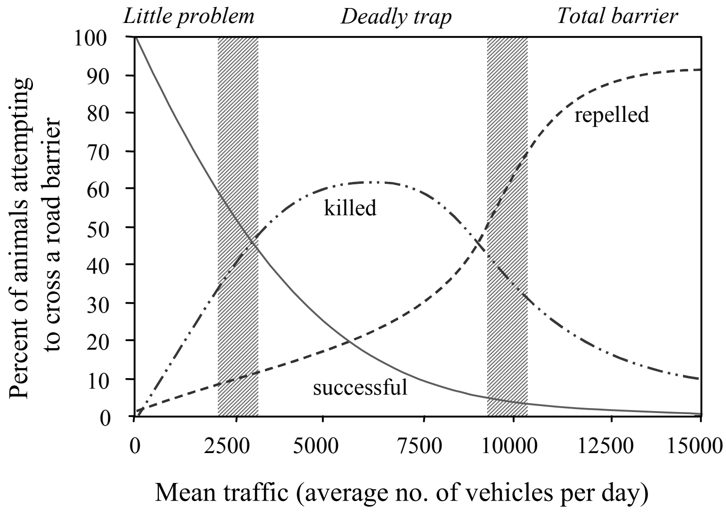

Figure 7. Conceptual model on the effect of traffic volume on the percentage of animals that successfully cross a road, are repelled by traffic noise and vehicle movement, or get killed as they attempt to cross. The model is based on empirical data indicating that most collisions occur on intermediate roads (compare to Berthoud 1987, Skölving 1987, Müller & Berthoud 1997, paper IV).

Once an animal has taken a step onto the road, the risk of colliding with vehicles will increase with traffic volume, vehicle speed, road width, and the presence of obstacles such as gullies or central wire railings that slow down animals or prevent their exit from the road. Clearly, mobile animals may have a greater chance to slip between cars on a trafficked road than slow moving species. Mader (1981) suggested that the chance of survival increases logarithmically with the velocity of the animal, i.e., the faster the animal, the greater the chance to escape from a road before the next vehicle arrives. Hels & Buchwald (2001) calculated collision risks for amphibians and small mammals as the product of animal speed, vehicle width, traffic density, and the angle at which the animal crosses the road (i.e., a measure of road width). Their model suggested that traffic volumes of less than 4,000 vehicles per average day might kill most amphibians trying to cross a road, whereas the mortality risk for faster species, such as small mammals, may only be marginal. Field observations lend support to this notion, for example, traffic densities of 60 cars/h can kill more than 90% of female toads (*Bufo bufo*) migrating across roads (Van Gelder 1973). However, these models do not account for differences in flight or defensive behaviour among animals. Animals that are aware of moving vehicles or even recognize the danger may be able to avoid collisions although they move slowly. For the driver of a car, on the other hand, it may be easier to avoid a frog resting on the road than a hare that tries to run away from the vehicle making abrupt turns and stops.

For the planning of roads, however, it may be most important to understand the relationship between traffic parameters and the actual frequency of collisions with wildlife. In paper IV, I describe that the probability of moose-vehicle collisions increased logarithmically with traffic volume and vehicle speed: Roads with low traffic volumes but high speed limits embedded the highest risk of accidents. Reduction of vehicle speed appeared as the most effective measure to reduce collision risks (Figure 6).

Environmental factors

Animal-vehicle collisions are most likely to occur where trafficked roads run through or between preferred wildlife habitats, or where roads and roadsides provide attractive resources to wildlife. Forest habitat, for example, is an important prerequisite for deer-vehicle accidents in Austria (Kofler & Schulz 1987), France (Berthoud 1987), in the USA in Illinois (Finder et al. 1999), Iowa (Hubbard et al. 2000), and Pennsylvania (Puglisi et al. 1974, Bashore et al. 1985), as well as in Sweden (Almkvist et al. 1980). Moist forests, young pine plantations, and clear cuts with high proportion of deciduous vegetation provide important staple forage for moose in Sweden (e.g., Bergström & Hjeljord 1987, Cederlund & Okarma 1988, Faber & Lavsund 1999), whereas roe deer preferably feed on grasses and herbs in more open habitats (Cederlund et al. 1980). Accordingly, I observed that moose-vehicle collisions were more frequent in areas with high proportions of forest and wetland, while the numbers of collisions with roe deer were increased in rural (open and agricultural) habitats (paper III). The probability of moose-vehicle collisions also depended on the distance to the nearest forest cover and the amount of forest in proximity to a road (paper IV). The model predicted that an increase of 100 m in distance to the nearest forest can reduce collision risks by 15% (paper IV).

A Spanish study on vertebrate mortality on roads suggested that environmental measures and habitat quality had a much higher effect on the species-specific frequency of fauna casualties than road features (Gonzalez-Prieto et al. 1993). The highest collision frequencies occurred in undisturbed areas, whereas fewer took place close to human habitations where wildlife habitat was of lower quality and animal densities were reduced. Similarly, in Sweden, Göransson et al. (1978) observed increased frequencies of road killed mammals and birds in urban (suburban) and forest habitats compared to in open, agricultural areas, a pattern which reflects differences in population densities between these habitats.

The effect of habitat on collision risks, however, depends also on the composition of the wider landscape and the juxtaposition of the road relative to important landscape elements. Where the preferred habitat is extensive and common, animal-vehicle accident sites tend to be more randomly distributed (e.g., Allen & McCullough 1976, Bashore et al. 1985). Where the favourable habitat is patchy and coincides with infrastructure, and where linear landscape features such as riparian corridors, fence rows or other transport infrastructure funnel animals alongside or across a roadway, collision risks will locally be increased and accident sites more aggregated (e.g., Feldhamer et al. 1986, Kofler & Schulz 1987, Lehnert et al. 1996, Lodé 2000, Nielsen et al. 2003, Clevenger et al. 2003).

Traffic casualties in otters (*Lutra lutra*), for example, were most likely to occur where roads cross over watercourses along which otters move (e.g., Philcox et al.

1999). The probability for deer-vehicle collisions in Illinois, USA, is significantly increased where public recreational land near roads and the presence of adjacent gullies and riparian travel corridors is intersected by roads (Finder et al. 1999). Hubbard et al. (2000) observed that the likelihood for accidents with white-tailed deer was increased where highways bridged over (riparian) travel corridors for deer. Also, where exclusion fences terminate or are interrupted by interchanges and connecting infrastructure, collision risk will be increased (e.g., Ward 1982, Feldhamer et al. 1986, Clevenger et al. 2001). Road kills in Dutch hedgehogs, for example, were more likely to occur where railway corridors, along which hedgehogs foraged, intersected with trafficked roads (Huijser 2000). In Denmark, more road-killed foxes and roe deer were found near interchanges than elsewhere along the studied highways (Madsen et al. 1998). This was explained by the design of interchanges, including the extent of forestation and fencing between the roads that attracts but traps animals in the road junction. Similarly, I observed that the risk of moose-vehicle collisions was increased where private roads connected to highways (paper IV). This may probably be due to moose using minor roads as travel corridors. However, where private roads connected to bridges or tunnels providing a safe passage, collisions occurred less frequently (paper III).

In addition, temporal factors also may influence the effect of habitat and landscape composition on collision risks. The work of Almkvist et al. (1980), for example, suggested that during daylight the risk for moose-vehicle collisions in forested areas was four times greater than in open habitats, whereas the risk during night was about the same in both habitat types. Studies on moose-train collisions in Norway demonstrated strong interactions of temporal and spatial factors such as lunar phase, snow cover, temperature, and time of day in determining collision sites (e.g., Andersen et al. 1991, Gundersen & Andreassen 1998, Gundersen et al. 1998).

Mitigation against animal-vehicle collisions

Various measures to counteract animal-vehicle collisions have been tested through the years, yet only few have proven effective (Reed & Ward 1987, Romin & Bissonette 1996, Putman 1997, Forman et al. 2003). Most counteractive measures implemented today seek to prevent animals from crossing a road (by means of fences, gullies, reflectors, and olfactory or acoustical repellents) or to reduce their presence in the road corridor (by means of roadside clearance, additional feeding or salt lick sites, and population control) (e.g., Müller & Berthoud 1997, Keller et al. 2003). Only exceptionally attempts have been made to alter traffic patterns by reduced speed limits or by temporary road closing, or even to adjust road schemes as to avoid high-risk areas (Keller et al. 2003). Measures aimed at increasing the awareness of a driver by means of warning signs or public education are also used, yet mostly in relation to larger animals (e.g., Romin & Bissonette 1996).

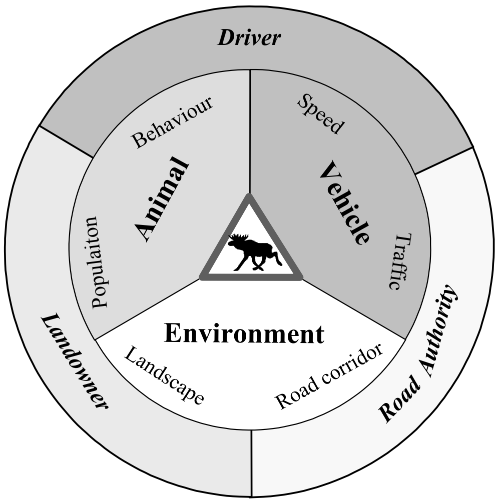

Figure 8. Factors that influence the occurrence of animal-vehicle collisions can be attributed to the vehicle, the animal, and their environment, including the road corridor and surrounding landscape. They relate to the partial responsibilities of the driver, road authority, and wildlife manager/landowner in counteracting collisions. Effective mitigation concepts need to involve all three perspectives.

Typically, mitigation measures against animal-vehicle collisions aim at increasing human traffic safety rather than reducing road mortality to wildlife (e.g., Forman et al. 2003, Keller et al. 2003). This anthropocentric perspective usually views the animal as the intruder on the road, without realising that it is the road and its traffic that have encroached on an animal's habitat in the first place. Recently, a new mitigation approach has been proposed that considers fences and other counteractive measures as part of an integrated 'landscape permeability and traffic safety concept' that aims at remedying habitat fragmentation due to transport infrastructure in the same way as it increases traffic safety (Keller &

Bekker 2003). Counteracting animal-vehicle collisions thereby calls for integration of road design, traffic regulation, and land use and thus addresses all three actors involved in animal-vehicle collisions: The animal, the driver, and the road with its traffic (Figure 8). Thus, responsibilities for counteracting animal-vehicle collisions are in part with the road authority (who decides about road localisation, design and traffic velocity), the driver (who determines the actual travel speed and can avoid animals in time), and the landowner or wildlife manager (who influences distribution of wildlife habitat relative to a road and thereby affects animal movements and abundances).

Exclusion fences

Among the various mitigation measures against ungulate-vehicle collisions that have been tested on Swedish roads since the 1970's (e.g., Anonymous 1980, Björnstig et al. 1986, Skölving 1987, Lavsund & Sandegren 1991), only exclusion fencing and roadside clearing have proven to work efficiently. Small-scale experiments suggested that fencing can reduce the rate of accidents with moose locally by more than 80%, and with roe deer by up to 55%, while the clearance of forested roadsides from palatable or attractive forage for ungulates may result in a 20% reduction in ungulate-vehicle collisions (Almkvist et al. 1980, Skölving 1985, Nilsson 1987). I also observed that the presence of fences significantly reduced the probability of moose-vehicle collisions per km road (Figure 9). Together with traffic volume and vehicle speed, fencing appeared as the dominant road factor determining collision risks (paper IV).

Fencing and roadside clearance have become a standard in Swedish road management. More than 5,000 km of roads or approximately 34% of motorways and national roads have been fenced during the past 25 years, and recent traffic safety policy aims at a significant extension of mitigation fencing (A. Sjölund, SNRA, pers. comm.). Nevertheless, the overall effect of fencing on the numbers of collisions is probably only marginal: About half of all collisions recorded since 1975 occurred on national roads. If all fences were equally efficient (80% effective in moose and 55% effective in roe deer, see above) and all other factors influencing animal-vehicle collisions were held constant over time, we may expect a 13.6% reduction in risk for moose-vehicle collisions, and a 9.4% reduction in risk for roe deer collisions nationwide over the past 25 years. These numbers, however, are smaller than the observed year-to-year variation in collision numbers and thus cannot be confirmed from accident statistics.

It seems obvious that a complete reduction in animal-vehicle collisions can only be achieved by erecting impermeable barriers that separate animals and vehicles. Such measures, however, are costly and only economically beneficial on high-speed roads where the risk for human injury in animal-vehicle collisions is substantial. On minor roads with intermediate speed limits, there is less economic gain for road authorities to erect wildlife-proof fences, although the number of collisions with animals may be considerably higher than on high-speed roads (Figure 6, paper IV). This implies that in order to reduce collision numbers (instead of the severity of accidents), a larger proportion of intermediate roads should be fenced.

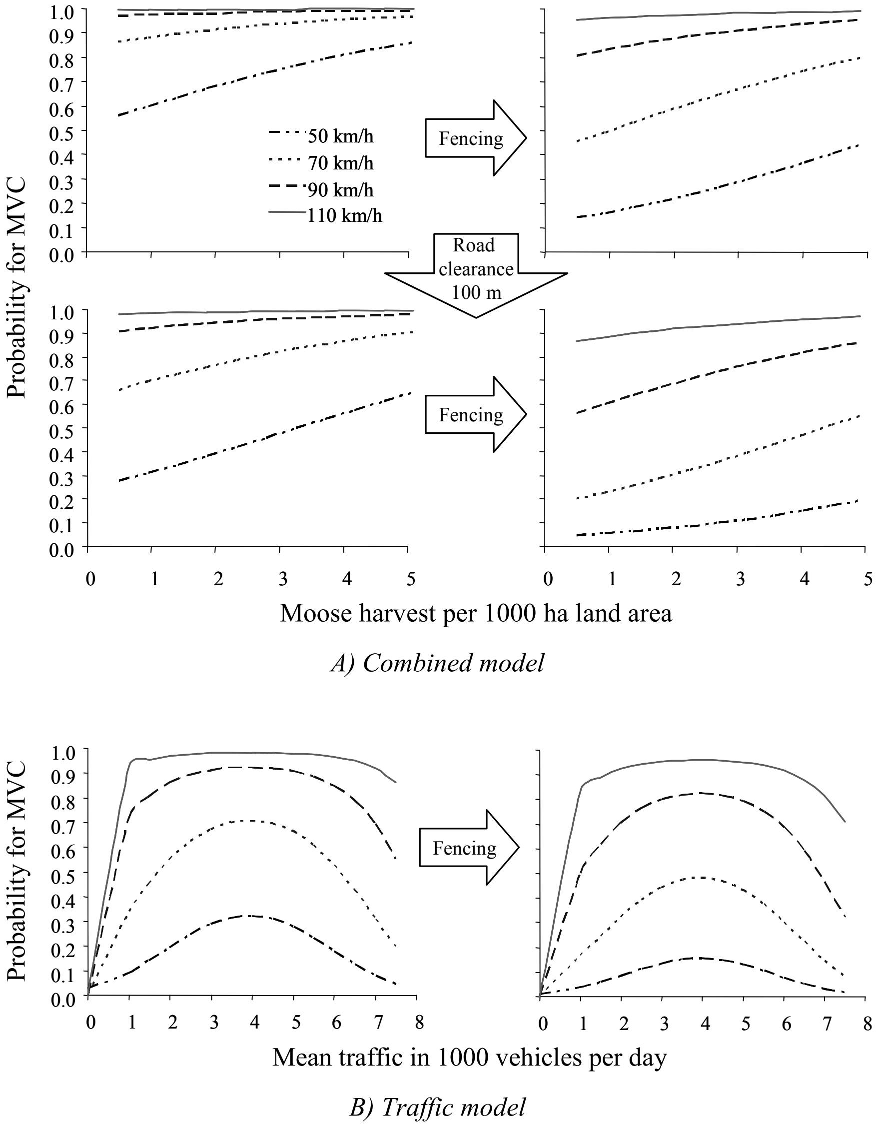

Figure 9. Visualisation of the combined effects of vehicle speed, traffic volume, fencing, moose abundance (game bag statistics) and proximity of forest on the likelihood for at least one MVC occurring per kilometre over a ten years period. A) Predictions of the combined model for roads with traffic volume of 5,000 vehicles per average day and with all other variables included in the model kept constant at the observed means. B) Predictions of the traffic model with intercepts forced through the origin.

Extended fencing, on the other hand, increases the risk of isolation effects on wildlife and may even reduce the efficacy of fences as animals determined to cross a road may force a barrier and eventually break through (Nilsson 1987, Seiler et al. 2003). Fences too short, however, may not actually reduce the risk for accidents but only shift the problem towards the end of the fences (e.g., Ward 1982, Foster & Humphrey 1995, Clevenger et al. 2001). In addition, economic constraints in planning and design may result in suboptimal fences that are only partially effective and pretend to provide a higher road safety than they actually do. Wallentinus (2000), for example, reported from a 15-year monitoring study along a partially fenced road segment in Sweden that moose accidents were actually more common on a fenced road stretch than on an unfenced part. In paper III, I describe that density of moose-vehicle collisions within Swedish parishes was not affected by amount of fencing, but occurrence of conventional road bridges that may provide alternative passage to moose, and this, in turn, did reduce collision frequencies.

Fauna passages

To counteract isolation and further increase traffic safety, SNRA now recommends combining road fences with passages especially adapted to wildlife at locations where collisions are most frequent or the need for continued wildlife movement is high. Such locations may exist where fences terminate and linear landscape elements and topographic features funnel animals across the roadway (e.g., Bashore et al. 1985, Feldhamer et al. 1986, Bennett 1991, Lehnert et al. 1996, Madsen et al. 1998, Finder et al. 1999, Hubbard et al. 2000). Exact localisation and adapted design of wildlife passages appeared to be crucial requisites in determining their usage by wildlife (e.g., Olbrich 1984, Clevenger & Waltho 2000, Keller & Bekker 2003). However, various observations confirmed that even conventional road bridges and tunnels may provide passage to wildlife and thereby reduce the likelihood of animals crossing roads at-grate (e.g., Yanes et al. 1995, Rodriguez et al. 1996, Clevenger & Waltho 2000). Ongoing field studies suggest that the size and openness of road underpasses positively affects usage by roe deer or moose, whereas badgers and foxes seem to prefer narrower passages (A. Seiler, unpubl. data). Snow tracking data from a fenced highway in northern Sweden (Seiler et al. 2003), for instance, illustrated that moose were reluctant to enter narrow road underpasses and instead chose to charge a highway fence with the consequent risk for collisions with vehicles. Similarly, Hubbard et al. (2000) observed that the likelihood for accidents with white-tailed deer in Iowa, USA, was increased where roads bridged over travel corridors for deer. The authors believed that deer did not accept these conventional passages and instead chose to cross over the road.

Nevertheless, I found that in Sweden the risk for moose-vehicle collisions decreased where tunnels or bridges separated intersecting roads. The density of road passages had a significant effect on density of collisions with moose and roe deer per parish (paper III). Where private roads directly connected to a main road but bridges or tunnels were absent, however, the risk for moose-vehicle collisions was elevated, irrespective of whether this road was fenced or not (paper IV).

It remains to be investigated how efficient conventional road bridges or tunnels are compared to adapted wildlife passages. It is possible that even small changes in design and width of conventional passages could provide sufficient efficiency to reduce isolation effects and increase traffic safety. Recommendations for minimum dimensions of adapted wildlife passages have been proposed earlier. For example, Olbrich (1984) concluded from field inventories on 788 bridges and tunnels in Western Germany that effective wildlife passages should exceed a relative width (width*height/length) of 0.75 for roe deer and 1.5 for red deer (*Cervus elaphus*) and fallow deer (*Dama dama*). These minimum requirements are not far from standard dimensions used for conventional road underpasses. In practise, it seems more likely to find support for the adaptation (enlargement) of conventional road underpasses and bridges than for the construction of passages exclusively designated to wildlife (e.g., Keller & Bekker 2003).

Reduced animal density

Another, rather compelling but little discussed, mitigation option is the reduction of animal populations in the vicinity of roads. The observed relationship between collision numbers and harvest statistics in, e.g., ungulates (paper III) suggests that intensive population control might reduce the number of animal-vehicle collisions (e.g., Keller et al. 2003).

Certainly, large-scale reductions in animal densities may have a counteractive effect on collision risks, but it will be difficult to find political and public support for such action even if the species is abundant and widespread. Local reductions, on the other hand, are more easily achieved, but may not necessarily give the desired effect. In their survey of mitigation measures applied across the United States, Romin & Bissonette (1996) reported that only one of two states that tried to reduce deer-vehicle collisions through intensified hunting indicated success.

Almkvist et al. (1980), for example, expressed doubt as to whether local management for reduced moose density would decrease the frequency of moose-vehicle collisions. Joyce & Mahoney (2001) observed that numbers of moose-vehicle collisions along the Trans-Canada Highway in Newfoundland were elevated in areas of both very scarce and very dense moose populations. I found no correlation between annual moose harvest and density of moose-vehicle collisions among parishes, but instead a significant influence of road density, forest habitat and occurrence of underpasses and bridges (paper III).

As discussed before, it is an animals' activity and mobility rather than the density of the population that influences risks for collisions with vehicles locally. Local density reduction alongside roads, however, would perturb population structure, distort established territories, and thereby increase an animals' mobility. Reduced densities in otherwise attractive habitats may further provoke immigration by inexperienced dispersers that are more likely to attempt to cross a road and collide with vehicles. Thus, a local reduction in animal density may only give a momentary effect, or even increase the risk for collisions.

In conclusion, I know of no empirical study that has yet been published on the preceding question; however, there is anecdotal data on moose-vehicle collisions in Sweden lending support to the assumption. For example, collisions with moose tend to be most frequent during the first years after construction of a new road but lessen after 2-3 years. Also, problems with animals forcing entry through a road fence seem to occur mainly during the first two to three years after a fence has been raised (Kjell Ståhl, SNRA, pers. comm.). This seems probable because resident moose may either be killed (due to the new road dissecting their home ranges; e.g., Reilly & Green 1974, Jones 2000) or gradually adapt their movements to the new road or fence and learn to cope with traffic and the risk of collision – at least to some degree.

Conclusions

Animal-vehicle collisions are a common phenomenon worldwide, causing injury or death to millions of animals and hundreds of human passengers each year (e.g., Romin & Bissonette 1996, Groot-Bruinderink & Hazebroek 1996, Forman et al. 2003). Studying and mitigating animal-vehicle collisions can be empowered as part of traffic safety programs or in the context of habitat fragmentation or wildlife management, but for complete success, a holistic approach that addresses both drivers and animals in their shared (road) environment is needed. In fact, in many cases, animal-vehicle collisions are not primarily a conservation problem but must be dealt with from a political and ethical standpoint. Thus, it is not solely in the hand of an engineer, economist, or ecologist to judge whether counteraction is necessary. Instead, there is need for interdisciplinary co-operation to develop adequate, goal-efficient mitigation concepts.

In Sweden, most wildlife species are not immediately threatened by today's road traffic. Mitigation measures are therefore focused primarily on increasing traffic safety for humans. Game management is another important factor stimulating the implementation of counteractive measures such as wildlife passages. In some species, for instance the badger, hunting is probably overtaken by road traffic as the major cause of mortality. Road mortality is especially harmful to species with slow reproduction and low population densities. Regional differences in habitat quality and dispersion can produce large variation in the significance of road traffic to population dynamics. Thus, although nationwide road-kill estimates may appear to be within acceptable levels, impacts at a regional or local scale can be substantial.

At present, neither the Swedish Environmental Protection Agency nor animal welfare organisations have yet become aware of, or seem to be interested in, this issue. Nevertheless, animal-vehicle collisions are now considered as an integrated part of the ecological impact of infrastructure and thereby subject to proposed environmental quality goals of the transport sector. Statistics on animal-vehicle collisions can provide a useful tool to quantify and evaluate environmental impacts of transport infrastructure as well as to monitor trends in wildlife populations.

If counteraction is required (or desired), more knowledge about spatial and temporal factors determining collisions risks are needed. I showed that the local risk for collisions with moose, for example, can be predicted reasonably well from remotely sensed landscape data and official road traffic data. The spatial and temporal clumping of animal-vehicle collisions implies, however, that patterns observed at one scale may not apply at another scale. Local pattern may not support a general conclusion, while broad-scale dependencies and trends may tell relatively little about relationships at a local level. In addition, a correlation between animal density, traffic intensity and collision numbers seems convincing, while a dose-effect relationship may be curvilinear or even reversed. Since research on animal-vehicle collisions should address both humans and animals, investigations should also be at multiple scales.

Typically, mitigation measures against animal-vehicle collisions seek to prevent animals from entering a roadway. Fences, warning reflectors, scent repellents, and wildlife passages have been used to guarantee unobstructed, safe roads to drivers. However, it seems it is usually a vehicle that strikes an animal. The significance of vehicle speed in models on moose-vehicle collisions, for example, underlined the importance of responsibility by an individual driver. With better knowledge on risk distribution and adequate preventive behaviour, many drivers might be able to avoid colliding with animals. To achieve effective mitigation against animal-vehicle collisions, there is clearly a need for a holistic approach that includes an integrated management of surrounding landscapes (directing animal movements), of roads (creating barriers and passages), of animal populations (protection of resident animals near roads), as well as a better understanding of driver behaviour (awareness and responsible driving).

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