


Road mortality in Swedish mammals: results of a drivers' questionnaire

Andreas Seiler, J-O. Helldin & Christiane Seiler

Seiler, S., Helldin, J-O. & Seiler, C. 2004: Road mortality in Swedish mammals: results of a drivers' questionnaire. - *Wildl. Biol.* 10: ~~xxx-xxx~~ 

We present new estimates on the national road kill for nine large and medium-sized mammals in Sweden. Our estimates are based on 705 drivers' reports on the number of animals accidentally hit during individually chosen reference periods. During 1960-2000, a total of 881 animal-vehicle collisions were reported based on 243.6 million driven kilometres, representing 0.37% of the overall mileage driven in Sweden during 1992, the mean reference year of all replies. The collision frequencies ranged from 0.07 incidents per million kilometres for medium-sized mustelids, over 0.42 for badgers *Meles meles* to 1.11 for hares *Lepus* spp. Our data suggest that during 1992, 7,000-13,500 moose *Alces alces*, 43,500-59,000 roe deer *Capreolus capreolus*, 63,500-81,500 hares, 22,000-33,000 badgers and 6,500-12,500 red foxes *Vulpes vulpes* may have been killed on Swedish roads. Among these game species, the extrapolated nation-wide road kill ranged between 7 and 97% of the average annual harvest, and between 1 and 12% of the assessed total populations in 1992. Our results are in agreement with other independent road kill estimates for Sweden. The data suggested an overall increase in the frequency of road kills over the past 40 years, which partly can be attributed to changes in traffic volume and wildlife population sizes (game bags). In most species, the estimated levels of nation-wide road mortality are not alarmingly high, although local impacts may be significant. In badgers and hares, the ratio of the estimated road kill to the annual harvest increased two fold, suggesting a steady increase in the relative importance of road mortality. We conclude that interviews with drivers can provide a cheap and useful index of wildlife traffic mortality.

Key words: ecological impact, infrastructure, mammals, road kills, traffic casualties, wildlife management

Andreas Seiler, J-O. Helldin & Christiane Seiler, Swedish University of Agricultural Sciences, Department of Conservation Biology, Grimsö Wildlife Research Station, SE-730 91 Riddarhyttan, Sweden - e-mail addresses: andreas.seiler@nvb.slu.se (Andreas Seiler); j-o.helldin@nvb.slu.se (J-O. Helldin); christiane.seiler@nvb.slu.se (Christiane Seiler)

Corresponding author: Andreas Seiler

Received 13 December 2002, accepted 13 October 2003

Associate Editor: Sigurður Snorrason

Collisions between motorised vehicles and wild animals have attracted public attention for many decades (e.g. Stoner 1925, Dickerson 1939, Haugen 1944, McClure 1951, Ueckermann 1964, Way 1970, Hansen 1982,

Van den Tempel 1993, Caletrio, Fernandez, Lopez & Roviralta 1996). The numbers of wildlife casualties on roads and railways have constantly grown as traffic and vehicle speeds have increased and infrastructure net-

works expanded. Today, road-killed animals are probably seen by many more people than their living conspecifics, and wild animal carcasses have become a common view in modern transportation corridors (e.g. Knutson 1987). In their review on ecological effects of roads, 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".

Estimates made by the Humane Society of the United States during the 1960s suggested a minimum of one million animal road kills per day (Lalo 1987). In Spain, extensive surveys revealed a minimum of 10^7 vertebrate traffic kills per year (about 31/km road; Caletrio et al. 1996). In the Netherlands, Jonkers & De Vries (1977) reported an estimate of 0.6 million bird and 0.2 million mammalian road victims annually, but a more recent study by Van den Tempel (1993) has suggested that this figure may actually be much higher (2 million birds in the Netherlands). Field inventories in Belgium were extrapolated to a nation-wide road kill of 4 million vertebrates annually (Rodts, Holsbeek & Muyldermons 1998). Hansen (1982) estimated that as many as 1.5 million mammals, 3.7 million birds and more than 3.1 million amphibians were killed annually on Danish roads. The numbers of road kills are staggering, but are they significant from an ecological point of view?

For many rare species worldwide, especially amphibians and reptiles, traffic is considered a threat to their survival (e.g. Blaustein & Wake 1990, Rodriguez & Delibes 1992, Fahrig, Pedlar, Pope, Taylor & Wegner 1995). Traffic also imposes a problem to many large and medium-sized mammals, (e.g. Boscali 1987, Madsen 1990, Van der Zee, Wiertz, Terbraak & Van Apeldoorn 1992, Clarke, White & Harris 1998), and even in common game species, road mortality can be of significance to the management or harvest of local populations (e.g. Romin & Bissonette 1996, Putman 1997, Child 1998). In small and abundant species, such as rodents, voles, rabbits and many birds, traffic mortality is currently considered of little importance (e.g. Haugen 1944, Bergmann 1974, Göransson, Karlsson & Lindgren 1978, Bennett 1991, Caletrio et al. 1996). However, irrespective of whether or not road mortality is significant to the conservation or management of a species, there is growing economical, ethical and political concern, let alone reasons of traffic safety that demand mitigation against animal-vehicle collisions (e.g. Knutson 1987, Fehlberg 1994, Romin & Bissonette 1996, Schwabe & Schuhmann 2002).

Little is known about road mortality in small and medium-sized mammals in Sweden. Studies on wildlife

casualties on roads date back to 1962 (Bengtsson 1962) and the 1970s (Bolund 1974, Göransson et al. 1978). Based on comprehensive field inventories, Göransson et al. (1978) estimated an annual minimum of 1.0 million bird casualties and 0.5 million casualties of medium-sized mammals (excluding small mammals, ungulates and large carnivores). For most species, they considered this road mortality to be within tolerable limits. Since this study was conducted, however, the traffic flow on Swedish roads has increased with about 50%, the length of motorways has doubled (Anon. 2000) and the number of police recorded ungulate-vehicle collisions has multiplied by 14 (Seiler in press). It seems reasonable to believe, that the road mortality has increased also in other species. A recent estimate of avian road kills, for example, suggested that as many as 8.5 million birds were killed on Swedish roads in 1995 (Svensson 1998).

We present new estimates of the numbers of mammalian road kills in Sweden and discuss the importance of road mortality from an ecological point of view. Our estimates are not based on field inventories of road kills, but on drivers' responses to a questionnaire during 2001.

Material and methods

We collected information on animal-vehicle collisions in Sweden based on answers to a standardised questionnaire to Swedish car drivers. The questionnaire was distributed via e-mail lists, the Internet (<http://grimso-slu.se/djurotrafik>) and was published via radio and newspapers during 2001. In the questionnaire, we asked drivers to estimate the total mileage they had driven and the number of collisions they had had with wild mammals larger than mice during a time period they were free to choose, but for which they were confident that they could remember any incident. This reference period could span from one year to the entire period during which a person had possessed a driving licence. In order to obtain collision data that were comparable to the official hunting statistics covering the years 1960-2000, we restricted the analysis to responses with reference periods of up to a maximum of 40 years. If collisions were reported, we asked for species, number of individuals and approximate location.

For each species for which we received > 10 collision reports, we calculated the mean collision frequency (MCF) as the ratio between the number of reported collisions and the total reported mileage driven by all respondents. Species with < 10 reported incidents were

grouped with ecologically similar species or were excluded from further calculations. MCF-values were multiplied with the total mileage driven in Sweden during the mean reference year (i.e. the average reference year over all replies was 1992) to obtain estimates for the overall national road kill. We calculated 95% confidence limits for the number of reported collisions according to the Poisson distribution (Crow & Gardner 1959, in Krebs 1989) as the distribution of incident numbers per species was highly skewed towards zero.

We assumed that the frequency of collisions per driven kilometre would relate directly to the abundance of a species and to its susceptibility to road traffic. For a given species, variations in collision frequencies in space or time were therefore considered to reflect changes in population densities. In lack of better abundance estimates, we used harvest statistics as indices of animal abundances and tested for correlation with MCF between counties and reference years. Hunting is not regulated through a licensing system for any of the reported mammal species, except moose *Alces alces*. Variation in animal abundance may thus directly affect harvest statistics, provided a constant hunting effort. Even in moose, however, Seiler (in press) observed strong relationships between moose harvests on national and county levels and the number of police reported moose-vehicle collisions in Sweden.

MCF-values for individual reference periods were calculated as the number of collisions per million kilometres driven averaged for all respondents referring to the same period. County MCF-values were obtained from replies with specified collision sites and calculated as the number of reported collisions related to the official traffic per counties during the mean reference year 1992 (Anon. 2000). Game bag statistics and estimations of wildlife population sizes in Sweden during the early 1990s were obtained from The Swedish Association for Hunting and Wildlife Management (Anon. 1992). Data on police reported ungulate-vehicle collisions between 1970 and 1999 were obtained from the Road Accident Database of the Swedish National Road Administration (SNRA; Seiler in press).

Estimates of the total annual mileage driven by all motor vehicles on Swedish roads, including private, municipal and national roads, during 1950-1999 were obtained from Edwards, Nilsson, Thulin & Vorwerk (1999). The average annual mileage driven per motor vehicle was estimated by the Swedish Motor Vehicle Inspection Company (SMVIC; Svensk Bilprovning AB) from periodic safety inspections on motor vehicles older than two or three years.

We expected the responses to our questionnaire to be biased towards a higher proportion of positive answers, i.e. answers that reported collisions with animals, than would be expected from a random sample, because we assumed that people who collided with wild mammals might feel more encouraged to reply to our questionnaire than people who did not remember or did not experience such accidents. To control for this possible bias, we personally contacted colleagues at the Swedish Agricultural University, the Swedish National Road Administration and the Swedish National Road & Transport Research Institute. These controlled replies (N = 106) were compared to those returned by the public (N = 599) with respect to driven mileage, length of reference period and ratio of positive to negative answers.

All calculations were performed with the statistical software package StatView 5 (SAS Institute Inc. 1998). For all tests, the significance level was set to $P < 0.05$. Only two-tailed tests were applied. In repeated statistical tests on the same data set, we used the sequential Bonferroni correction (Holm 1979) to adjust significance levels and reduce the risk of Type 1 errors.

Results

During 2001, we obtained a total of 705 useful replies to our questionnaire; of these 48.7% (N = 343) reported collisions with large and medium-sized mammals, amounting to a total of 594 reported road kills. The individual reference periods varied from the preceding year (2000) back to 1960, with 1992 being the mean reference year of all replies. On average, each respondent referred to $16,462 \pm 817$ km ($\pm 95\%$ C.I.) per year, which, according to the SNRA and the SMVIC, lies close to the national average driven per vehicle and year in Sweden (ca 16,000 km). All answers combined referred to 243.59 million kilometres, representing 0.37% of the total mileage driven by all vehicles combined in Sweden during the mean reference year 1992 (65.28 billion km). Each reported collision from our survey would thus represent 268 incidents if extrapolated to the national level.

There was no difference in the reported annual or total mileage driven between controlled (N = 106) and public (N = 599) replies (Table 1). Group status did not affect the ratio of positive (with reported collisions) to negative (without reported collisions) answers ($G^2 = 0.306$, $df = 1$, $P = 0.580$). People who reported collisions with wild mammals, however, referred to a significantly higher annual mileage than those who gave negative replies (Table 2). The distribution of respondents among

Table 1. Analysis of variance of the reported annual and total mileage and the numbers of reference years comparing replies from a control group (N = 106) and a public group (N = 583), and positive (N = 329) and negative (N = 360) answers (Collisions Yes/No). Professional drivers that reported an average annual mileage of > 50,000 km (N = 16) were excluded from this analysis.

	DF	SS	F	P
Annual mileage				
Control/Public	1	1812779	2.40	0.1221
Collisions Yes/No	1	88987258	117.61	<0.0001
Residual	659	498634695		
Total mileage				
Control/Public	1	1818846284	2.22	0.1372
Collisions Yes/No	1	74052057715	90.17	<0.0001
Residual	659	541202387508		
Number of reference years				
Control/Public	1	3	0.03	0.8747
Collisions Yes/No	1	5294	48.82	<0.0001
Residual	684	72629		

counties reflected the number of inhabitants per county in 1992 ($R^2 = 0.175$, $F_{1,20} = 5.45$, $P = 0.0301$).

All this indicates that our survey reached a small but representative sample of the Swedish drivers, and that extrapolation from the reported collisions to a national estimate of road kills should be legitimate.

Most frequent among the reported collisions were accidents with hares *Lepus* spp. (30% of all collisions), roe deer *Capreolus capreolus* (21%), badger *Meles meles* (11%) and red squirrel *Sciurus vulgaris* (10%), whereas collisions with red fox *Vulpes vulpes*, hedgehog *Erinaceus europaeus* and moose were reported in only 4-5% of the replies (Table 3). No reports were received on collisions with large carnivores such as wild boar *Sus scrofa* or otter *Lutra lutra*. Due to the small sample sizes and the high risk of erroneous identification, we grouped polecat *Mustela putorius* (N = 6), mink *Mustela vison* (N = 7) and pine marten *Martes martes* (N = 4) as 'medium-sized mustelids'. Brown hares *Lepus europaeus* and mountain hares *Lepus timidus* were grouped as

Table 2. Results of logistic regression analysis on the effects of group membership (Control/Public) and reported annual mileage on the likelihood of a return to our questionnaire reporting at least one animal-vehicle collision. Collisions were reported in 531 of the 705 returns.

Collisions ratio	DF	L-L	χ^2	P
Intercept	1	-476.88		
Reported annual mileage	1	-419.93	113.90	<0.0001
Control/Public	1	-419.93	0.00	0.9615

'hares'. Reports on collisions with reindeer *Rangifer tarandus* (N = 5), fallow deer *Dama dama* (N = 2) and red deer *Cervus elaphus* (N = 1) were excluded from further calculations due to their small sample sizes.

Among the nine species or species groups included in the analysis, mean collisions frequencies per species or group ranged from 0.07 incidents per million kilometres driven in medium-sized mustelids to 1.11 collisions per million kilometres in hares (see Table 3). If extrapolated to the total road kill during the mean reference year 1992, these estimates accounted for 1-12.5% of the assessed population sizes. The ratio of road kill to annual game bag ranged on average from 7% in medium-sized mustelids to 97% in badger.

Mean collision frequencies were not constant over time but changed with the length of the reference periods, resulting in generally higher estimates of the national road kill as the maximum period length decreased from 40 to 10 years. In three of nine species (badger, hares and roe deer), the MCF-values increased significantly as the number of reference years decreased ($R^2 > 0.19$, $F_{1,30} > 6.60$, $P < 0.0156$; significant in a sequential Bonferroni-test). In badger, red fox, hares and roe deer, the changes in the MCF-values correlated with the changes in the average annual game bag for the corresponding reference periods (adjusted $R^2 > 0.375$, $F_{1,35} > 22.6$, $P < 0.0001$; significant in a sequential Bonferroni-test). The MCF-values also correlated with moose har-

Table 3. National estimates of the total number of animal-vehicle collisions in Sweden in relation to game bags and estimated population sizes during 1992. Collision estimates are based on 705 drivers' reports, referring to a total of 243.59 million kilometres driven between 1960 and 2000, with 1992 as the mean reference year. Mean frequencies of collisions per million kilometres driven (MCF) are extrapolated to national road kill estimates by multiplication with the total mileage driven in Sweden in 1992 (65.28 billion kilometres). Game bag statistics and population estimates derive from The Swedish Association for Hunting and Wildlife Management (Anon. 1992).

Species	N	MCF	Road kill (95% C.I.)	Game bag	Road kill % /game bag	Population size	Road kill % /population
Moose <i>Alces alces</i>	37	0.15	10000 (7000-13500)	99372	10.1 (7.1-13.6)	250000	4.0 (2.8-4.5)
Roe deer <i>Capreolus capreolus</i>	188	0.77	51000 (43500-59000)	372050	13.7 (11.7-15.9)	1000000	5.1 (4.4-5.9)
Hares <i>Lepus</i> spp.	270	1.11	72500 (63500-81500)	207200	35.0 (30.6-39.3)	800000	9.1 (7.9-10.2)
Badger <i>Meles meles</i>	102	0.42	27500 (22000-33000)	28100	97.9 (77.5-118.1)	250000	11.0 (8.7-13.3)
Red fox <i>Vulpes vulpes</i>	34	0.14	9000 (6500-12500)	31300	28.8 (20.3-40.3)	100000	9.0 (6.4-12.6)
Medium-sized mustelids <i>Martes martes</i> , <i>Mustela</i> spp.	17	0.07	4500 (2500-7000)	62052	7.3 (4.1-11.4)	365000	1.2 (0.8-2.2)
Rabbit <i>Oryctolagus cuniculus</i>	32	0.13	8500 (5500-12000)	71500	11.9 (8.0-16.6)	150000	5.7 (3.8-7.9)
Red squirrel <i>Sciurus vulgaris</i>	93	0.38	25000 (20000-30000)	-	-	200000	12.5 (10.1-15.1)
Hedgehog <i>Erinaceus europaeus</i>	38	0.16	10000 (7000-14000)	-	-	-	-
Domestic dog <i>Canis familiaris</i>	10	0.04	2500 (4500-14000)	-	-	-	-
Domestic cat <i>Felis catus</i>	60	0.25	16000 (12000-20500)	-	-	-	-

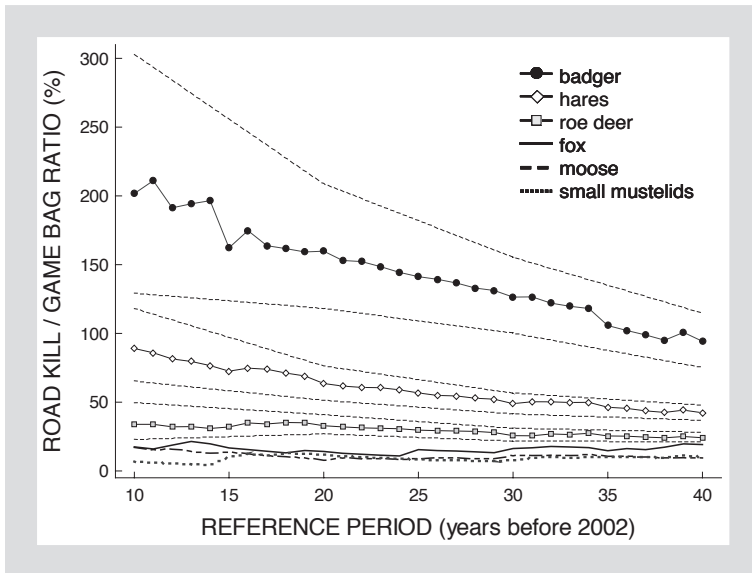


Figure 1. Change in ratio between the estimated road kills in Sweden and the average game bag (with 95% C.I.) in relation to the length of the reference periods covering the past 40 years (1960-2000). In badger and hares, the ratio increased two-fold as the maximum number of reference years decreased from 40 to 10 years.

vest data, but to a lesser degree (adjusted $R^2 = 0.123$, $F_{1,35} = 6.1816$, $P < 0.018$). In badger and hares, however, the increase in the MCF-values was faster than the increase in annual game bags, causing the ratio of estimated national road kill to the annual harvest to multiply (Fig. 1). Also in the remaining species, the mean ratios increased, but the changes were not significant.

To test for large-scale spatial correlation between collision frequencies and harvest statistics, we compared county MCF-values with county game bags per square kilometre during the mean reference year 1992. In roe deer ($R^2 = 0.264$, $F_{1,20} = 7.18$, $P = 0.0144$) and moose ($R^2 = 0.319$, $F_{1,20} = 9.372$, $P = 0.0062$) the correlations were significant, but this was not the case in the other species. County MCF-values for roe deer also correlated with differences in the average number of police reported deer-vehicle collisions per county and kilometre during 1985-1999 ($R^2 = 0.504$, $F_{1,20} = 20.317$, $P = 0.0002$). In moose, the trend was similar, but it was not significant ($R^2 = 0.147$, $F_{1,20} = 3.447$, $P = 0.0781$).

Discussion

Extent of collision mortality and effects on population dynamics

Seen from an individual driver's point of view, vehicle collisions with large and medium-sized mammals are relatively rare events. According to our survey, an

average driver may experience one collision with any one of the eleven species or species groups listed in Table 3 during 15 years of driving. The average odds of colliding with a moose in Sweden may be as low as one in 357 years of driving or one per 6.6 million driven kilometres. Collision with a hare is more likely, although it may still take one million kilometres of driving to experience such an accident. Seen in a national perspective, however, animal-vehicle collisions are rather common. On an average day, about 12 moose and 68 roe deer collisions are officially registered by the Swedish police, and these collisions make up more than 60% of the daily number of all police reported road accidents (Seiler in press). About half of all respondents to our questionnaire reported collisions with large and medium-sized

mammals, yet many more reported collisions with smaller mammals, birds and other vertebrates (which we did not ask for specifically), or they described 'near' accidents. Animal-vehicle collisions, especially those involving large mammals, are often traumatic incidents and are therefore well remembered by the drivers, although they usually produce only minor damage to the vehicles and seldom cause physical injuries or death.

For the animals involved, on the other hand, road accidents are almost always lethal. Earlier Swedish studies suggested that road accidents are lethal for > 80% of all moose and 94% of all roe deer (Almkvist, André, Ekblom & Rempler 1980). For smaller species, the chance of survival is probably even smaller. Our data indicate that 7,000-13,500 moose, 43,500-59,000 roe deer, 63,500-81,500 hares, 22,000-33,000 badgers and 6,500-12,500 red foxes may have been killed on Swedish roads during 1992 (95% C.I.). Furthermore, additional collisions with small mammals, birds and other vertebrates occur. According to Svensson (1998), the road traffic in Sweden probably kills one bird per 10,000 vehicle kilometres which would equal 6.5 million traffic-killed birds during 1992. Overall, our data indicate that the number of collisions with animals is primarily a function of how much a person drives.

Our study suggests that in several of the commonly occurring mammal species in Sweden, road traffic causes an average loss of 1-12% of the estimated popu-

lation sizes, approximating 10-100% of the annual game bags. What does this imply? To evaluate the importance of road mortality to a species, it must be related to the population size, growth rate and other sources of mortality. As a rule of thumb, the larger the proportion of road kills is of all deaths, the more likely it is that traffic is a 'key factor', unless the road mortality is compensated for by increased survival or fecundity of the remaining individuals, or mainly influences the already 'doomed surplus' (e.g. Southwood & Henderson 2000). Thus, in game species such as the moose that are mainly regulated through hunting (Sylvén 2003), our estimated proportional road traffic loss of 4-5% of the population is likely not influential at the population level, but it may still locally restraint the allowable harvest of the species (e.g. Seiler in press). Deer road mortality in Europe is commonly regarded rather as an economical and traffic-safety issue than an ecological problem (Groot-Bruinderink & Hazebroek 1996).

Species that are especially exposed to road traffic are typically wide-ranging habitat generalists, whereas species that are sensitive to road mortality are long-lived and slow reproducing (Verkaar & Bekker 1991, Forman, Sperling, Bissonette, Clevenger, Cutshall, Dale, Fahrig, France, Goldman, Heanue, Jones, Swanson, Turrentine & Winter 2003). Such behaviour and life history traits are combined in the badger (Anderson & Trehwella 1985, Seiler, Lindström & Stenström 1995) and the hedgehog (Huijser 2000). Indeed, road traffic is considered the largest single cause of death in British and Dutch badgers, charging > 20% of the population and being responsible for a decline in several local populations (Harris, Cresswell, Reason & Cresswell 1991, Van der Zee, Wiertz, Terbraak & Van Apeldoorn 1992, Clarke et al. 1998). We estimated a comparably lower mortality rate due to road traffic (11%) among Swedish badgers, but the rate seems to be increasing and, due to strong regional differences in badger habitat and distribution (Bevanger & Lindström 1995), the effect on marginal populations may be more pronounced than suggested from the national average (A. Seiler, unpubl. data). In hedgehogs, road traffic probably kills up to 26% of the Dutch population (Huijser 2000) and up to 19% of the Swedish population (Göransson et al. 1978), with local impacts substantially affecting both population recruitment and survival.

Methodological considerations

Our data are rough estimates and only give a very simplified picture of the road mortality in Sweden. Our estimates of the national road kill in Sweden are based on only 0.37% of the total mileage driven by all vehicles

in Sweden during the mean reference year of 1992, which means that each collision report must be multiplied by factor of 268 to produce national road kill numbers. As our questionnaire was distributed mainly electronically on the Internet, people without access to the Internet may not have had the possibility to participate in the survey. Also, we primarily addressed people with special interest in wildlife or traffic, such as hunters, field biologists or colleagues from universities and other official authorities. Thus our sample is not representative for the entire Swedish human population. Nevertheless, it seems unlikely that these groups of people experienced a different risk for animal-vehicle collisions than the Swedish average driver. More importantly, however, people who have experienced collisions with wild animals may have felt more encouraged to reply to our questionnaire than those who have not. We therefore expected the returns to be biased towards a higher proportion of positive answers, but we did not find any difference in the ratio of positive to negative answers, nor in the driven mileage or the length of the reference period between public returns and controlled replies. The mean annual mileage driven per respondent was similar among the groups and close to the national average. In addition, the distribution of public replies on counties reflected the variation in the number of inhabitants per county.

Another potential bias in our data derives from the fact that the respondents were free to choose their individual reference period. Although we specifically asked for an independent definition of the reference time, we can not exclude that the onset of this period may still have been influenced by the first well remembered accident. If this was the case, the individual collision frequencies would have been overestimated. More importantly, however, it appears that the risk that people who referred to especially long reference periods may have forgotten incidents that occurred a long time ago, especially if these collisions involved only small animals. This would lead to an underestimation of the collision frequencies and may partly account for the inverse relationship observed between the MCF-values and the length of the reference period in some species. However, the observed correlations between game bags as indices of population trends and MCF-values indicate that the increase in MCF-values may actually reflect an increase in animal abundance. For example, a strong correlation between deer density, deer harvest and deer-vehicle collisions has been observed by several authors (e.g. McCaffery 1973, Groot-Bruinderink & Hazebroek 1996, Seiler in press).

Despite various potential sources of bias our results

appear reasonable in comparison with other independent road kill estimates for Sweden. For example, Göransson et al. (1978) conducted intensive field inventories of road kills in southernmost Sweden during 1973-1976 and extrapolated their findings to produce national road kill estimates. Since their study, the road traffic has increased by 50%, and it seems reasonable to assume that road mortality has also increased in proportion. To obtain comparable road kill estimates for this earlier period, we extrapolated our MCF-values from 1992 with the total mileage driven in Sweden during 1974 (46.4 billion km; Edwards et al. (1999)). Provided that the mean collision frequencies were similar during Göransson et al.'s (1978) study and our survey, our data would suggest a nation-wide road kill of 14,000-21,000 red squirrels, 5,000-9,000 red foxes, 5,000-10,000 hedgehogs, 15,000-24,000 badgers and 4,000-9,000 rabbits during 1974. Assuming that the ratio of road-killed brown hares to mountain hares is similar to the ratio in the hunters' harvest (50.2% during 1973-1976), then our survey suggests a road kill of 17,000-22,000 brown hares in 1974. These figures are in good agreement with Göransson et al.'s (1978) estimates of 24,000 road killed brown hares, 21,000 red squirrels, 10,000 red foxes and 5,000 hedgehogs. Conversely, Göransson et al. (1978) estimated that only 7,000 badgers and 41,000 rabbits were killed on roads annually. Göransson et al.'s (1978) high figure of rabbit casualties is probably biased by the geographical location of their field study in the southernmost part of Sweden; their estimate of the proportional road traffic loss (2.7-10.3% of the total rabbit population) is remarkably close to ours (3.8-7.9%). The only striking divergence between the results reported by Göransson et al. (1978) and our study is the estimate for badger; our estimate of an overall road traffic loss of 8.7-13.3% of the population is 4-6 times higher than the estimate of Göransson and his co-workers.

Another independent road kill estimate derives from police reported ungulate-vehicle collisions. Almkvist et al. (1980) suggested that police records of collisions with moose and roe deer represented about 39% of the true number of incidents during the late 1970s. If this applies to 1992 as well, there were about 55,000 collisions with roe deer and 11,500 accidents with moose in Sweden (based on 21,534 officially registered incidents with roe deer and 4,596 accidents with moose). Our estimates of the nationwide collisions with moose and roe deer closely fit these estimates.

Independent road kill estimates for badger were obtained from mark and recapture studies at Tovetorp (Ahnlund 1980) and Grimsö Wildlife Research Station (Erik Lindström, unpubl. data). In both areas com-

bined, road traffic was responsible for an average of 34% of the known deaths (N = 38), compared to a 45% loss due to hunting. If these two studies are representative at a national level, badger road kills should approximate $\frac{2}{3}$ of the annual game bag. Our estimate of the nationwide road kill in badger indeed ranges within 77-118% of the official harvest.

Conclusion

For most species included in our survey, the level of nationwide road mortality does not appear to be a threat to the survival of the species. Yet, the impact is likely to vary between regions and, locally, road mortality can probably be a significant problem, if not to the survival of a species then to its management. To what extent road density or traffic volume may actually limit population growth in wild mammals, and how this may depend on circumstances, are matters to be further investigated. For this, more accurate estimates of road kills and population sizes are needed.

Our results indicate that drivers' questionnaires can be a practical and inexpensive way of assessing road mortality at a large scale. To improve the statistics, reference periods should be standardised and shortened (e.g. to one year), and driven mileages should be reported more exactly than what was possible to obtain in our study. We agree with e.g. McCaffery (1973), Case (1978), Göransson & Karlsson (1979), Rolley & Lehman (1992) and Loughry & McDonough (1996), who recommended using road kill indices for the monitoring of large and medium-sized mammals.

Acknowledgements - the study was financed by the Swedish National Road Administration. Financial support was also supplied through scholarships from Oscar och Lili Lamms Stiftelser, Olle och Signhild Engkvists Stiftelser and the Centre for Biodiversity. We are grateful for the wide public interest in the study and all voluntary replies we received. Special thanks to Alejandro Rodriguez, Rick Mace and Per Angelstam, and two anonymous referees, who critically read and commented on earlier drafts of this manuscript.

References

- Ahnlund, H. 1980: Aspects of the population dynamics of the badger (*Meles meles*). - PhD thesis, University of Stockholm, Department of Zoology, Stockholm, 103 pp.
- Almkvist, B., André, T., Ekblom, S. & Remppler, S.A. 1980: Slutrapport Viltolycksprojekt. (In Swedish with an English

- summary: Final report of the Game Accident Project). - Swedish National Road Administration, TU146:1980-05, Borlänge, Sweden, 117 pp.
- Anderson, W. & Trehwella, W.J. 1985: Population dynamics of the badger (*Meles meles*) and the epidemiology of bovine tuberculosis (*Mycobacterium bovis*). - Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 310: 327-381.
- Anonymous 1992: Swedish Game - Biology and management. - Swedish Hunters' Association, Uppsala, 159 pp.
- Anonymous 2000: Statistical Yearbook of Sweden. - Statistiska centralbyrån, Stockholm, Stockholm, 710 pp.
- Bengtsson, S.A. 1962: En fallviltundersökning. - Fältbiologen 3: 9-15. (In Swedish).
- Bennett, A.F. 1991: Roads, roadsides and wildlife conservation: a review. - In: Saunders, D.A. & Hobbs, R.J. (Eds.); Nature conservation 2: The role of corridors. Surrey Beatty & Sons, Chipping Norton, pp. 99-118.
- Bergmann, H.H. 1974: Zur Phänologie und Ökologie des Strassentods der Vögel. - Vogelwelt 95: 1-21. (In German).
- Bevanger, K. & Lindström, E.R. 1995: Distributional history of the European badger *Meles meles* in Scandinavia during the 20th century. - Annales Zoologici Fennici 32: 5-9.
- Blaustein, A.R. & Wake, D.B. 1990: Declining amphibian populations: a global phenomenon? - Trends in Ecology and Evolution 5: 203-204.
- Bolund, L. 1974: Trafikdöd. - Djurskyddet 82: 92-95. (In Swedish).
- Boscali, G. 1987: Wolves, bears and highways in Italy. - In: Bernard, J.-M., Lansiaert, M., Kempf, C. & Tille, M. (Eds.); Actes du colloques "Route et fauna sauvage". Strasbourg, 1985. Ministère de l'Équipement, du Longement, de l'Aménagement du Territoire et des Transports, Colmar, France, pp. 237-239.
- Caletrio, J., Fernandez, J.M., Lopez, J. & Roviralta, F. 1996: Spanish national inventory on road mortality of vertebrates. - Global Biodiversity 5: 15-18.
- Case, R.M. 1978: Interstate highway road-killed animals: a data source for biologists. - Wilson Society Bulletin 6: 8-13.
- Child, K.N. 1998: Incidental mortality. - In: Franzmann, A.W. & Schwartz, C.C. (Eds.); Ecology and management of the North American moose. Smithsonian Institution Press, Washington, pp. 275-302.
- Clarke, G.B., White, P.C.L. & Harris, S. 1998: Effects of roads on badger *Meles meles* populations in south-west England. - Biological Conservation 86: 117-124.
- Dickerson, L.M. 1939: The problem of wildlife destruction by automobile traffic. - Journal of Wildlife Management 3: 104-116.
- Edwards, H., Nilsson, G., Thulin, H. & Vorwerk, P. 1999: Trafikarbetet uttryckt i fordonskilometer på väg i Sverige 1950-1997. - Väg- och Transportforskningsinstitut, VTI rapport 439, Linköping, 60 pp. (In Swedish).
- Fahrig, L., Pedlar, J.H., Pope, S.E., Taylor, P.D. & Wegner, J.F. 1995: Effect of road traffic on amphibian density. - Biological Conservation 73: 177-182.
- Fehlberg, U. 1994: Ecological barrier effects of motorways on mammalian wildlife - an animal protection problem. - Deutsche Tierärztliche Wochenschrift 101: 125-129.
- Forman, R.T. & Alexander, L.E. 1998: Roads and their major ecological effects. - Annual Review of Ecology and Systematics 29: 207-231.
- Forman, R.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R., Goldman, C.R., Heanue, K., Jones, J.A., Swanson, F.J., Turrentine, T. & Winter, T.C. 2003: Road ecology - Science and Solutions. - Island Press, Washington, 481 pp.
- Göransson, G. & Karlsson, J. 1979: Changes in population densities as monitored by animals killed on roads. - In: Hytteborn, H. (Ed.); The use of ecological variables in environmental monitoring. Proceedings from the first Nordic Oikos conference, 2-4 October 1978, Uppsala, Sweden. National Swedish Environmental Protection Board, PM 1151, pp. 120-125.
- Göransson, G., Karlsson, J. & Lindgren, A. 1978: Vägars inverkan på omgivande natur. II Fauna. (In Swedish with an English summary: Influence of roads on the surrounding nature. II Fauna.). - Swedish Environmental Protection Agency, SNV PM 1069, Stockholm, 124 pp.
- Groot-Bruinderink, G.W.T.A. & Hazebroek, E. 1996: Ungulate traffic collisions in Europe. - Conservation Biology 10: 1059-1067.
- Hansen, L. 1982: Trafikdræbte dyr i Danmark. (In Danish with an English summary: Road kills in Denmark.). - Dansk Ornitologisk Forenings Tidsskrift 76: 97-110.
- Harris, S., Cresswell, W., Reason, P. & Cresswell, P. 1991: An integrated approach to monitoring badger (*Meles meles*) population changes in Britain. - In: McCullough, D.R. & Barrett, R.H. (Eds.); Wildlife 2001: Populations. Elsevier Applied Science 58, London, pp. 295-311.
- Haugen, A.O. 1944: Highway mortality in southern Michigan. - Journal of Mammalogy 25: 177-184.
- Holm, S. 1979: A simple sequentially rejective multiple test procedure. - Scandinavian Journal of Statistics 6: 65-70.
- Huijser, M.P. 2000: Life on the edge. Hedgehog traffic victims and mitigation strategies in an anthropogenic landscape. - PhD thesis, Wageningen University, Wageningen, NL, 165 pp.
- Jonkers, D.A. & De Vries, G.W. 1977: Verkeersslachtoffers onder der fauna. - Nederlandsa Vereniging tot bescherming van vogels, Zeist, NL, 190 pp. (In Dutch).
- Knutson, R. 1987: A field guide to common animals of roads, streets, and highways. - Ten Speed Press, Berkeley, USA, 88 pp.
- Krebs, C.J. 1989: Ecological Methodology. - Harper Collins Publishers, New York, 654 pp.
- Lalo, J. 1987: The problem of road kill. - American Forests 72: 50-52.
- Loughry, W.J. & McDonough, C.M. 1996: Are road kills valid indicators of armadillo population structure? - American Midland Naturalist 135: 53-59.
- Madsen, A.B. 1990: Otters (*Lutra lutra*) and traffic. - Flora og Fauna 96: 39-46.
- McCaffery, K.R. 1973: Road kills show trends in Wisconsin

- deer populations. - *Journal of Wildlife Management* 37: 212-216.
- McClure, H.E. 1951: An analysis of animal victims on Nebraska's highways. - *Journal of Wildlife Management* 15: 410-420.
- Putman, R.J. 1997: Deer and road traffic accidents: Options for management. - *Journal of Environmental Management* 51: 43-57.
- Rodriguez, A. & Delibes, M. 1992: Current range and status of the Iberian lynx (*Felis pardina*) in Spain. - *Biological Conservation* 61: 189-196.
- Rodts, J., Holsbeek, L. & Muyldermons, S. 1998: Dieren onder onze wielen. - Koninklijk Belgisch Verbond voor de Bescherming van de Vogels, Vubpress, Brussel, 190 pp. (In Dutch).
- Rolley, R.E. & Lehman, L.E. 1992: Relationships among raccoon road-kill surveys, harvests, and traffic. - *Wildlife Society Bulletin* 20: 313-318.
- Romin, L.A. & Bissonette, J.A. 1996: Deer-vehicle collisions: Status of state monitoring activities and mitigation efforts. - *Wildlife Society Bulletin* 24: 276-283.
- Schwabe, K.A. & Schuhmann, P.W. 2002: Deer-vehicle collisions and deer value: an analysis of competing literatures. - *Wildlife Society Bulletin* 30: 609-615.
- Seiler, A. in press: Trends and spatial pattern in ungulate-vehicle collisions in Sweden. - *Wildlife Biology*.
- Seiler, A., Lindström, E.R. & Stenström, D. 1995: Badger activity and abundance in relation to fragmentation of foraging biotopes. - *Annales Zoologici Fennici* 32: 37-45.
- Southwood, T.R. & Henderson, P.A. 2000: *Ecological Methods*. - Blackwell Science Ltd., Oxford, 575 pp.
- Stoner, D. 1925: The toll of the automobile. - *Science* 61: 56-58.
- Svensson, S. 1998: Birds kills on roads: is this mortality factor seriously underestimated? - *Ornis Svecica* 8: 183-187.
- Sylvén, S. 2003: Management and regulated harvest of moose (*Alces alces*) in Sweden. - Doctoral thesis, Swedish University of Agricultural Sciences, Uppsala, 36 pp.
- Ueckermann, E. 1964: Wildverluste durch den Strassenverkehr und Verkehrsunfälle durch Wild. - *Zeitschrift für Jagdwissenschaft* 10: 142-168. (In German).
- Van den Tempel, R. 1993: Vogelslachtoffers in het wegverkeer. (In Dutch with an English summary: Bird casualties in road traffic). - *Vogelbescherming Nederland, Ministerie van Verkeer en Waterstaat, Directoraat-Generaal Rijkswaterstaat, Delft, The Netherlands*, 75 pp.
- Van der Zee, F.F., Wiertz, J., Terbraak, C.J. & Van Apeldoorn, R.C. 1992: Landscape change as a possible cause of the badger *Meles meles* L. decline in the Netherlands. - *Biological Conservation* 61: 17-22.
- Verkaar, H.J. & Bekker, G.J. 1991: The significance of migration to the ecological quality of civil engineering works and their surroundings. - In: Van Bohemen, H.D., Buizer, D.A.G. & Littel, D. (Eds.); *Nature engineering and civil engineering works*. Pudoc, Wageningen, The Netherlands, pp. 44-62.
- Way, J.M. 1970: Wildlife on the motorway. - *New Scientist* 47: 536-537.