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Trends and spatial patterns in ungulate-vehicle collisions in Sweden

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I studied trends and the spatial variation in ungulate-vehicle collisions (UVC) in Sweden varying the spatial resolution in order to test the hypothesis that UVC are proportional to animal density and traffic volume. 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 UVC were studied at national, county and district level covering periods of 30, 16 and 12 years, respectively. During 1970-1999 the overall number of reported collisions with moose *Alces alces* and roe deer *Capreolus capreolus* was closely correlated with changes in annual game bags and the increase in traffic volume. Large-scale spatial variations in UVC also showed a strong correlation with harvest and traffic. The ratio of collision numbers to harvest, however, increased significantly over time, suggesting a growing importance of traffic over ungulate management. With increased resolution, other environmental factors such as preferred habitat, road density and the presence of road underpasses that can provide passages for wildlife, gained significance over ungulate density and traffic volume. My results suggest that the relationship between animal abundance, road traffic, mitigation measures and collision numbers are not linear. For future prediction, evaluation and mitigation of UVC in Sweden, improved knowledge about passage design, fence location, and the occurrence of UVC in time and space is needed.

Key words: Alces alces, automobile, Capreolus capreolus, infrastructure, mitigation, moose, road accidents, roe deer, traffic casualties, traffic safety

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Collisions between motor vehicles and wild ungulates have increased substantially in Europe and North America over the past decades (Ueckermann 1987, Lehnert, Romin & Bissonette 1996, Groot-Bruinderink & Hazebroek 1996). Although ungulate-vehicle collisions (UVC) do not usually cause concern for species extinction (e.g. Groot-Bruinderink & Hazebroek 1996), they are a serious problem in regard to traffic safety, social economics, wildlife management and animal welfare (Child & Stuart 1987, Lavsund & Sandegren 1991, Hartwig 1991, Fehlberg 1994, Schwabe & Schuhmann 2002). In the United States for example, it was estimated that more than half a million deer *Odocoileus* spp. accidents occurred in 1991 (Romin & Bissonette 1996). Similarly, in Europe (excluding Russia), approximately 500,000 collisions occur each year, causing over one billion Euro in material damage (Groot-Bruinderink & Hazebroek 1996). In Sweden, UVC accounted for over 60% of all road accidents reported to the police during the 1990s (Swedish National Road Administration, SNRA, database), with an estimated cost exceeding 100 million Euro per year. On average, Swedish police records until 1999 included approximately 4,500 moose *Alces alces* collisions (MVC) and 24,000 roe deer *Capreolus capreolus* collisions (RVC) each year. In addition, about 3,000 collisions with domestic reindeer *Rangifer tarandus* in the northern counties, 200 collisions with red deer *Cervus elaphus* and fallow deer *Dama dama*, 50 collisions with wild boar *Sus scrofa*, and 250-300 collisions with other wild animals were also registered nationwide each year (SNRA, database). However, not all collisions are detected by the driver, reported to the police, or registered by the SNRA, so the actual numbers of collisions with ungulates are likely to be more than twice as high (Almkvist, André, Ekblom & Rempler 1980). A recent drivers' questionnaire suggested that the true annual numbers of collisions may exceed 10,000 incidents involving moose and 51,000 incidents involving roe deer (Seiler, Helldin & Seiler 2004). Fortunately, < 5% of all animal-related traffic accidents cause human injury, although 10-15 collisions per year are fatal to the vehicle occupants (Seiler & Folkeson 2003). For the involved animals, however, collisions with vehicles are almost always fatal. Approximately 92% of all moose and 98% of all roe deer involved in police-reported vehicle collisions in Sweden died as a consequence of the accident (Almkvist et al. 1980).

Various measures to mitigate UVC have been tested in Sweden (Almkvist et al. 1980, Björnstig, Eriksson, Thorson & Bylund 1986, Skölving 1985), but only exclusion fencing and roadside clearing have proven to work cost-efficiently (Niklasson & Johansson 1987, Nilsson 1987; see also McDonald 1991, Clevenger, Chruszcz & Gunson 2001). Roadside clearance and exclusion fencing have become a standard in Swedish road management. As of 2001, more than 5,000 km of highway have been fenced for moose. The SNRA now plans to significantly expand the fencing and combine fences with specially designed wildlife passages, both to counteract potential barrier effects on moose and to further increase traffic safety (A. Sjölund, SNRA, pers. comm.). However, there is no evaluation of the overall effect of fences or passages on UVC in Sweden, and it has been questioned whether the current understanding of ungulate-vehicle relationships is sufficient to meet future mitigation needs (Putman 1997, Seiler & Folkeson 2003).

In theory, collisions between ungulates and vehicles can only occur where and when both come together. The probability of collisions should therefore be a function of the abundance of animals and vehicles. Various studies suggest that patterns in the distribution of UVC relate to variations in ungulate density and traffic volume, but that topography, amount and distribution of preferred habitat, road characteristics, vehicle speed and other factors can modify this relationship (e.g. Bashore, Tzilkowski & Bellis 1985, Finder, Roseberry & Woolf 1999, Joyce & Mahoney 2001, Nielsen, Anderson & Grund 2003). For example, coniferous forests (especially clearcuts and young plantations) provide important habitats for moose in Sweden and are thus visited by moose more frequently than the less preferred agricultural areas (e.g. Bergström & Hjeljord 1987, Cederlund & Okarma 1988). Consequently, the frequency of moose collisions is higher on roads proximate to young coniferous forests than on roads passing through agricultural areas (Almkvist et al. 1980). Similarly, Kofler & Schulz (1987) observed that collisions with roe deer in Austria were more frequent where roads were located between forest and fields, which reflects the species' preference for rural habitats (e.g. Cederlund, Ljungquist, Markgren & Stålfelt 1980).

Thus, with sufficient knowledge of ungulate abundance, habitat distribution and road and traffic characteristics, it should be possible to predict the risk of UVC and determine appropriate mitigation measures. Ungulate-vehicle collisions are usually spatially and temporally aggregated, which implies that patterns observed at one scale may not necessarily apply at another scale (e.g. Wiens 1989). In my study, I placed special emphasis on the effects of broad landscape scale, testing whether trends and densities of UVC can be explained by estimates of traffic intensity and ungulate abundance. At a finer scale, I also evaluated the influence of habitat, fences and road passages on the occurrence of UVC.

Material and methods

Study design

I used multivariate regression analysis to study factors associated with trends and spatial variations in UVC within and among Swedish administrative units (Fig. 1). Trends in UVC were studied relative to changes in traffic and ungulate harvest at (i) national level between 1970 and 1999, (ii) within counties between 1985 and 1999, and (iii) at the district level between 1986 and 1997. Spatial patterns in UVC, harvest statistics, landscape parameters, road density and traffic volume were studied among (i) 22 counties over a period of 15 years (1985-1999), (ii) 95 districts (from seven counties) covering 12 consecutive years (1986-1997), and (iii) 311 parishes (in 36 districts in three counties) over a period of five years (1993-1997).

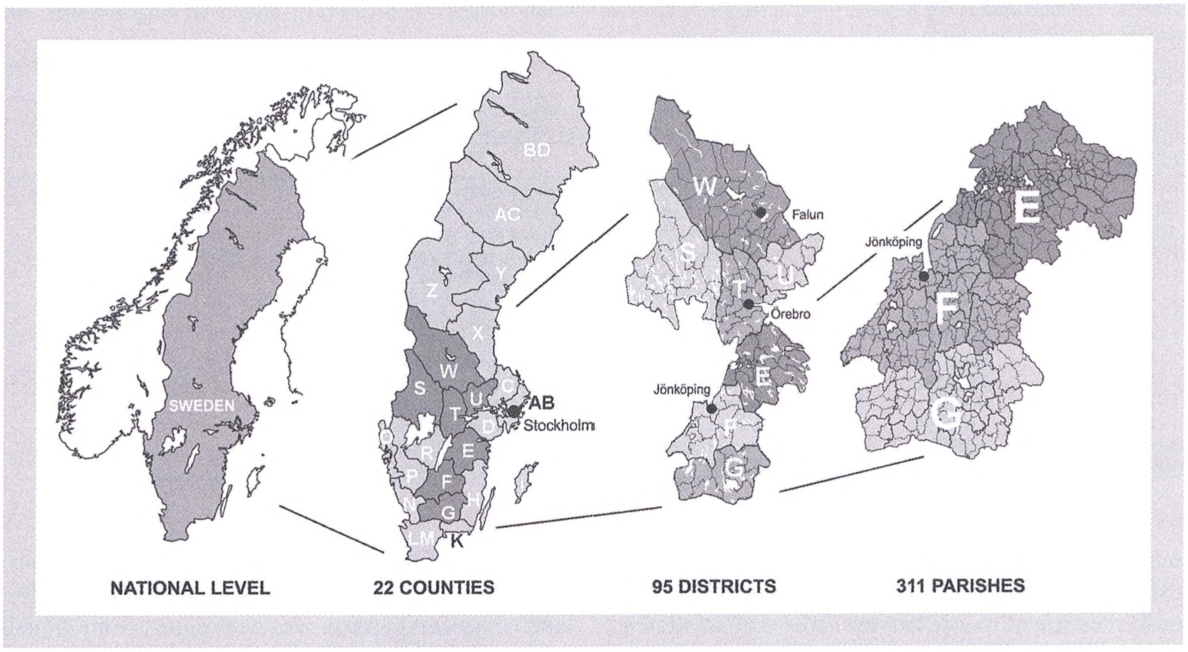

Figure 1. Spatially nested levels of data: Trends in ungulate-vehicle collisions were studied at national level during 1970-1999, at county level during 1985-1999 and at district level during 1986-1997. Spatial patterns were studied among 22 Swedish counties, 95 moose hunting districts within seven counties, and among 311 parishes within three counties during 1993-1997.

These spatially nested levels were due to differences in the extent and the resolution of available data, but allowed for comparisons of large-scale data with long temporal continuity (i.e. national and county level) with small-scaled data covering a greater spatial variation (i.e. district and parish level). The county level is the only reliable spatial resolution for roe deer hunting statistics, whereas moose harvest data are also available at the district and parish levels. Moose populations are typically managed at the district level, but individual hunting teams operate within smaller areas that encompass one or a few individual moose home ranges. The average size of a moose home range (~10 km^2/moose; Cederlund & Okarma 1988) was set at the minimum size for the selection of parishes. Mitigation measures such as wildlife fences or underpasses are best evaluated at the parish level due to the limited extend of available data on their occurrence. At the national and county levels, most data on road traffic, ungulate harvest and collisions were readily available from statistical yearbooks and official databases. At the district and parish levels, all parameters were quantified from official databases and statistics that I linked to digital maps on land cover, administrative borders and roads.

Ungulate-vehicle collisions

Swedish car drivers are obliged to report any vehicle accident involving ungulates to the police, irrespective of where or when it occurred. Since 1970, the SNRA have kept UVC records in a national Road Accident Database. Prior to 1985, only summary statistics were available, but for the period 1985-1999, the database provides information on the exact location of each accident. After 1999, the database was limited and now only records accidents involving human injury or death, which is < 5% of all UVC. The Road Accident Database does not include information on the age or sex of the animals involved. If not stated otherwise, I refer to UVC-densities as the annual frequency of accidents with moose and roe deer per hundred kilometres of public road.

Hunting statistics

Data on the annual harvest of moose and roe deer were used to index trends and spatial variations in the abundance of these species. Although game bag statistics tend to less accurately reflect trends in ungulate populations than hunter observations or pellet counts (Ericsson & Wallin 1999, Solberg & Sæther 1999), only the annual game bag data covered a sufficiently large area or time period required for the analysis. Hunting statistics for moose and roe deer at the national and county levels were provided by the Swedish Association for Hunting and Wildlife Management. At the district and parish levels, moose harvest data were compiled from County Ad-

Table 1. Variables used in the stepwise forward regression analyses at the three spatial levels county (I), district (II) and parish (III); see also Fig. 1.

LEVEL	Dependent variable	
I - III	MVC	Density of moose-vehicle collisions/100 km public road
I - III	RVC	Density of roe deer-vehicle collisions/100 km public road
LEVEL	Independent variables	
I - III	MHT	Moose harvest/1000 hectar land and year
only I	RHT	Roe deer harvest/1000 hectar land and year
only I	MOUNTAIN	Proportion of mountainous land/area (arcsine transformed)
I - III	WETLAND	Proportion of wetland/area (arcsine transformed)
I - III	FOREST	Proportion of forest/area (arcsine transformed)
I - III	URBAN	Proportion of urban habitat/area (arcsine transformed)
I - III	ROAD<70	Density of local roads with speed limits < 70 km/hour (km/km^2)
I - III	ROAD70	Density of county roads with speed limits of 70 km/hour (km/km^2)
I - III	ROAD90	Density of major roads with speed limits of 90 km/hour (km/km^2)
I - III	ROAD110	Density of highways with speed limits of 110 km/hour (km/km^2)
I - III	ROADS	Density of all public, state administered roads (km/km^2)
I - III	TRAFFIC	Kilometres driven by all vehicles combined/average day or year
only III	FENCED	Proportion of public roads with fence against UVC
only III	PASSAGE	Density of road underpasses/100 km public road

ministrative Board records. No roe deer hunting statistics exist at the district or parish level. To obtain a comparable measure of moose harvest across administrative units, I calculated the annual density of moose shot per 1,000 ha of land, quantified from digital topographic maps.

Road and traffic data

The length of public roads and averaged traffic volumes at the national and county levels were combined from data in Statistical Yearbooks of Sweden (Statistics Sweden 1970-2000), from Edwards, Nilsson, Thulin & Vorwerk (1999), and from digital road maps provided by the SNRA. For each area, I calculated the overall traffic volume ('TRAFFIC') as the summed kilometres driven by all vehicles combined during an average day or year. The density (km/km^2) of public, i.e. state administered roads, was separately calculated for roads with different speed limits ('ROAD<70, ROAD70, ROAD90, ROAD110'; Table 1). These speed categories largely coincide with road standards such as local roads, county roads, national roads and international roads, but do not necessarily relate to traffic volume.

Exact information on the location of wildlife fences was available for only three counties and was therefore considered at the parish level only. I calculated the proportion of unfenced public roads ('UNFENCED'), and the density of road underpasses and bridges ('PASSAGE') per hundred kilometres of road. The passages were constructed for private or local roads crossing larger highways or motorways, but may occasionally be used by wildlife as well (A. Seiler, unpubl. data).

Land cover

Data on the composition of land cover at the county level were obtained from Swedish Statistical Yearbooks (Statistics Sweden 2000). Within districts and parishes, land cover composition was determined from digital topographic maps provided by the Swedish National Land Survey. Major land cover types were distinguished as forest (including deciduous and coniferous forest), wetland (peat bogs, mires), open land (mostly agricultural land), urban areas and mountains (see Table 1).

Statistics

Land cover proportions were transformed using the arcsine transformation to compensate for skewed distributions (Zar 1999). I used univariate and stepwise multivariate regression analyses, as well as analyses of covariance to evaluate the influence of the selected independent environmental variables on the number and density of UVC. To reduce intercorrelation between the predictor variables, I omitted those variables from further use that were highly ($R > 0.75$) correlated with others (Zar 1999). As the proportion of open land inversely relates to the proportion of forest, I excluded this category from further regression analysis. If required by the logic of the relationship, for example when testing the correlation between road length and collision numbers, intercepts were set at zero. In stepwise multiple regression analyses, the required minimum F-value to enter a new independent variable was set at $F = 4$. In all analyses, the significance level was set at $P < 0.05$. In repeated statistical tests on the same dataset, I used the sequential Bonferroni correction (Rice 1989) to adjust the significance level and reduce the risk of Type I errors. Calculations were performed using the statistical software package STATISTICA (StatSoft 1999).

Table 2. Multiple regression results for trends in vehicle collisions with moose and roe deer in relation to traffic intensity (billion kilometres driven by all motor vehicles) and the nationwide annual harvest in both species between 1970 and 1999 in Sweden. For moose: overall model $P < 0.0001$, $R^2 = 0.85$, $F(2,27) = 77.92$; for roe deer: overall model $P < 0.0001$, $R^2 = 0.94$, $F(2,27) = 218.84$.

Species	Variables	Coefficient	SE	Partial F	Partial P	multiple R^2
Moose	Intercept	-1272	569			
	Traffic	60.85	15.12	15.2	0.0004	0.853
	Harvest	0.029	0.0031	93.2	<0.0001	0.765
Roe deer	Intercept	-25649	3123			
	Traffic	845.09	103.52	347.7	<0.0001	0.925
	Harvest	0.022	0.0079	7.57	0.0105	0.942

Results

Trends in moose and roe deer-vehicle collisions

Between 1970 and 1999, UVC in Sweden showed significant variation (Fig. 2). The steadily increasing traffic (about 1.5% increase per year) and changes in the annual harvest in moose and roe deer as an index of ungulate abundance explained 85% and 94% of the trends in MVC and RVC, respectively (Table 2). In both species, harvest statistics appeared as the primary correlate with the number of collisions over time, while traffic explained most of the residual variation (moose: univariate $R^2 = 0.72$, $N = 30$, $P < 0.0001$; roe deer: univariate $R^2 = 0.15$, $N = 30$, $P = 0.036$).

Practically all variation in annual MVC between 1970 and 1980, when MVC increased approximately 6.6 fold from 902 incidents to 5,951, can be explained by the concurrent increase in moose harvest and traffic intensity (multivariate adjusted $R^2 = 0.99$, $N = 11$, $P < 0.0001$). After the peak in 1980, however, traffic continued to increase, whereas moose harvest and MVC decreased slightly but remained correlated (univariate $R^2 = 0.22$, $N = 19$, $P = 0.026$). However, during both the increasing and decreasing phases, changes in MVC seemed to precede changes in moose harvest by two years (for the entire period: $R^2 = 0.81$, $N = 28$, $P < 0.0001$; for the increase phase 1970-1980: $R^2 = 0.98$, $N = 17$, $P < 0.0001$; for the decrease phase 1981-1999: $R^2 = 0.69$, $N = 19$, $P < 0.0001$). In roe deer, no time lag was observed in the correlation between collision numbers and the annual harvest. The annual harvest of roe deer was significantly correlated with the extent of collisions between 1970 and 1993, when RVC numbers rose 30.5 times; from 925 to 24,797 ($R^2 = 0.93$, $N = 24$, $P < 0.0001$). After 1993, harvest numbers dropped significantly, but RVC remained at a high level, probably due

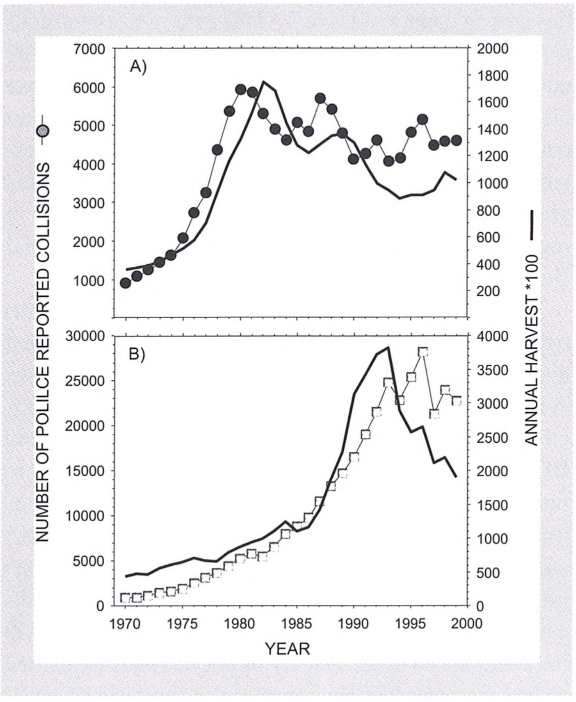

Figure 2. Trends in ungulate harvests correlate significantly with the number of police reported vehicle collisions with moose (A; $R^2 = 0.77$, $N = 30$, $P < 0.0001$) and roe deer (B; $R^2 = 0.81$, $N = 30$, $P < 0.0001$) during 1970-1999 in Sweden.

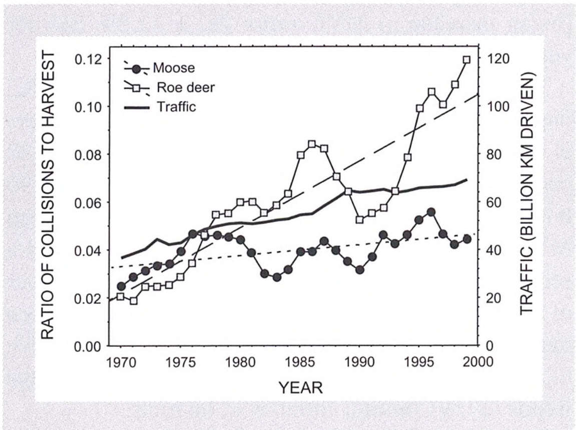

Figure 3. Development in the ratio of vehicle collision numbers to the annual harvest in roe deer and moose compared with the annual change in traffic volume in Sweden. The mean annual increase rate in the collision/harvest ratio in roe deer (6.8%) was significantly higher than the change in traffic (2.3%; $t = 26.37$, $df = 56$, $P < 0.0001$), whereas there was no difference in increase rate between traffic (2.3%) and the moose ratio (2.2%).

Table 3. Results of stepwise forward regression models on the density of vehicle collisions with moose and roe deer at the three levels of spatial resolution county, district and parish. For all models, F-to-enter was set at 4. Coefficients and R^2-values refer to full multivariate models. For description of the included variables, see Table 1.

Level	Variable	Step	Coefficient	SE	Partial F	Partial P	Multiple R^2
Moose-vehicle collisions							
COUNTY (N = 22)	*Intercept*		*1.288*	*0.730*			
1985-1999	MHT	1	1.102	0.202	29.78	<0.0001	0.598
DISTRICT (N = 95)	*Intercept*		*-3.796*	*1.444*			
1986-1997	MHT	1	0.806	0.196	28.49	0.0001	0.234
F(3.91) = 21.43	WETLAND	2	0.106	0.028	17.99	0.0002	0.360
	FOREST	3	0.078	0.027	8.42	0.0046	0.414
PARISH (N = 311)	*Intercept*		*0.912*	*1.218*			
1993-1997	ROAD70	1	-0.047	0.015	75.48	0.0015	0.196
F(7.303) = 36.84	WETLAND	2	0.105	0.019	33.59	<0.0001	0.275
	ROAD90	3	0.14	0.022	30.82	<0.0001	0.341
	FOREST	4	0.052	0.014	30.07	0.0002	0.400
	PASSAGE	5	-0.141	0.039	14.20	0.0003	0.427
	ROAD110	6	-0.090	0.024	5.52	0.0002	0.437
	TRAFFIC	7	0.0165	0.0046	12.64	0.0004	0.460
Roe deer-vehicle collisions							
COUNTY (N = 22)	*Intercept*		*9.589*	*3.225*			
1985-1999	RHT	1	1.078	0.210	26.30	<0.0001	0.568
DISTRICT (N = 95)	*Intercept*		*7.38*	*9.33*			
1986-1997	WETLAND	1	-0.656	0.147	32.74	<0.0001	0.260
F(3.91) = 18.16	URBAN	2	1.436	0.360	11.84	0.0001	0.345
	FOREST	3	0.263	0.126	4.32	0.0405	0.374
PARISH (N = 310)	*Intercept*		*0.891*	*4.727*			
1993-1998	ROAD90	1	1.14	0.13	137.56	<0.0001	0.309
F(6.303) = 51.69	URBAN	2	1.480	0.189	38.32	<0.0001	0.385
	PASSAGE	3	-1.043	0.258	23.43	0.0001	0.429
	FOREST	4	0.226	0.077	18.41	0.0036	0.462
	ROAD110	5	-0.69	0.15	7.86	<0.0001	0.475
	TRAFFIC	6	0.127	0.029	18.78	<0.0001	0.506

to the continued increase in traffic (univariate R^2 = 0.79, N = 6, P < 0.0001). However, the ratio between collision numbers and the annual harvest in roe deer increased with a significantly higher rate per year (6.8 ± 13.0% SD) than expected from the increase in traffic (2.3 ± 3.0% SD; t = 29.71, df = 56, P < 0.0001). For moose, there was no difference between the increase rates (mean increase in MVC ratio: 2.2 ± 12.5% SD per year; Fig. 3).

The strong relationships between trends in UVC, ungulate harvest and traffic observed at the national level were not observed at finer scales. Only in three of 22 counties (county LM, H and X), and in none of the 90 hunting districts, were univariate regressions between MVC densities and moose harvest significant after a sequential Bonferroni correction. In roe deer, only four of 22 counties revealed a significant relationship between harvest and accident numbers over time (county LM, N, P and Y). There was no effect of traffic on the trends in UVC within counties or districts.

Spatial variations

County level

Geographic differences in the abundance of moose and roe deer, indexed on the basis of game bags, appeared as the primary correlates with UVC at the county level, explaining 57% of the variation in collision densities among counties (Table 3). This pattern has been consistent over time; in any year between 1985 and 1999 counties with a larger harvest in roe deer or moose also suffered a higher frequency of RVC or MVC than counties with smaller game bags (Fig. 4). Linear regression of annual county harvests and UVC densities yielded P-values of < 0.007 in moose, and < 0.010 in roe deer (all of which were significant in a sequential Bonferroni test).

Maximum average density of MVC (8.6/100 km) occurred in county S, which also showed the highest average game bag (5.5 moose/1,000 ha land; Table 4). A minimum of 1.7 and 2.4 MVC/100 km were reported in the very southern and northern counties (LM and BD; see Fig. 1), where average moose harvests were below 1.1 moose/1,000 ha. Similarly, RVC densities were smallest in the northernmost counties (BD and AC; < 0.5 RVC/100 km) where roe deer harvests were marginal, but peaked with 50 RVC/100 km in the south-eastern counties K and H with harvests >25 deer/1,000 ha. Differences in the density of public roads explained a significant part of the variation in the ratio of collision numbers to harvest (moose: R^2 = 0.95, df = 21, P < 0.0001; roe deer: R^2 = 0.51, df = 21, P = 0.0001; intercepts set at zero). In moose, the ratio varied from 1.5%

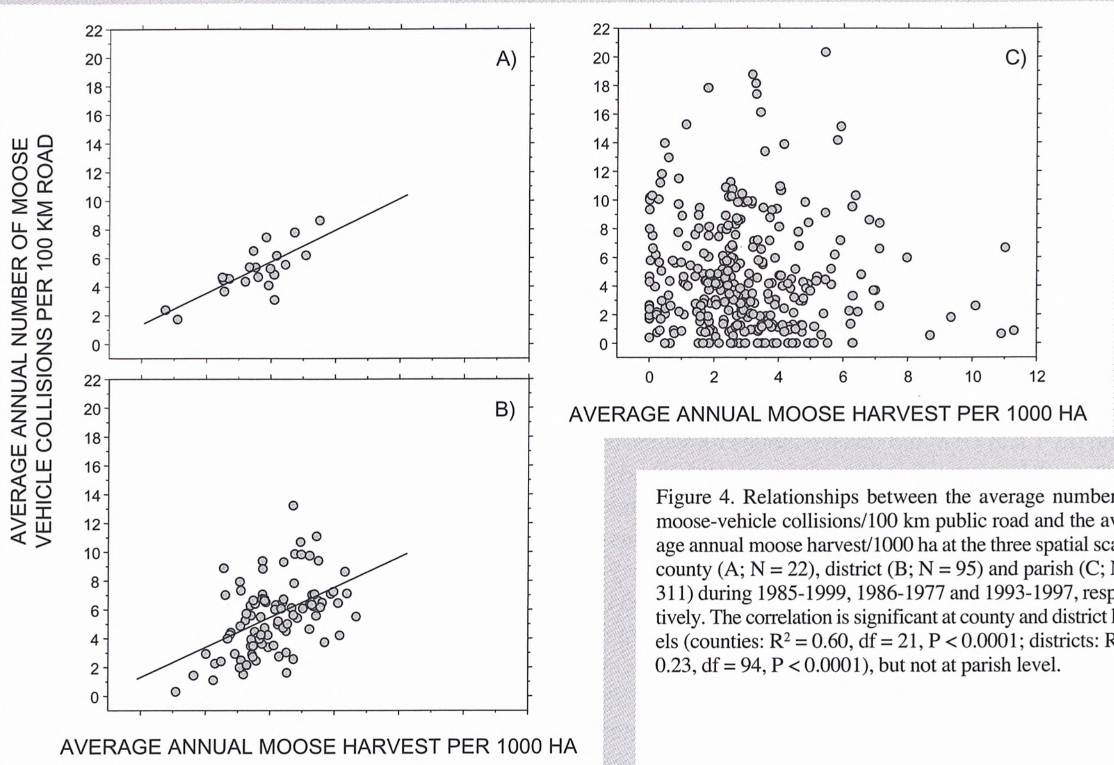

Figure 4. Relationships between the average number of moose-vehicle collisions/100 km public road and the average annual moose harvest/1000 ha at the three spatial scales county (A; N = 22), district (B; N = 95) and parish (C; N = 311) during 1985-1999, 1986-1977 and 1993-1997, respectively. The correlation is significant at county and district levels (counties: $R^2 = 0.60$, df = 21, $P < 0.0001$; districts: $R^2 = 0.23$, df = 94, $P < 0.0001$), but not at parish level.

to 19.3% in individual years and counties, averaging 5.8% at national level (see Table 4). In roe deer, the ratio ranged within 2-92.6% (see Table 4).

County land cover correlated with ungulate harvests, but was subordinate in its effect on UVC and did not enter the multivariate models. Moose harvests

Table 4. Descriptive statistics for all variables included in multiple regression analyses. For explanation of variables, see Table 1.

	Counties (N = 22)				Districts (N = 95)				Parishes (N = 311)			
Variables	Mean	SD	Min	Max	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
MVC /100km	5.07	1.66	1.73	8.63	5.63	2.39	1.10	13.2	4.65	3.87	0	20.3
MHT / 10km^2	3.43	1.16	0.72	5.50	4.20	1.08	1.63	6.67	2.94	1.98	0	11.3
MVC/MHT %	5.83	3.05	1.51	19.3	5.28	3.87	0.91	21.9	12.8	20.5	0	200
RVC /100km	29.5	15.7	0.55	50.0	26.2	11.8	1.41	52.2	35.4	25.1	1.51	137
RHT / 10km^2	14.5	9.95	0	30.4	-	-	-	-	-	-	-	-
RVC / RHT % *	12.2	11.9	2.01	92.6	-	-	-	-	-	-	-	-
MOUNTAIN %	11.0	9.22	1.44	35.6	-	-	-	-	-	-	-	-
WETLAND %	6.85	5.35	1.02	17.8	5.80	6.35	0.07	26.2	4.32	7.20	0	46.9
FOREST %	60.6	12.8	34.6	80.8	75.4	10.8	44.1	92.1	64.0	22.7	2.6	94.2
OPEN %	16.8	12.9	0.61	51.7	16.9	12.1	0.78	53.2	29.3	22.9	2.7	97.4
URBAN %	4.73	3.36	0.51	14.2	1.89	1.38	0	7.21	2.41	5.10	0	43.0
ROAD<70**	4.56	2.94	0.52	10.3	3.25	2.98	0	23.2	4.44	6.39	0	45.5
ROAD70**	24.0	10.7	3.12	37.1	20.3	10.3	1.62	43.3	33.3	14.1	4.97	92.1
ROAD90**	9.30	3.30	3.26	15.1	9.09	5.12	0.59	32.1	10.6	9.27	0	46.9
ROAD110**	2.53	2.65	0	11.0	1.32	2.95	0	15.6	2.97	8.53	0	58.3
ROADS**	40.4	17.2	9.06	65.5	34.0	16.0	3.00	67.5	51.2	18.4	19.9	127
TRAFFIC ***	2.06	1.04	0.75	5.22	313	297	36.9	1649	42.8	50.4	1.22	432
FENCED	-	-	-	-	-	-	-	-	4.42	9.62	0	45.5
PASSAGE	-	-	-	-	-	-	-	-	1.86	5.28	0	45.7
Area (km^2)	18536	22540	2941	98911	869	593	94	3829	85.5	58.6	10.1	381

* The ratio of collision to harvest is based on individual areas and years (county N = 330; district N = 1,140, parish N = 1,550).

** Road densities are given as 100 km/km^2.

*** Traffic at county level is given as billion kilometres driven per year, at district and parish levels as 1,000 km per day.

were largest in counties dominated by forests ($R^2 = 0.44$, df = 21, P = 0.0008), whereas roe deer harvests increased with the proportion of urban habitats ($R^2 = 0.45$, df = 21, P = 0.0007) and decreased with an increasing proportion of wetlands ($R^2 = 0.64$, df = 21, P > 0.0001).

District level

At the scale of moose management districts, the relationship between moose harvest and MVC was weaker than at county level, but still significant ($R^2 = 0.23$, df = 94, P < 0.0001). Correlations were significant in three (E, T and U) of the seven counties for which data were available, yet none of the regressions remained significant in a sequential Bonferroni test. In general, however, districts with a large average moose harvest during 1986-1997 also suffered a high frequency of moose vehicle collisions during the same period (see Fig. 4). Multivariate regression suggested that an additional 18% of the variation in MVC among districts was explained by differences in the proportion of wetland and forest (see Table 3). The ratio of accidents to moose harvest increased with road density ($R^2 = 0.64$, df = 94, P < 0.0001; intercept set at zero) and traffic volume ($R^2 = 0.41$, df = 94, P < 0.0001; intercept set at zero). Within individual years and districts, the ratio reached as high as 40%, but averaged 5.9% over the 12 years (see Table 3).

No hunting statistics were available at the district level for roe deer. However, stepwise multiple regressions showed that the proportion of wetlands, urban areas and forests per district explained 37% of the variation in RVC (see Table 3).

Parish level

Within moose management districts, at the level of individual parishes, there was no relationship between MVC and moose harvest (see Table 3). However, the density of UVC increased with the proportion of forest cover, the density of roads with speed limit of 90 km/hour and with traffic volume. High-speed roads and underpasses were correlated with a decrease in UVC densities, whereas fencing had no effect. The ratios of MVC to moose harvest averaged 12.8% over all parishes, but in individual areas and years, up to four times more moose were involved in road accidents than were killed by hunters (see Table 3). Differences in the road density explained 32% of the variation in the ratio among parishes ($R^2 = 0.32$, df = 300, P < 0.0001; intercept set at zero).

Discussion

Trends

The significant change in ungulate-vehicle collisions that occurred in Sweden during the past three decades can mainly be attributed to the increase in ungulate density and vehicle traffic. Game bag statistics, as an index of ungulate abundance, were the primary correlate with collision numbers in this analysis, whereas traffic explained a significant part of the residual variation and retained collision numbers at high levels while population sizes declined. Trends in moose and roe deer populations have been strongly biphasic due to changes in food availability, predation and harvest regimes. Large-scale changes in forestry created favourable habitat conditions for moose, which, coupled with restrictive and selective hunting quotas and a virtual lack of large predators, accelerated the growth of the population during the 1970s (Lavsund & Sandegren 1989). By the winter of 1981/82, the Swedish moose population was estimated at approximately 315,000 animals, which was probably one of the highest national moose densities recorded worldwide (Lavsund & Sandegren 1989). The considerable damage to forestry and agriculture due to high moose densities and the drastic increase in MVC called for a substantial reduction in the Swedish moose population (Cederlund & Markgren 1987). Consequently, hunting quotas peaked with more than 175,000 moose shot in autumn 1982. Quotas were reduced to approximately 100,000 animals in the following years (Swedish Association for Hunting and Wildlife Management, database). Moose-vehicle collisions followed a similar pattern, although changes in MVC preceded changes in the harvest by two years. Also the Swedish roe deer population went through a significant increase and expansion during the 1980s and early 1990s (Swedish Association for Hunting and Wildlife Management, database). The increase was likely a response to a series of mild winters, coupled with the outbreak of Sarcoptic mange that significantly reduced the population of the red fox *Vulpes vulpes* (Lindström, Andrén, Angelstam, Cederlund, Hörnfeldt, Jäderberg, Lemmell, Martinsson, Sköld & Swenson 1994, Cederlund & Liberg 1995) which is the main predator on roe deer fawns. In 1993, roe deer harvest peaked at 382,000 animals. Since then, roe deer densities and game bags dropped substantially, due in part to the recovering populations of red fox and Eurasian lynx *Lynx lynx* (Andrén, Liberg & Sand 1999). The number of RVC remained consistent over the early years, but stabilised after 1993 at > 20,000 per year.

As with moose, the deviation between trends in RVC and roe deer harvest is probably a result of the steadily increasing traffic. In contrast to moose, however, the ratio of collisions to harvest in roe deer has increased three times faster than traffic. This suggests a non-linear relationship between traffic volume, harvest and accident numbers or the influence of a fourth, maybe behavioural, factor that makes it difficult to foresee future trends in RVC. Also in The Netherlands, the increase in RVC during 1985-1995 was five times as high as the increase in roe deer densities or traffic volume (Groot-Bruinderink & Hazebroek 1996). A similar pattern was described by Oosenbrug, Mercer & Ferguson (1991), who observed that a 46% increase in traffic and a 23% increase in moose harvest produced an 89% increase in MVC during 1983-1989 in Newfoundland. One complication in projecting moose collision numbers from harvest and traffic statistics is the time lag of 1-2 years between actual population densities and harvest statistics. The time lag occurs because the numbers of hunting licenses in any given year are based on previous years' game bags and population surveys (e.g. Cederlund & Markgren 1987). My results suggest a time lag of two years between MVC and moose harvest, but no time lag in roe deer. Roe deer hunting in Sweden is not regulated by licenses as is moose hunting, so that game bags may directly relate to changes in roe deer densities. Rather than predicting ungulate collision numbers from current hunting statistics, it may thus be more appropriate to use accident statistics in the planning of future hunting quotas. Using road kill statistics (corrected for traffic volumes) as a large-scale index of wildlife populations has been suggested previously (Jahn 1959, McCaffery 1973, Hicks 1993).

Spatial patterns

Strong relationships between trends and spatial patterns in ungulate densities and UVC have been found in many studies (e.g. Bellis & Graves 1971, Désiré & Recorbet 1987, Oosenbrug et al. 1991, Jaren, Andersen, Ulleberg, Pedersen & Wiseth 1991), but not in all (e.g. Del Frate & Spraker 1991, Groot-Bruinderink & Hazebroek 1996). McCaffery (1973), for example, observed significant correlations between antlered buck harvest and road kills in white-tailed deer *Odocoileus virginianus* in 28 of 29 management areas in Wisconsin. Puglisi, Lindzey & Bellis (1974) reported positive relationships between county deer population estimates, deer harvest and collision numbers among 15 counties in Pennsylvania. My findings suggest that county UVC and district MVC were significantly related to harvest statistics.

Adaptive management of ungulate populations may appear as an implicative measure against UVC, albeit it is hardly considered as a possible option (e.g. Putman 1997, Keller, Alvarez, Bekker, Cuperus, Folkeson, Rosell Pagés & Trocmé 2002). Large-scale reductions in ungulate densities may likely have a counteractive effect on UVC, but it will be difficult to find political or public support for such action. Local reductions, on the other hand, can more easily be achieved, but may not have 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 UVC and local deer populations through intensified hunting indicated success. Joyce & Mahoney (2001) documented that the risk of MVC along the Trans-Canada Highway in Newfoundland was elevated in areas with both scarce and dense moose populations, but reduced in intermediate areas. The authors expressed doubt as to whether a simple management for reduced moose densities would decrease MVC. Also Almkvist et al. (1980) questioned the effect of local density control on traffic safety, as they did not find a significant relationship between local moose harvests, i.e. density, and the local frequency of MVC in Sweden during the 1970s. Similarly, I observed that there was no relation between moose harvest and the density of collisions at parish level, although it was significant at the district and county level. Despite the strong relationship between trends in harvest, traffic and UVC at the national level, there was no consistent relationship within counties and, especially, nor within moose hunting districts.

The more complex patterns at higher spatial resolution are likely due to the emerging influence of local factors such as the animal's habitat use and behaviour, proximity to and juxtaposition of preferred habitat near roads, road and roadside specifications, vehicle speed, or the presence of mitigation measures (e.g. Bashore et al. 1985, Hartwig 1993, Finder et al. 1999, Hubbard, Danielson & Schmitz 2000, Madsen, Strandgaard & Prang 2002). UVC are usually spatially and temporally aggregated, which implies that patterns observed at broad scale may not necessarily apply at a finer scale. Also, local density measures may produce a misleading picture of local collision risks as density necessarily refers to comparatively large areas encompassing many individuals' home ranges. Harvest data may provide a reasonable index of moose abundance at broad scales, encompassing several management areas or populations, but will fail to reflect local variations in abundance at finer scales, if the spatial extent covers but a few individual home ranges and hunting licences are decided upon other criteria than local animal abundance.

At the parish level, UVC densities were significantly related to preferred habitat, road density and occurrence of underpasses. For moose, clearcuts and young forests provide important staple forage. Wetlands, marsh-lands and moist coniferous forests are preferred habitats especially during snow free periods (e.g. Markgren 1974, Bergström & Hjeljord 1987, Cederlund & Okarma 1988) as they provide sources of protein and sodium (e.g. Jordan 1987). Conversely, roe deer in Sweden are more often found in rural habitats, agricultural land and clearcuts, while feeding on grasses and herbs primarily during the summer months (Cederlund et al. 1980). This may explain why the RVC density was increased with the proportion of urban areas at the parish and district levels.

In addition, collision densities were positively correlated with the density of roads with speed limits of 90 km/hour (i.e. major national roads), but inversely related to minor roads (70 km/hour) and motorways (110 km/hour). At lower speeds, drivers presumably have more reaction time to prevent such collisions. Roads with high speed limits and traffic volumes are more often protected by fences or extensive roadsides than minor roads. Also, heavy traffic may deter animals from entering the roadway and thereby prevent UVC from occurring (e.g. Skölving 1987, Berthoud 1987).

Mitigation measures

I found a significant inverse correlation between the density of road passages and the density of both MVC and RVC among parishes. This suggests that even conventional road bridges and tunnels may reduce animal-vehicle collisions. The use of such passages by animals has been documented elsewhere (e.g. Rodriguez, Crema & Delibes 1996, Yanes, Velasco & Suarez 1995, Clevenger & Waltho 2000). Conversely, Hubbard et al. (2000) observed that the density of bridges increased the likelihood of UVC in Iowa, probably because bridges were associated with travel corridors that funnel deer across the roads (e.g. Finder et al. 1999).

In contrast to my expectations, there was no effect of fencing on the density of UVC at parish level. Earlier studies conducted by the SNRA indicated that fencing could reduce the risk of MVC by more than 80% and RVC by up to 55% (Skölving 1987, Niklasson & Johansson 1987). However, because only 4.5% of all public roads within the parishes I studied were fenced, the expected reduction in the number of collisions would be 3.6% in MVC and 2.5% in RVC. These values are well within the confidence limits of the variation in UVC densities among parishes. In addition, where fences terminate or get interrupted by local roads or water courses, accident rates tend to be increased (Ward 1982, Niklasson & Johansson 1987, Foster & Humphrey 1995). It is not uncommon that moose break through or jump over fences if they do not find a safer passage across the road (e.g. Nilsson 1987, Seiler, Cederlund, Jernelid, Grängstedt & Ringaby 2003). Thus the overall effect of fencing on UVC numbers may be smaller than previously suggested. Also at the national level, the effect of fencing is likely only marginal. In the past 25 years, approximately 5,000 km (34%) of motorways and major national roads have been fenced against wildlife (A. Sjölund, SNRA, pers. comm.). About half of all UVC recorded during this period, occurred on such roads. If all fences were equally efficient, we may thus expect a 13.6% reduction in the risk of moose-vehicle collisions, and a 9.35% reduction in the risk of roe deer collisions nationwide. Also these reductions are smaller than the variation in UVC from year to year. On the other hand, the proportion of UVC involving human injury or death in Sweden decreased from 5% in 1983 to 2.2% in 1999 (SNRA, database). This decrease contrasts the growing rate of human injuries in other, non-wildlife related road accidents (+20%) and may approve for some beneficial effect of fencing, particularly at high-speed roads. Nevertheless, fencing is probably still the most efficient and practical way to keep large ungulates off the road.

Conclusion

Successful prediction and mitigation of UVC must be done with respect to spatial and temporal scale. Although the correlation between ungulate densities and UVC is highly significant at large scale, local density control may not necessarily give the desired reduction in UVC occurrence. Technical mitigation measures such as fences or wildlife passages are site specific, but endure several decades. Fence or passage efficacy in preventing UVC is probably independent of the density of animals or vehicles. If combined with traffic adjustments, such as reduced speed limits or rerouting of traffic flow, traffic safety may further be improved. My findings suggest that passages for wildlife may be a realistic counteractive option for the road planner as already conventional road underpasses have a significant effect on UVC occurrence. For future prediction, evaluation, and mitigation of UVC in Sweden, improved knowledge about passage design, fence location, and the occurrence of UVC in time and space is needed. I strongly advise the SNRA to improve their road and road accident database at the national level.

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