

Road mortality in Swedish badgers (*Meles meles*): Effect on population

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Abstract

We evaluated the effect of road mortality on population dynamics in Swedish badgers and estimated the critical level of road mortality that the population can sustain without decline. We used life table analysis and matrix population models to assess a stable age-structure and population growth. Estimates of age structure, fecundity, and sex ratio among road-killed badgers were obtained from 76 carcasses that we collected from public roads during April to September 2001, and from existing estimates in literature. There was no difference in fecundity or sex ratio between our sample and literature data, but the age structure among road-kills was skewed towards a higher proportion of adults and subadults than expected from the population model. The difference in growth rates and predicted losses between the population model and three alternative roadless models in which mortality was reduced by a age-specific proportion solely attributed to road traffic, suggested that losses due to road traffic respond for 12-13% of the post-breeding population. Since the population model predicted a nearly stationary growth rate, these estimated mortality levels were considered equivalent to the maximum sustainable loss. The predicted critical loss was similar to independent estimates of the present number of road-killed badgers in Sweden. Assuming the number of road-killed badgers being proportional to traffic intensity, and with regard to the quantified sources of uncertainty, we predict that between 1978 and 2049 nationwide road traffic will kill more badgers than the population can sustain without declining. Thus, this critical threshold may already be exceeded in areas of low badger density and of high traffic loads. We recommend taking greater concern for this species when planning and maintaining roads in such areas in Sweden.

Keywords: Conservation, ecological impact, infrastructure, road-kill, sustainability, traffic casualties, wildlife management

Introduction

For many decades, road mortality in wildlife has been of concern to biologists (e.g. Stoner 1925, McClure 1951, Way 1970, Bennett 1991, and Seiler 2003). In many wild mammals, road traffic has probably become the leading direct human cause of death, and even in game species, the toll of the automobile can be substantial (Forman & Alexander 1998). Species that are most exposed to road traffic are typically wide-ranging animals and habitat generalists, while species that are sensitive to road mortality are long-lived and slow reproducing (Verkaar & Bekker 1991, Forman et al. 2003). Such behaviour and life history traits are typical for carnivores including the badger (*Meles meles*) (Van der Zee et al. 1992, Aaris-Sorensen 1995, Davies, Roper, & Shepherdson 1987, Revilla, Palomares, & Delibes 2001).

Badgers are well recognized among road-kills across Europe, and there are indications that road mortality can be substantial both at local and metapopulation level (Lankester et al. 1991, Griffiths, Griffiths, & Thomas 1993). Road traffic is considered the largest single cause of death in British badgers (Neal 1986), amounting to over 50,000 individuals per year or 20% of the population (Harris et al. 1991, Neal & Cheeseman 1996). Also in the Netherlands (Lankester et al. 1991, Wiertz 1993), and Denmark (Aaris-Sorensen 1995), road traffic probably kills between 15-20% of the living populations. Road mortality has been made responsible for local declines in British (Clarke, White, & Harris 1998) and Dutch badger populations (Van der Zee et al. 1992). Considerable effort with tunnelling and fencing of roads has been made in the Netherlands to reduce badger mortality to a level that allows the recovery of the population (Broekhuizen & Derckx 1996, Bekker & Canters 1997).

In Sweden, badgers are common throughout southern and central regions and many people, especially hunters, consider the species as being overabundant rather than rare. Badger density approximates 2-3 adults per km² in south-central Sweden (Seiler, Lindström, & Stenström 1995), but decreases substantially northwards. Individual badgers have been reported up to 67° north (Bevanger & Lindström 1995). Game bags, for example, averaged 20-25 badgers per 100 km² during 1983 to 2000 in southern Sweden, but less than one badger per 100 km² in the arctic-boreal Northwest (Swedish Association for Hunting and Wildlife Management, database). Official game bags in badgers have been relatively stable for the past two decades, averaging 28,000 animals (\pm 3,140 S.D.) each year, and it is commonly believed that the badger population keeps a rather constant size of up to 350,000 individuals, the largest national total in Europe (Bergström et al. 1992, Griffiths & Thomas 1993, Bevanger & Lindström 1995). Road mortality was for long not considered significant to the Swedish badger population, since inventories of road-kills made during the 1970's suggested as few as 7,000 badger casualties per year (Göransson, Karlsson, & Lindgren 1978).

However, a recent study suggested a four times larger loss due to road traffic: between 22,000 and 33,000 badgers were supposedly killed on Swedish roads in 1992 (Seiler, Helldin, & Seiler, in press). This trend is likely upward as traffic intensity increases steadily (about 1.5% per year, SIKa 2002). If road mortality

increases while other mortality factors remain constant, traffic will eventually kill more badgers than the population can sustain without declining. This critical level of road mortality depends on badger population dynamics, the proportional road mortality, and whether or not traffic losses can be compensated by increased fecundity or survival. In addition, if traffic kills selectively of age and gender, the impact of road traffic on badger populations may be more severe than suggested by the simple proportional loss. Empirical studies suggest that adults and fecund females are overrepresented among road-kills (e.g. Jefferies 1975, Ahnlund 1980a, Page, Ross, & Langton 1994). Thus, is there reason for concern?

In this paper, we explore the effect of road mortality on badger population dynamics using age-classified models based on published estimates of fecundity and mortality coupled with new data on age distribution among road-killed badgers. We provide an estimate of the critical level of road mortality that would cause the population to decline and predict the period during which nationwide road traffic eventually exceeds this threshold.

Models and data

Model design

We used life table analyses (Krebs 1989, Southwood & Henderson 2000) and age-classified matrix population models (Caswell 1989, Tuljapurkar & Caswell 1996) to study how altered survivorship under roadless conditions would affect population growth rate, and to identify the critical level of road mortality that would cause the population to decline provided all other factors being constant. Population growth rate λ and a stable age distribution \mathbf{a}_x were estimated from a transition model as the dominant eigenvalue and the right eigenvector of population matrix \mathbf{A} (Caswell 1989). In this model (the ‘null-model’), the probability of an individual female to survive from one year to another was given by age specific survival rate (p_x), and her contribution to population growth by age-specific fecundity rates (f_x ; pregnancy rate * litter size). We chose a post-birth pulse model considering only females, i.e., the stable age structure describes a female population immediately after birth.

Estimates of age-classified fecundity and survival were combined from Ahnlund (1980a). Ahnlund’s work was based on several hundred badger carcasses including 212 road-kills provided by Swedish hunters during 1971 to 1975, and a mark and recapture study involving 86 badgers at Tovetorp field station in south-central Sweden (Fig. 1) during 1976 to 1979 (Ahnlund 1980a). Additional information on survivorship was taken from an unpublished mark and recapture study on 78 badgers trapped within the Grimsö Wildlife Research Area in south-central Sweden (Fig. 1) during 1982 -1989 (Erik Lindström, unpublished work). The sensitivity of the matrix model to uncertainties in survival and fecundity estimates was explored by arbitrarily varying the parameters by $\pm 10\%$ of the original value.

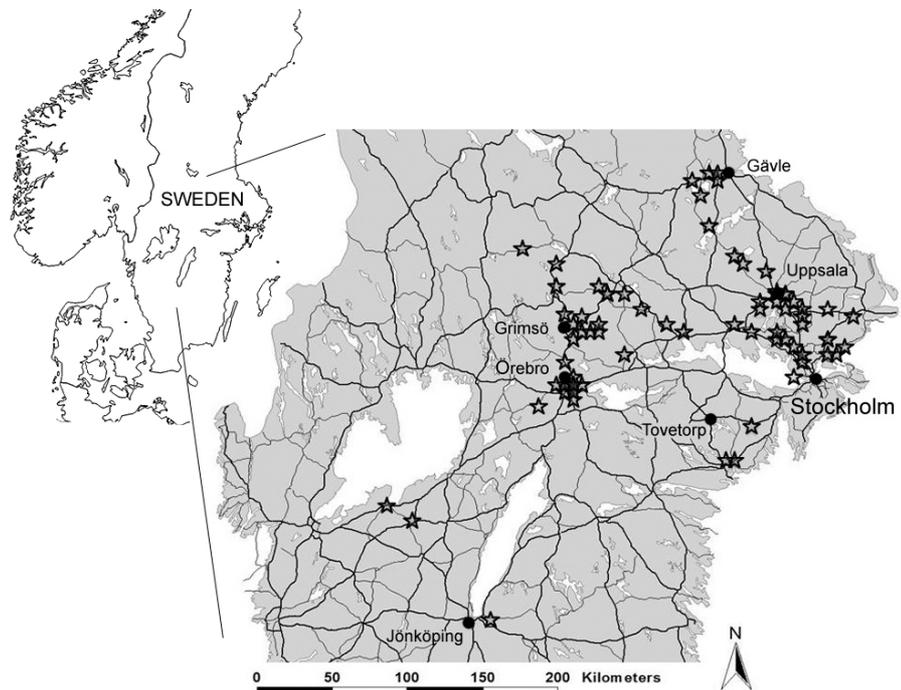


Figure 1. Distribution of road-killed badgers collected during 2001.

New estimates of the age- and sex distribution among road-kills were obtained from 76 badger carcasses collected from public roads in south-central Sweden during mid April to September 2001 (Fig. 1). This period covers most of the time badgers are active above ground and thus potentially exposed to road traffic. The carcasses were aged from counts of *cementum annuli* (conducted at Matson's Laboratory, Montana, USA) and examined for blastocysts and placental scars to measure female fecundity (cf. Ahnlund 1980a). We tested whether demographic variables of this road-killed sample differed from those described by Ahnlund (1980a) and from those estimated by the population null-model.

Through reducing adult and juvenile post-emergence mortality by the proportion assumed to be solely attributed to road traffic, we simulated population dynamics in a roadless environment. The difference in population growth rates between roadless and 'normal' populations provided an estimate of the effect of road traffic on badger population dynamics. For that, we assumed that road mortality is entirely additive and not compensated by changes in hunting pressure or female fecundity. The reduction in mortality was adjusted according to i) the age distribution among deaths produced by the null-model (dx_1), i.e., the risk for road mortality is independent of age; and ii) the age distribution observed among road-kills in a) this study (dx_2), and b) Ahnlund (1980a) (dx_3). In the following, these three alternatives are referred to as model 1, 2, and 3. We estimated the proportional road-kill in badgers from the differences between the total losses predicted by the population null-model and the three roadless models. Since the null-model suggested a stationary population, this difference was considered

equivalent to the critical level of road mortality that would cause the population to decline. Finally, we estimated the time period during which the steady increase in road traffic (about 1.5% per year, Edwards et al. 1999) would approach this critical threshold.

Model assumptions & parameter estimates

1. The transition matrix considered only females and assumed an equal sex ratio. Empirical evidence suggests an equal sex ratio among adult as well as among juvenile badgers (Ahnlund 1980a, Anderson & Trehwella 1985, Neal & Cheeseman 1996). Estimates on sex ratio and age structure among road-killed badgers were obtained from i) a sample of 76 badger carcasses that we collected from roads in south-central Sweden during mid April to late September 2001; and ii) from 212 badger carcasses examined by Ahnlund (1980a).
2. Age of first reproduction was set at two years. Females typically mate at the age of one, i.e., during their second year of life, but implantation is delayed until the following January or February, with the first litter produced in March, at the age of two (Ahnlund 1980b, Cheeseman et al. 1988, Harris & Cresswell 1988).
3. Litter sizes vary slightly with female age but seem to be rather similar among different populations, averaging 2 to 3 cubs per female (Anderson & Trehwella 1985). Pregnancy rates on the other hand, seem to decrease with increasing population density (Cresswell et al. 1992, Woodroffe & Macdonald 1995): In south-central Sweden, badger densities were typically below 3 individuals per km² (e.g., Seiler, Lindström, & Stenström 1995), yet most (88%) of all females older than one year were pregnant (Ahnlund 1980a). In high-density populations of Woodchester Park (25 adults/km², Rogers et al. 1997) and Wytham woods (38 adults/km², Macdonald & Newman 2002), however, pregnancy rates were reduced to 35% and 29%, respectively. In our model, we exclusively used Ahnlund's estimates based on placental scar counts (Table 1).
4. Maximum age for a female badger in our model was set at 10 years. This is in concordance with observations from free-living badgers, although captive badgers may attain a much higher age (Ahnlund 1980a, Neal & Cheeseman 1996). The number of individuals older than 5-6 years is probably very small and their effect on population dynamics is only marginal (Lankester et al. 1991).
5. Mortality among adults and subadults was estimated at a constant rate of 25%, as suggested by Ahnlund (1980a), Anderson & Trehwella (1985) and Lankester et al. (1991). The Grimsö mark & recapture study (Lindström, unpublished work) produced a similar estimate of 23% that could be subdivided into a summer mortality of 10% and a winter mortality of 15% (based on 24 known deaths of 79 marked badgers during 14 seasonal trapping events). We considered adult mortality in the Swedish population to be independent of gender, age, and population density. Yet there is some indication for density dependence in adult mortality in high-density populations in the UK (Rogers et al. 1997, Macdonald & Newman 2002).
6. Mortality among juveniles was distinguished into a pre- and post-emergence period. Among new born badgers, a significant loss of about 25% occurs during

the first 8-12 weeks of life in spring, when the cubs are still inside the natal den (Ahnlund 1980a, Rogers et al. 1997). This pre-emergence mortality may be due to disease or starvation caused by e.g., the death of lactating females. First after their emergence from the natal den, young badgers are directly exposed to road traffic or hunting (trapping). Estimates of juvenile post-emergence mortality from spring to autumn vary between 30% in England (Rogers et al. 1997, Macdonald & Newman 2002) to 37% in Sweden (Ahnlund 1980a). To this adds a supposedly age independent winter mortality of approximately 15% (of those that survived summer and autumn). Thus, on average, about 60% of the cubs born in March are likely to die during their first year of life (Ahnlund 1980a).

7. Hunting/poaching, traffic accidents, diseases, starvation and injuries have been identified as the main causes of mortality in badgers (Neal & Cheeseman 1996). Road traffic contributes with 67% of all badger mortality in Woodchester Park (Rogers et al. 1997), 44% in Wytham Woods (Macdonald & Newman 2002) and about 50% in other areas in the UK (Jefferies 1975, Harris & Cresswell 1988, Cheeseman, Wilesmith, & Stuart 1989) and in the Netherlands (Wiertz 1993). In the mark and recapture study at Tovetorp (Ahnlund 1980a), 50% of the known deaths (N=14) were due to traffic, compared to 25% (N=24) in the much less roaded Grimsö area (Lindström, unpublished). Hunting was responsible for 36%, respectively 50% of the mortality in the two Swedish areas, while the remaining 14-25% were due to other, undefined causes. If corrected for lifetime losses, the contribution of traffic to all known mortality increased to 36% in the Grimsö study. In our models, we have deliberately chosen an average of 40% as estimate of the proportional nationwide road mortality in Swedish badgers.

8. The number of road-killed badgers in Sweden has been estimated to between 22,000 and 33,000 in 1992 (Seiler et al., in press). This figure derived from a questionnaire with drivers who reported animal-vehicle collisions they experienced over the past 40 years, and relates to a total traffic volume of 65 billion vehicle kilometres driven in Sweden during the average year 1992. Thus, the number of road-killed badgers per million kilometres driven would average 0.42 (0.34 – 0.51; 95% C.I.). With the assumptions that the number of road-killed badgers is directly proportional to traffic intensity, and that the badger population density remains constant, future road-kills can be extrapolated from traffic estimates using the above conversion factor.

9. Estimates of the size of the Swedish badger population range from 250,000 (Bergström et al. 1992) to 350,000 individuals (Griffiths & Thomas 1993). During the past two decades, the official badger game bag has been relatively stable around 28,000 badgers per year (Swedish Association for Hunting and Wildlife Management, database). This is commonly taken as indication for a stable population.

10. Traffic intensity in Sweden during 1992 was estimated to 65.3 billion vehicle kilometres (Edwards et al. 1999) and the expected annual increase is 1.5% per year (SIKA 2002).

Results

Stable age structure

From the estimates on age-specific survival (p_x), and birth rates (m_x), the transition matrix estimated the stable age structure (a_x) and a λ of 1.003. Per capita birth and death rates approached 0.4, resulting in a net reproductive rate $R_0 = 1.014$ and a cohort generation time $T_c = 4.614$. Thus, according to the null-model, the Swedish badger population should be nearly stationary.

Table 1. *Life table of badgers based on average age-specific survival and birth rates, as given in Ahnlund (1980a), and the stable age distribution (a_x) calculated in a Leslie matrix population model. Per capita birth and death rates approached 0.4, which implies that the population is nearly stationary.*

Age class	stable age structure	survial rate *	prop. living between age x and x+1	prop. dying between age x and x+1	pregnancy rate	per capita litter size	daughters per female '
<i>age x</i>	<i>a_x</i>	<i>p_x</i>	<i>l_x</i>	<i>d_x</i>			<i>m_x</i>
0	0.40	0.75 / 0.536	1.00	0.60	-	-	0.00
1	0.16	0.75	0.40	0.10	-	-	0.00
2	0.12	0.75	0.30	0.08	0.46	1.94	0.45
3	0.09	0.75	0.23	0.06	0.91	2.36	1.07
4	0.07	0.75	0.17	0.04	0.94	2.55	1.20
5	0.05	0.75	0.13	0.03	0.94	2.11	0.99
6	0.04	0.75	0.10	0.02	0.94	2.46	1.16
7	0.03	0.75	0.07	0.02	0.94	2.33	1.10
8	0.02	0.75	0.05	0.01	0.94	2.17	1.02
9	0.02	0.75	0.04	0.01	0.94	1.93	0.91
10	0.01	-	0.03	0.03	0.94	1.93	0.91

* *pre- / post-emergence juvenile survival*

' *female fecundity estimates are based on placental scar counts*

Road-kills

Thirty-one of the 76 road-killed badgers we collected from roads in south-central Sweden were obtained during April to June and the remaining 45 during July to September. Sex ratio among these road-kills was close to parity (55% males; $\chi^2=0.52$, $df=1$, $p=0.469$) and there was no difference in the age distribution between the sexes (for age classes 0 to 5+, Mann-Whitney $U=13.0$, $N=6;6$, $p=0.423$). However, females were found more frequently during spring ($N=23$), especially April, than during autumn (July–September, $N=11$) ($\chi^2=4.23$, $df=1$, $p=0.039$). Juveniles ($N=5$) first occurred in August and September. There was no

difference in the number of males found between spring (N=22) and autumn (N=20).

Also in Ahnlund's (1980a) study, the sex ratio among road-killed badgers was close to parity and the age distribution did not differ between the sexes. Similar to our observations, Ahnlund found more females during the period January to June (winter and spring) than during the summer and autumn months. From July to December, juveniles made up 26% in this sample, which is similar to the pattern we found in our autumn sample (N=45; contingency table tests based on age classes 0 to 3+; $\chi^2=1.73$, $df=3$, $p=0.630$).

However, for the whole year, we found significantly fewer juveniles and more 2-year old badgers, than Ahnlund (1980a) did ($\chi^2=22.11$, $df=3$, $p<0.0001$; Fig. 2), or than suggested by the null-model for post-emergence deaths (for N=73, $\chi^2=55.43$, $df=3$, $p<0.0001$; Fig. 2). Also Ahnlund's sample of road-kills differed significantly in its age structure from the null-model (for N=212, $\chi^2=16.87$, $df=3$, $p<0.0001$; Fig. 2). On the other hand, we found no difference in average litter sizes and pregnancy rates between our road-killed females and those observed by Ahnlund (1980a) and used in the transition model (Table 2).

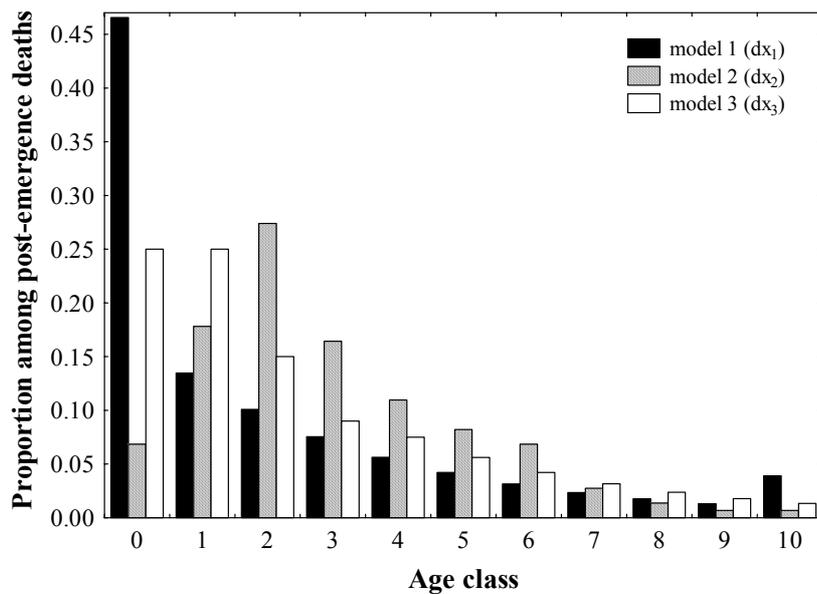


Figure 2. Proportions of badgers dying during age x as obtained from model 1 assuming age independent road mortality (dx_1) and from samples of road-kills from model 2 (dx_2) and model 3 (dx_3 ; Ahnlund 1980a). Ahnlund distinguished only between age classes 0 to 3+. We estimated the distribution of older ages from an exponential decay curve assuming a constant 25% mortality. Pre-emergence losses among juveniles are excluded.

Table 2. Average litter sizes and pregnancy rates of badgers, as calculated from placental scars compared between our sample of road-killed females and those examined by Ahnlund (1980a) and used in the population model. Standard deviations are given in brackets. *P*-values refer to difference in *t*-tests.

Litter size	Road-kills: this study		Ahnlund (1980a)		<i>p</i> -value
	Mean (S.D.)	N	Mean (S.D.)	N	
Age					
2	1.33 (0.58)	3	1.94 (0.66)	54	0,123
3	2.25 (0.96)	4	2.36 (0.96)	61	0,824
4+	2.50 (1.00)	4	2.55 (0.80)	132	0,642
Pregnancy rates					
Age					
2	0.30 (0.48)	10	0.46 (0.50)	107	0,353
3	1.00 (0)	4	0.91 (0.29)	66	0,431
4+	0.67 (0.52)	6	0.94 (0.24)	143	0,012

Roadless mortality

The survivorship curves for the null-model and model 1 showed typical type III-IV pattern (*sensu* Slobodkin 1962), i.e., mortality acts most heavily on juveniles but is constant among the older age classes. Survivorship curves for model 2 and 3, on the other hand, were skewed towards an increased survival among adults, whereas juveniles were underrepresented among the observed road-kills (Fig. 3). Despite these differences, all three roadless models resulted in similar estimates of the proportional road-kill: If road traffic stands for 40% of all mortality in badgers older than 8-12 weeks, the losses due to traffic should correspond to between 12% and 13% of the spring population (Table 3). For a population of 300,000 individuals, one may thus expect 38,000 badgers being road-killed each year. Since the null-model suggested a nearly stationary population ($\lambda=1.003$), this loss should be equivalent to the maximum road-kill that the model population can sustain without a change in growth rate. Any uncompensated change in mortality will thus directly affect population growth. An 10% increase in road mortality, for example, would reduce λ with up to 6%, whereas a 40% reduction of mortality, as simulated by the three roadless models, produced growth rates that were 18-22% increased from the null-model (Fig. 4). Thus, if all road mortality could be prevented, the badger population would have the potential to increase by 18-22% annually. Again, model 1 yielded the smallest effect on growth rate, but the differences between the models' predictions were small.

As expected from the differences in age structure between the models, model 1 was more sensitive to changes in juvenile mortality, whereas adult mortality and female fecundity had greater effect in model 2 and 3 (Fig. 5). To test the sensitivity of the model to parameter changes, we deliberately increased the proportional mortality attributed to road traffic by 10%. Under roadless conditions, this change would increase growth rates with 4-5%, and the estimated critical road-kill with about 3% compared to the original roadless models.

Table 3. Estimation of the proportional road-kill from the difference in deaths between the null-model and three roadless models assuming that road traffic is responsible for 40% of the mortality among badgers older than 8-12 weeks. For details of the roadless models, see text. Proportion of dead (d_x) and survival rates (p_x) refer to post-emergence age structures, whereas the resulting proportional losses are calculated from the post-breeding (pre-emergence) age distribution (compare Table 1).

age x	'null-model' (including road mortality)		prop. losses			age structure among dead			roadless survival rates			predicted losses (excluding road mortality)		
	$p_{x,0}$	deaths 0	$d_{x,1}$	$d_{x,2}$	$d_{x,3}$	$p_{x,1}$	$p_{x,2}$	$p_{x,3}$	deaths 1	deaths 2	deaths 3			
0 (post)	0.536	0.239	0.529	0.068	0.250	0.722	0.560	0.624	0.183	0.232	0.213			
1	0.750	0.040	0.119	0.178	0.250	0.850	0.900	0.960	0.024	0.016	0.006			
2	0.750	0.030	0.089	0.274	0.150	0.850	1.000	0.919	0.018	0.000	0.010			
3	0.750	0.022	0.066	0.164	0.090	0.850	0.997	0.885	0.013	0.000	0.010			
4	0.750	0.017	0.050	0.110	0.075	0.850	0.970	0.901	0.010	0.002	0.007			
5	0.750	0.013	0.037	0.082	0.056	0.850	0.971	0.901	0.008	0.001	0.005			
6	0.750	0.009	0.028	0.068	0.042	0.850	0.996	0.902	0.006	0.000	0.004			
7	0.750	0.007	0.021	0.027	0.032	0.850	0.882	0.902	0.004	0.003	0.003			
8	0.750	0.005	0.016	0.014	0.024	0.850	0.838	0.903	0.003	0.003	0.002			
9	0.750	0.004	0.012	0.010	0.018	0.850	0.838	0.903	0.002	0.003	0.002			
10	0.000	0.012	0.034	0.003	0.013	0.400	0.040	0.155	0.007	0.011	0.010			
<i>sum</i>		0.398						<i>sum</i>	0.279	0.272	0.271			
<i>difference to null-model losses:</i>									11.9%	12.6%	12.7%			

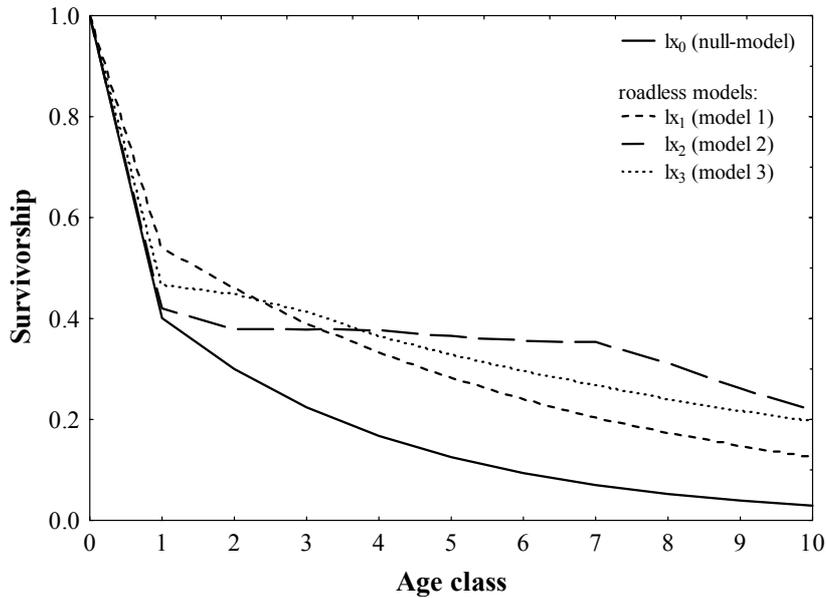


Figure 3. Survivorship curves of badgers, derived from the population null-model (plain line) and three roadless models (dotted lines) assuming a 40% reduced roadless mortality calculated from three different age distributions among road-kills. For details on the roadless models, see text.

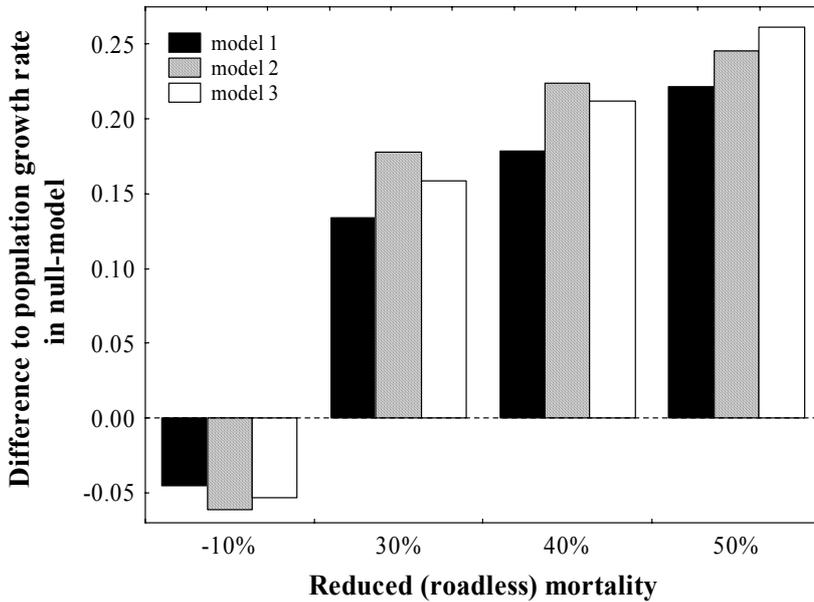


Figure 4. Effect on population growth rate of reduced mortality calculated for three roadless models assuming that traffic is responsible for 30%, 40%, or 50% of all mortality among badgers older than 8-12 weeks. For details on the models, see text. For comparison, the results of a 10% increase in all post-emergence mortality are given.

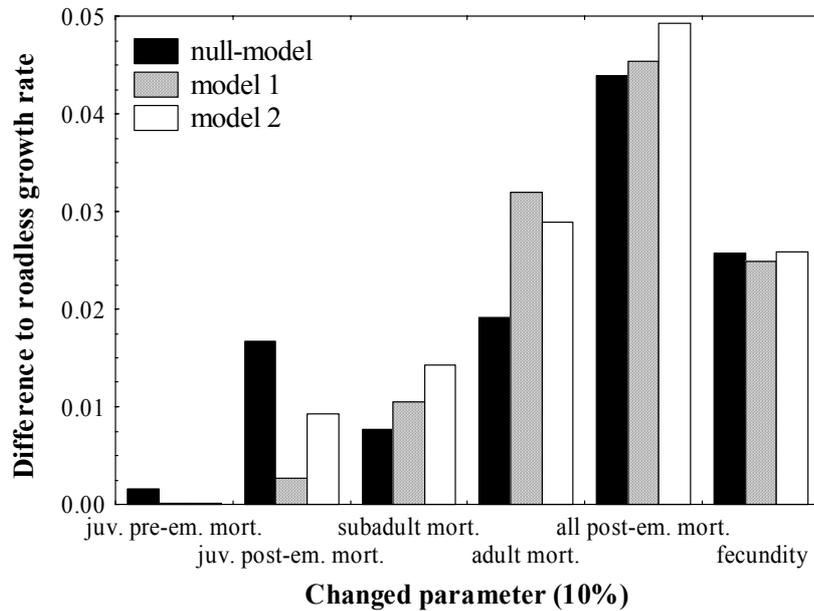


Figure 5. Effect on population growth rate of a 10% change in partial mortalities and fecundity in the 3 roadless models. For example, a 10% reduction in adult mortality would raise λ population growth rate with about 3% in model 2 and 3 based on observed age distributions among road kills, but only with 1.9% in model 1 that assumes no age dependence in road mortality. For details on the models, see text.

Predicted threshold

Provided that the number of road-killed badgers is directly proportional to road traffic (0.42 badger casualties per million kilometres driven; Seiler et al., in press), nationwide road traffic intensity should rise to about 90 billion vehicle kilometres before the increased mortality would limit badger population growth. Provided a steady 1.5% increase in traffic (SIKA 2002), this critical threshold may be exceeded in the year 2018. However, uncertainties in the parameter estimates add broad confidence limits to this prediction. For example, if the badger population tallies only 250,000 individuals and the overall contribution of road traffic to all post-emergence mortality is 30% instead of the assumed 40%, then the rate of casualties will be 0.51 rather than the average 0.42 per million km. This implies that the critical traffic intensity would have been exceeded already in 1978 (Fig. 6).

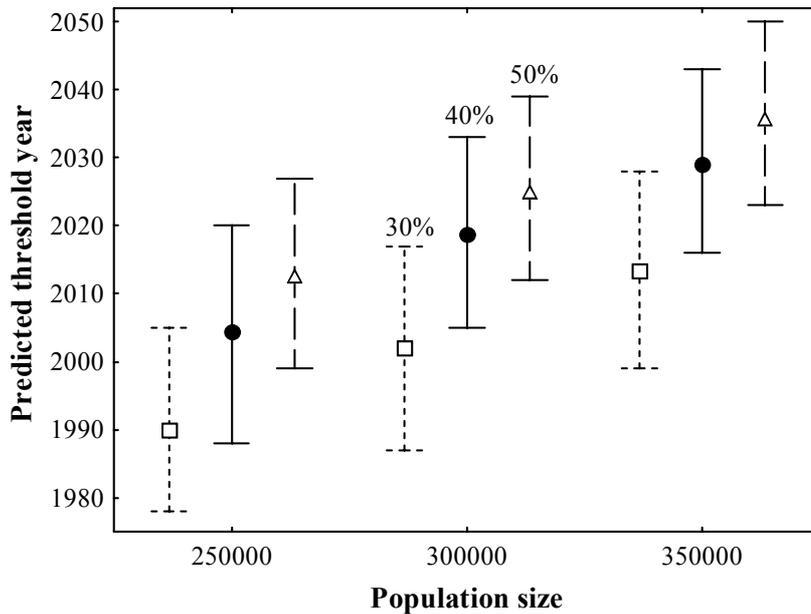


Figure 6. Variation in the predicted threshold year when nationwide road traffic is assumed to approach the critical level of road mortality in badgers. The figure is based on model 1, assuming a proportional road mortality of 30-50% and a total population size of 250,000 to 350,000 individuals. The predicted time ranges are calculated from a mean frequency of 0.42 (0.34-0.52, 95% C.I.) road-killed badgers per million kilometres driven.

Discussion

Critical level of road mortality

Our models predicted that somewhere between 1978 and 2049 (mean = 2018), the steadily increasing road traffic would produce a road kill that exceeds the critical level that the Swedish badger population can sustain without decline. The critical time period depends on the relative contribution of road traffic to all post-emergence mortality (assumed to range from 30-50%), the relationship between traffic intensity and the number of road-killed badgers (assumed to be proportional with 0.34 – 0.51 incidents per million km), and the actual size of the population (estimated at 250,000 to 350,000). Thus, even if nationwide road traffic is not yet limiting badger population growth, it may very well do so in the near future.

Uncertainties in the estimates of mortality and fecundity add further variation to the prediction, but their effect on the estimated critical level (simulated by a 10% change in the parameter values) was small compared to the influence of the uncertainty in population size. Changes in the survival of adults and subadults had greater effect on population growth rates than changes in juvenile survival; a

pattern which is typical for large mammals with low intrinsic rates of increase (Heppell, Caswell, & Crowder 2000). However, although there were significantly more adults and subadults and fewer juveniles in the road-killed samples than in the modelled population, the predicted critical level of road-mortality was resistant to differences in age structure between the models. According to the models, 12-13% of the spring population may be killed by vehicles before traffic mortality limits population growth. This percentage is well within the range of what Seiler et al. (in press) estimated as the total number of road-killed badgers in 1992 (8.7-13.3% of a population of 250,000 individuals). This result contradicts common belief according to which road traffic has no significance to the Swedish badger population (Göransson, Karlsson, & Lindgren 1978, Griffiths & Thomas 1993). Although badger road mortality in Sweden appears less than compared to other countries, it is in line with estimates from the Netherlands, England and Denmark, where road traffic is more intense and responsible for a loss of up to a 10-20% of the national badger populations (Harris et al. 1991, Lankester et al. 1991, Wiertz 1993, Aaris-Sorensen 1995, Neal & Cheeseman 1996).

There is, however, substantial regional and local variation in traffic volume and badger density, which implies that in areas with traffic loads above the national average, road-mortality probably exceeds the predicted threshold. Likewise, in areas with very little traffic, the impact on badger populations of road traffic may still be insignificant. Differences in traffic volume between Swedish counties are up to 6-fold, with the highest loads in the counties of Stockholm and Scania and least in the northernmost counties. Scania, on the other hand, produces an annual harvest in badgers that is more than a magnitude larger than compared to northern, boreal, areas (about 25 badgers/100 km² compare to less than one per 100 km², Swedish Association for Hunting and Wildlife Management, database). Badgers in the boreal zone associate with agricultural land use, as they depend on richer soils and select areas of higher productivity than what is available throughout the matrix of the boreal coniferous forest (Seiler 1992, Bevanger & Lindström 1995, Broseth, Knutsen, & Bevanger 1997). Due to food dispersion, badgers in boreal habitats have wider ranges than badgers in richer landscapes (Seiler, Lindström, & Stenström 1995). Since also roads and traffic are linked with human settlement and agriculture, boreal badgers may indeed be relatively more exposed to and affected by road traffic than their southern conspecifics. Unfortunately, there are no county statistics on road-killed badgers to test this hypothesis. If it applies, however, the overall impact of road traffic in badger populations will be more significant than suggested by our models.

Age structure and population growth

Evaluating the significance to population dynamics of single mortality factors, such as road traffic, requires population models that consider age- and sex-specific mortality risks. We based our models on age-specific mortality and fecundity estimates established by Ahnlund (1980a). These estimates concur with results from other European studies that have been used in previous badger population models (e.g., Anderson & Trehwella 1985, Lankester et al. 1991). However, even if mortality and fecundity are well documented, a number of assumptions have to be made that may influence the model's outcome.

Analysis of life tables, for example, assumes a stable age structure, i.e., considers mortality and fecundity to be constant over time (Southwood & Henderson 2000). This assumption may seem unrealistic, but many larger mammals, including badgers, may indeed approximate a stable age structure, especially if population sizes have remained constant over longer time. We chose to calculate a stable age structure at the time of birth from a transition matrix using average mortality and fecundity estimates as only input. Age structures obtained from trapped or killed individuals, on the other hand, are usually biased due to the sampling method and the time of the year when sampling is done (Caughley 1974). Most reported age structures in badgers refer to autumn samples and are thus not representative for the population age structure at the time of birth (during early spring). Generally, about 25-30% of autumn populations tend to consist of juveniles, while subadults account for 20-25% and adults for the remaining part (Ahnlund 1980a, Anderson & Trehwella 1985, Rogers et al. 1997, Macdonald & Newman 2002). To assess the population age structure at birth from these autumn samples, one must account for differential summer mortality in adults and juveniles, and include pre-emergence mortality among juveniles (see model assumption and parameter estimates). With these adjustments, the age distribution at birth will approximate 40% juveniles, 20% subadults, and 40% adults. This is indeed close to the stable age structure that we obtained from the transition matrix (i.e., 40% juveniles, 16% subadults, 44% adults).

Thus, provided a stable age structure and an equal sex ratio, per capita birth rates should approximate 0.4. This is identical with the value obtained from Ahnlund's (1980a) estimates based on counts of placental scars, but smaller than the birth rate (0.6) estimated by Anderson & Trehwella (1985) from counts of blastocysts. However, blastocyst counts usually produce larger litter estimates than counts of placental scars, because pre-implantation losses and eventual adsorption of fetuses are not considered (Woodroffe & Macdonald 1995). The per capita death rate calculated in our model (0.4), was in line with studies from England ($d=0.37$, Anderson & Trehwella 1985), Switzerland ($d=0.37$, Wandeler & Graf 1982), and field data from Sweden ($d=0.46$, Ahnlund 1980a). Consequently, the number of deaths should approximate the number of newborn cubs and the Swedish badger population should produce a growth rate of $\lambda=1$, as suggested by our model.

Indeed, the Swedish badger population has for long been considered stationary (Bergström et al. 1992, Griffiths & Thomas 1993, Bevanger & Lindström 1995). In addition, badger game bags have been relatively stable over the past two decades (about 28,000 culls per year; database of the Swedish Association for Hunting and Wildlife Management), and there has been no major change in the hunters' attitude towards badger culling during this period.

Additive or compensatory mortality

If the Swedish badger population is close to stationary, the present number of road-killed badgers should approximate the critical level and any uncompensated increase in mortality, as due to increased road traffic, should cause the population to decline. If increased road mortality can be compensated by reduced hunting

mortality or increased fecundity, or if it mainly affects the “doomed surplus”, the model will suggest a lower critical level than the badger population can cope with. Whether mortality is additive or compensatory depends on population density and habitat quality as well as the killed individuals’ status in the population.

There is evidence from other studies on road-kills that the risk of being killed in traffic is specific of age and gender. Road-kills may thus not be a random sample of the population as a whole (Hodson & Snow 1965, Berthoud 1980, Dixon, Shawyer, & Sperring 1996). One may assume that inexperienced, active, and highly mobile individuals may be more exposed to road traffic and thus run a greater risk of being killed in traffic than older, stationary individuals with established territories. For example, O’Gara & Harris (1988) observed that road-killed mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) were of generally poorer body condition, and of younger or older age than those killed by predators. Loughry & McDonough (1996) found that although road-killed armadillos (*Dasypus novemcinctus*) provided a representative picture of the demography of the adult population, information on age structure was misleading. Our sample of road-killed badgers, as well as Ahnlund’s material, contained significantly more one and two year old badgers and fewer juveniles than expected from the modelled, post-emergence distribution of deaths. Since juveniles are less mobile than adults and spend most of their time close to the natal den (Cresswell & Harris 1988), this result may be expected.

Several authors observed seasonality in the sex ratio among road-killed badgers, with an overrepresentation of males in late winter and of females in spring samples, reflecting increased activity associated with mating and nursing behaviour (Jefferies 1975, Anderson & Trehwella 1985, Neal 1986). During spring, lactating females may be especially exposed to road traffic as they have greater energy demands while nursing cubs and may have to range over wider areas to obtain sufficient food than during other times of the year. Since the loss of lactating females likely implies the death of her cubs, the impact of road mortality on pre-emergence juvenile mortality will increase with the proportion of fecund females among spring road-kills. This effect may be especially elevated in poor habitats, such as the boreal forest, where food resources are scarce during this time of the year (Seiler 1992). In addition, the large proportion of young females among spring road-kills, as observed by Jefferies (1975), Ahnlund (1980a), Aaris-Sorensen (1995), and this study, probably reflects dispersal of subdominant females triggered by raised intrasexual aggression during spring. If dispersal increases the chance to reproduce successfully, as suggested by Woodroffe, Macdonald, & daSilva (1995), the loss of these subdominant but fecund females may be as significant to population recruitment as the loss of territorial females. Also this effect will be more noticeable in poorer habitats and in low density populations.

Thus, there is reason to believe that road mortality in badgers is partly compensatory, especially in high-density populations in southern Sweden, as it primarily affects active and mobile individuals that anyway experience an increased mortality risk. In poor habitats, such as in northern boreal forests, the relative contribution of these individuals may be significant to population recruitment. Consequently, the effect of road mortality under poorer conditions

may rather be additive. Again, regional differences in habitat quality suggest that badgers in boreal environments and close the northern edge of their distributional range are more affected by road traffic than badgers from richer habitats in the south.

Conclusions

Our models suggest that, 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 be substantial. Especially in poorer habitats, such as northern boreal forests, population growth may already be limited by road mortality. In richer areas with traffic loads above average, road traffic probably exceeds hunting as the leading cause of death in badgers, but the effect on population recruitment may be compensatory. Even though the effect of road mortality is not entirely additive, we conclude that nationwide road traffic is probably close to the limit that the Swedish badger population can sustain without declining. 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.

Since there is no data on the spatial distribution of road-killed badgers, analyses of this pattern must remain a future task. For the protection of badgers, we recommend increased efforts on counteracting measures such as fences and badger tunnels to reduce badger road mortality in the most critical areas.

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