The effect of road kills on amphibian populations

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Abstract

The diurnal movement patterns of *Triturus vulgaris, Triturus cristatus, Pelobates fuscus, Bufo bufo, Rana temporaria,* and *Rana arvalis* were investigated during five breeding seasons (1994–1998). Two main questions were addressed: (1) What is the probability of an individual amphibian getting killed when crossing the road? and (2) What fraction of the amphibian populations gets killed by traffic? The rate of movement of 203 adult amphibians was recorded. Information on traffic loads was provided, and mortality risk was calculated depending on traffic loads and movement rate. The probability of getting killed ranged from 0.34 to 0.61 when crossing a road with a traffic load of 3207 vehicles/day, and from 0.89 to 0.98 when crossing a motorway. The number of amphibians killed on the road was estimated by systematic counts. Population sizes were estimated for all ponds within 250 m of the relevant highway stretch. Results indicate that about 10% of the adult population of *P. fuscus* and brown frogs (*R. temporaria* and *R. arvalis*) were killed annually by traffic at this site. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The decline of amphibian populations throughout the world is a well established fact that has received a lot of attention during the last 10 years (Blaustein and Wake, 1990; Wyman, 1990; Blaustein et al. 1994). Several factors have been proposed, but there seems to be a consensus about the fact that human activities are responsible for most of the declines. Road mortality is one factor which is potentially important but has received little attention (but see Fahrig et al., 1995). Traffic may be destructive to animal populations in two ways: directly, in the sense of actually killing individuals and indirectly, by fragmenting a population's habitat (Mader, 1984; Andrews, 1990; Mader et al., 1990; Groot Bruinderink and Hazebroek, 1996; Reed et al., 1996). Fragmentation in turn may lead to isolation of populations which again may result in a reduced population size and an increased stochastic risk of extinction (Bennett, 1990). As Fahrig et al. (1995) point out, traffic intensity throughout the world has increased in the last two decades and this goes for Denmark too (Anon.,

1998). Thus, it is likely that the toll of animal lives taken by traffic has increased accordingly.

Several studies have quantified road kills of many different taxa, e.g. toads (van Gelder, 1973, Cooke, 1995), birds, mammals, amphibians, and reptiles (Hansen, 1982; Fuellhaas et al., 1989), butterflies (Munguira and Thomas, 1992), snakes (Rosen and Lowe, 1994), mammals, birds, and reptiles (Drews, 1995), deer and other ungulates (Romin and Bissonette, 1996, Groot Bruinderink and Hazebroek, 1996). Due to their activity pattern, population structure, and preferred habitats, aquatic breeding amphibians are more vulnerable to traffic mortality than most other species. If they have to cross a road to get from their hibernation site to the breeding pond, or if a road runs through their terrestrial habitat, it may pose a serious threat to the population. Few studies, however, have related the number of road-killed individuals to the size of the total population, and as Huijser and Bergers (1997) mention, and Mallick et al. (1998) infer, a species often found killed on roads may simply reflect the presence of large thriving populations.

It is even more uncommon in the literature to relate road kills to the spatial organisation of the population. Vos and Chardon (1998), however, demonstrated a significant negative effect of road density on the occupation probability of ponds by moor frogs (*Rana arvalis*) in the Netherlands.

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Most studies regularly count road kills from slow moving vehicles, e.g. Hansen (1982), Rosen and Lowe (1994), Drews (1995), Mallick et al. (1998) or by foot, e.g Fuellhaas et al. (1989), Munguira and Thomas (1992). These assume that every victim is observed, which may be true for large conspicuous mammals, but is certainly not true for small animals. If an estimate of the total number of animals killed on a road in a given period of time is needed, one must quantitatively compensate for the number of animals that disappear from the road between censuses. Although often noted in the above mentioned studies, only Munguira and Thomas (1992) attempt to make this compensation.

The present study aimed at quantifying road kills in populations of six amphibian species: common newt (*Triturus vulgaris*), crested newt (*Triturus cristatus*), spadefoot toad (*Pelobates fuscus*), common toad (*Bufo bufo*), moor frog (*Rana arvalis*) and common frog (*Rana temporaria*). During a period of 5 years (1994–1998) the population sizes were estimated and road kills quantified (including corrections for animals not observed). The problem of quantifying road kills was approached from two different angles:

(1) by establishing a relationship between the probability of getting killed by crossing the road and (a) velocity of the animal, (b) diurnal activity pattern, (c) traffic intensity;
(2) by identifying the proportion of the populations killed on the road, and assessing the importance to the probability of population persistence.

2. Methods

2.1. Study site

The study site is located on the peninsula of Djursland, northern Denmark (56°26′N, 10°34′E). It is situated next to a two-lane road connecting two towns. The road is about 8 m wide, with a traffic intensity of ca. 3200 vehicles per 24 h. The speed limit is 80 km/h but the usual vehicle speed is 10–20 km/h higher. The landscape is dominated by intensively cultivated fields (mostly barley), with small woods and farms here and there. Ponds are quite numerous in the area; most of them are of natural origin (glacial formations), although some are artificially dug (peat bogs, gravel pits).

2.2. Population size estimates

Population sizes of *P. fuscus*, *R. temporaria* and *R. arvalis* were estimated in 1996 and 1997 for all ponds within a distance of 1000 m from the relevant road stretch (*n* = 14 ponds). Five of the ponds were completely encircled by drift fences in both years. Estimates

for the two *Rana* species were based on egg-clumps counted in 1996 and 1997, which corresponded very well with the number of females and males known to have entered the ponds by the pitfall traps. Moreover, the number of calling males was found to correspond well with the number of males known to be present in the pond. The number of egg clumps and the number of calling males were then used as a basis for an estimate of the population size in the ponds that were not fenced, assuming one egg clump per female and a sex ratio of unity. Population sizes of *T. vulgaris*, *T. cristatus* and *B. bufo* were estimated in the five fenced ponds only. Here, all adults of *P. fuscus* were caught by the fence in pitfall traps and were individually marked in both years. In the nine unfenced ponds, *P. fuscus* was assumed to be absent because there were no males calling either year. For *B. bufo*, the number of calling and/or visible males was assessed at the peak of the calling season and used as a basis of a population estimate.

2.3. Velocities and activity patterns of amphibians crossing roads

In order to establish a relationship between the probability for an amphibian of getting killed by crossing the road, data on velocity and diurnal activity pattern of the amphibians, and vehicle intensity, and diurnal variation, were needed. The velocity of adults of the six naturally occurring amphibian species was recorded during their spring migration to the breeding ponds (i.e. before spawning), as well as during their summer movements (in August) in 1996–1998. Some of the animals were spontaneous migrators, i.e. they were discovered on their way to the breeding pond (and their movement speed recorded directly), whereas some of the animals were caught in pitfall traps by the drift fences. They were then taken to a nearby paved area and released. Time spent and distance moved were then recorded from the time the animal started moving until it left the paved area. Pitfall traps were used to describe the amphibian diurnal activity pattern by emptying the traps at regular intervals during each 24 h period (April–May 1996 and 1997).

Traffic intensity (number of vehicles per 24 h, and frequency distribution during 24 h), and the number and frequency of different vehicle types occurring were provided by the Danish Road Directorate. Traffic intensity was recorded as the mean number of vehicles on the road in each 1-h interval in the months of April, May, June, and August 1996 (where amphibian activity and road kills were recorded).

2.4. Monitoring of road kills

A 600-m stretch of the road was monitored for road-killed adult amphibians every morning at dawn, in

order to minimise the number of corpses removed by day time scavengers (routine monitorings). Both sides of the road were carefully examined (one side at a time) by foot. All road victims were removed after recording in order to avoid double counts. This took place during the breeding period, and in late summer: 1995, 30 March–31 May and 27 July–1 September; 1996, 11 April–2 June and 1 August–2 September; 1997, 25 March–2 June and 29 July–1 September.

In addition to the routine monitoring, 19 control monitorings were conducted during peak spring migration (20–27 April, 1996 and 31 March–28 April, 1997), to assess the efficiency of our method of monitoring by foot. The control monitorings were spread evenly around the clock. Each road victim was recorded and the site carefully but invisibly marked, so as not to influence the probability of its recording during the routine monitoring. During control monitorings, victims were not removed from the road, so victims not recorded by the following routine monitoring must have disappeared or been missed. A few control monitorings were undertaken as direct continuations of the routine monitoring to check the number of extant victims missed.

The efficiency of monitoring was calculated using basic mark-recapture theory (Lincoln index, e.g. Begon, 1979). Let:

R = number of victims recorded by routine monitorings only, C = number of victims recorded by control monitorings only, B = number of victims recorded by routine *and* control monitorings, N = total number of victims.

Assuming that we are dealing with the same population of road kills for both routine and control monitoring and that the probability of missing an amphibian during routine monitoring is independent of the probability of missing it during control monitoring, then

$$\frac{B}{B+R} = \frac{B+C}{N} \tag{1}$$

and by rearranging (1), we get an estimate of the total number of victims ($\hat{N}$):

$$\hat{N} = \frac{(B+C)(B+R)}{B} \tag{2}$$

We define efficiency of routine monitorings (E) as the fraction of all victims found by routine monitorings:

$$E = \frac{R+B}{N} \tag{3}$$

Replacing N with the expression in (2), we get:

$$E = \frac{(R+B)B}{(B+C)(B+R)} = \frac{B}{B+C} \tag{4}$$

Substituting the expression for E in (3) into (4) yields:

$$\hat{N} = \frac{1}{E}(R+B)$$

Consequently, $F = 1/E$ is the factor to be multiplied by the number of road victims found by routine monitorings to get the estimated total number of road victims.

2.5. *Model for probability of getting killed when crossing the road*

The probability of surviving one road crossing [$P(\text{surv})$] is:

$$P(\text{surv}) = \frac{1}{\pi} \int_{\alpha=-\pi/2}^{\alpha=\pi/2} e^{-\frac{Na}{v\cos\alpha}} d\alpha$$

(cf. Eq. (10), Appendix)

where N = number of cars passing per time unit, a = killing width of car, v = velocity of animal and α = angle of road crossing.

This expression averages the survival probability for all possible crossing angles. Note that according to the expression, survival probability decreases exponentially with increasing traffic intensity (N), and increases exponentially with velocity of the animal. $\alpha = 0$ corresponds to perpendicular road crossing; in this case survival probability is at its maximum value. As the crossing angle deviates from perpendicular, $\cos\alpha$ — and thereby survival probability — decreases.

Our calculation is based on the fact that amphibians get killed if they are hit, even if only partly, by a wheel but usually not if they remain still under a passing vehicle (pers. obs.). Therefore, we calculated the killing width of vehicles (a) as twice the width of a tyre plus twice the body length of the species in question, assuming that the front and rear wheels traverse exactly the same part of the road. a was calculated as a weighted average of all vehicles occurring on this particular road: 72% cars (<2 t), 18% vans (between 2 and 3.5 t) and 10% trucks >3.5 t, 2% with single wheels and 8% with twin wheels) (Møller, pers. commun.). Tyre widths for cars, vans and trucks were 0.22 m, 0.24 m and 0.38 m/0.64 m (single wheels/twin wheels), respectively (Møller, pers. commun.). Anurans usually jump when passed by heavy vehicles (> 3.5 t; pers. obs.), so for such traffic twice the length of a jump was added to the width of the wheels instead of twice the length of the body. Finally, for all vehicles, a was increased by 5% which is an assessed fraction of vehicles that kill by their wind speed alone rather than by hitting the animals. a is thus proportional to the body length of the amphibians and ranges from 0.71 m (*P. fuscus*) to 0.77 m (*Triturus* spp.).

3. Results

3.1. Velocities, activity patterns and probability of getting killed by road crossing

We recorded velocities of 203 adult amphibians (Table 1): 185 were recorded during their spring migration (31 March–10 June) and 18 during their summer movements (30 July–24 August). All velocities were recorded between 2000 and 0230, reflecting the peak activity period. There was no significant difference between velocities of spontaneously and non-spontaneously moving individuals (Table 1). Because of this non-significant difference, we did not distinguish between spontaneous and non-spontaneous movers in the following analyses. Also, despite the low number of amphibians moving in summer, there was no significant difference between movement rates of adult amphibian individuals moving in spring and summer.

In the period of investigation, the sun set between 2000 and 2130 and rose between 0530 and 0700 and the activity patterns of the investigated amphibian species were concentrated at night (Fig. 1). It is clear, however, that the time of peak activity differed between species: most R. temporaria and R. arvalis were active soon after sunset whereas most B. bufo were active between 2200 and 2300. The two Triturus species and P. fuscus were later still, the latter with a distinct activity peak around midnight to 0200. There was a small rush-hour peak of traffic intensity around 0700 and a large peak around 1500. From 1500 to 0200, traffic intensity decreased steadily, reaching a minimum value of nine vehicles per hour in the middle of the night.

According to Eq. (12), the probability of getting killed increases to a maximum value with increasing traffic intensity. We investigated this for different velocities of amphibians, representative of the species in the study area, assuming perpendicular road crossing (Fig. 2) and for perpendicular road crossing in contrast to road crossing with all possible angles (Fig. 3). In order to investigate the significance of velocity only, α was set to 0.74 (mean of α) in both Fig. 2 and Fig. 3. Up to a

traffic intensity of 625 vehicles/h (15 000 vehicles/day), corresponding to a busy road, the velocity of the animals has a large influence on the probability of getting killed. Above this traffic intensity, the probability of getting killed during a road crossing is very close to 1 for all amphibian species investigated, whatever their velocity (within the range investigated).

We also calculated the probability of getting killed at different traffic intensities for velocities representative for hedgehog (Erinaceus europaeus, 45 m/min) and hare (Lepus europaeus, 120 m/min)(pers. obs.). For these two species, α was set to 2.0 m (total vehicle width), since, because of their size, they are killed by any part of a vehicle, not just the tyres. At these velocities, the probability of getting killed is far lower than for any of the amphibians considered (Fig. 2).

The angle of crossing clearly has an effect on the probability of getting killed (Fig. 3). The difference in probability of getting killed by perpendicular and random road crossing is most pronounced at medium
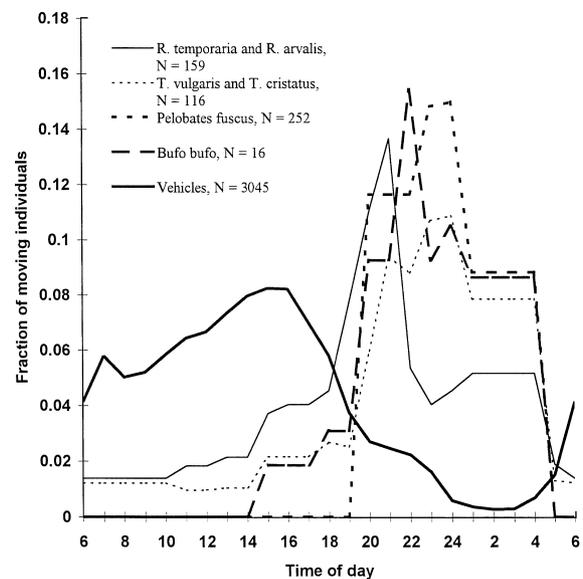

Fig. 1. Diurnal activity patterns of the six species of amphibians investigated and diurnal variation in vehicle intensity. Traffic data for April and May 1996.

Table 1
Mean speed and distance moved for the six naturally occurring amphibian species in the study area[a]

Species	Number of records		P	Mean distance moved (m ±S.D.)			Mean speed (m/min ±S.D.)		
	Sp	Non-sp		Sp	Non-sp	All	Sp	Non-sp	All
Triturus vulgaris	6	19	0.52	1.37(0.39)	1.28(0.65)	1.30(0.59)	0.69(0.49)	0.51(0.25)	0.55(0.32)
Triturus cristatus	0	7	–	–	1.66(0.81)	1.66(0.81)	–	0.99(1.01)	0.99(1.01)
Pelobates fuscus	8	40	0.18	2.81(3.04)	2.33(1.01)	2.41(1.50)	0.97(0.84)	1.50(0.99)	1.41(0.98)
Bufo bufo	38	0	–	3.63(2.67)	–	3.63(2.67)	0.93(0.82)	–	0.93(0.82)
Rana temporaria	11	19	0.06	2.77(2.03)	3.41(1.03)	3.18(1.48)	1.51(2.39)	2.39(1.94)	2.07(2.12)
Rana arvalis	20	35	0.59	5.29(3.05)	2.60(1.77)	3.58(2.64)	2.51(3.06)	1.76(2.18)	2.03(2.54)
Total	83	120	–	3.67(2.81)	2.37(1.38)	2.90(2.17)	1.37(1.93)	1.53(1.62)	1.46(1.75)

[a] Sp, undisturbed, spontaneous movement across pavement; Non-sp, movement after relocation to metalled road; P, P-value for H_0: movement speeds equal for spontaneous and non-spontaneous moving amphibians (Kruskal–Wallis test).

probabilities of getting killed — for slow movers this corresponds to a traffic intensity of about 1500 to 3000 vehicles per 24 h.

3.2. Diurnal variation in probability of death from crossing the road

In order to estimate diurnal variation in the probability of getting killed, species were grouped taxonomically, i.e. *Triturus* species, *Rana* species, *B. bufo*, *P. fuscus*. For any taxonomic group (k) at any time interval (j), the probability of getting killed ($P_{j,k}$(death)) was calculated as the mean probability of getting killed for all individuals in that particular group. Assuming perpendicular road crossing, Eq. (9) (cf. Appendix) reduces to:

$$P_{j,k}(\text{death}) = \frac{\sum_{i=1}^{n(k)} \left(1 - e^{-\frac{aN_j}{v_{i(k)}}} \right)}{n(k)}, \qquad (13)$$

where $n(k)$ is the total number of individuals in the taxonomic group in question (k), $v_{i(k)}$ denotes the velocity of one individual in group (k), and α is species specific. P(death) was then multiplied by the fraction of amphibians in this taxonomic group that are known from the recordings of diurnal activity pattern to be active in this particular time interval. Diurnal variation in the actual probability of getting killed was thus calculated, given the particular activity pattern and velocities of amphibians recorded, and the traffic

intensity pattern. Diurnal variation in the probability of getting killed by a single road crossing not only reflects diurnal variation in traffic intensity (Fig. 4) but more particularly, the diurnal movement pattern of the species, and to a lesser extent the velocity of the species. The probability of getting killed is very small in the day time with a small increase before dawn, reflecting the early rush-hour peak in traffic intensity late at night when the amphibians are still

Fig. 3. The effect on probability of getting killed by crossing the road randomly (*all angles*) compared to perpendicular road crossing (*perpendicular*) for three representative velocities of amphibians; 0.50 m/min corresponds to slow moving amphibians (mainly *Triturus* species), 1.50 m/min corresponds to *Pelobates fuscus*, and 9.00 m/min is the velocity of the fastest moving *Rana temporaria* and *Rana arvalis*.
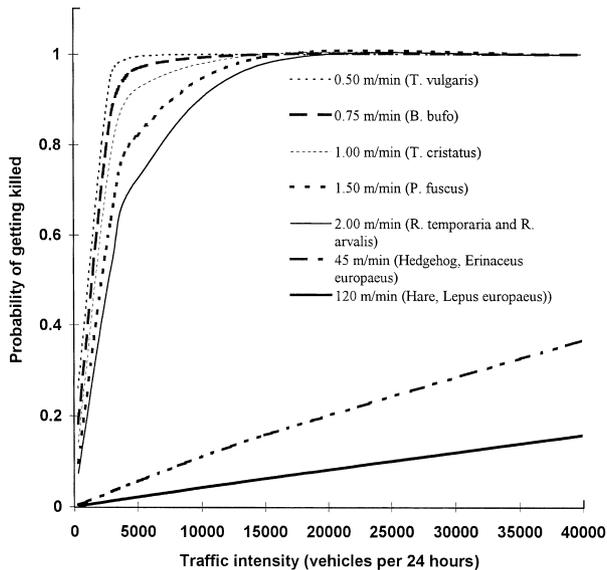
Fig. 2. Probability of getting killed for one individual of different species on the road, as a function of its velocity and traffic intensity, following the model: $P_{(\text{death})} = 1 - \frac{1}{\pi}\int_{\alpha=-\pi/2}^{\alpha=\pi/2} \frac{-Na}{e^{v\cos\alpha}} d\alpha$, and assuming perpendicular road ($\alpha = 0$). Velocities representative for different amphibian species are shown, together with velocities representative for hedgehog and hare. A traffic intensity of 3200 vehicles per 24 hours corresponds to the road investigated.
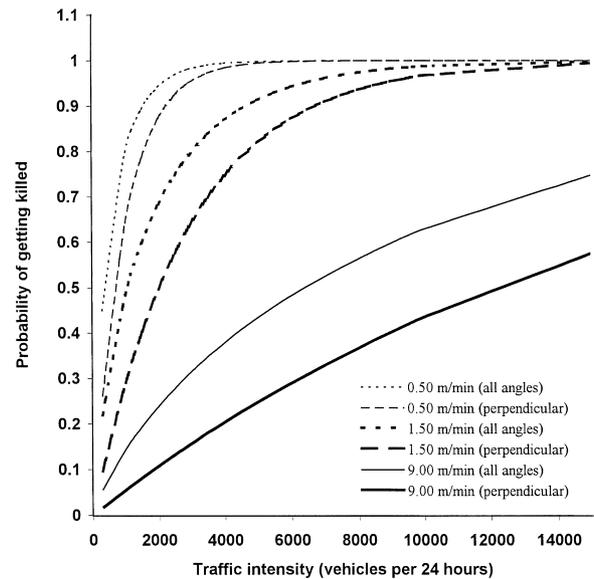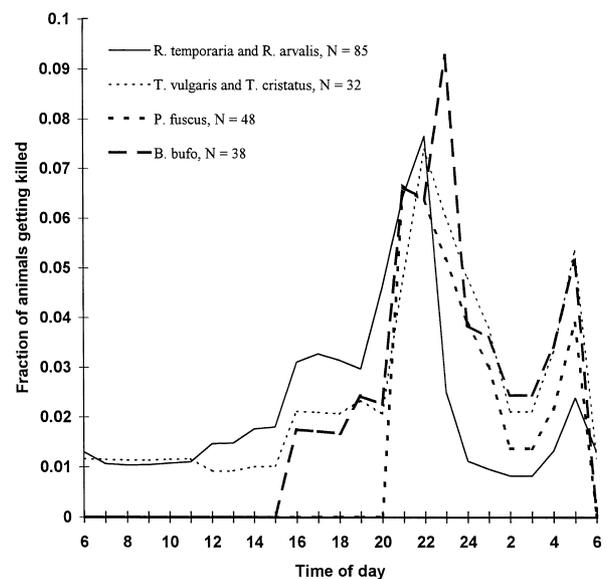
Fig. 4. Diurnal variation in probability of getting killed for the six amphibians species investigated. Probability of getting killed has been weighted by the movement pattern of the species.

Table 2
The efficiency of monitoring road victims by foot[a]

	Triturus vulgaris and *Triturus cristatus*	*Pelobates fuscus*	*Bufo bufo*	*Rana temporaria* and *Rana arvalis*
R	5	2	4	29
C	14	2	7	73
B	1	4	8	34
Total $= R + C + B$	20	8	19	136
$\hat{N}$	90.0	9.0	22.5	198.3
E^*	0.067	0.667	0.533	0.318
SE	0.065	0.192	0.129	0.045
$F = 1/E^*$	15.00	1.50	1.88	3.15

[a] The efficiency (E^*) with standard error is given as a fraction of road victims discovered out of the total (unknown) number (N). $R =$ number of victims recorded by routine monitorings only; $C =$ number of victims recorded by control monitorings only; $B =$ number of victims recorded by routine *and* control monitorings. The numbers are sums of 16 routine monitorings and 19 control monitorings, all by foot; F is the factor that converts, by multiplication, the number of victims found by routine monitorings ($R + B$) into the estimated total number of victims ($\hat{N}$).
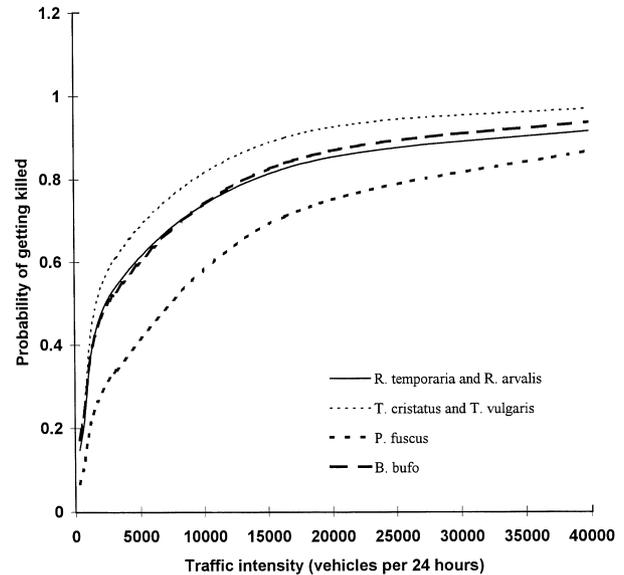

Fig. 5. Probability of getting killed for one individual of different amphibian species on the road, as a function of traffic intensity. Probability of getting killed has been weighted by movement pattern of the amphibian species and diurnal variation in traffic intensity.

active. However, the probability of getting killed reaches a peak just after sunset, owing to the activity pattern of the amphibians (Fig. 1).

Finally, the overall probability of getting killed by a single road crossing was found by summing up probabilities of getting killed for each of the 24 h-long intervals. This probability was also extrapolated to other traffic intensities (Fig. 5). Again, the difference in levels of probability of getting killed reflects the velocity and the diurnal activity pattern of the species. The slow moving salamanders face the highest probability of getting killed and the fast moving *Rana* species face a somewhat lower risk. The diurnal activity pattern for *P. fuscus* is complementary to that of vehicles and lowers the probability of getting killed considerably.

3.3. The efficiency of recording road deaths

The efficiency of monitoring of road victims by foot was estimated with the expression derived in the Section 2 (Table 2). The two *Rana* species were pooled since they are hard to distinguish as road kills. *Triturus vulgaris* and *T. cristatus* were pooled because of low numbers and taxonomic similarity.

Monitoring road victims by foot was surprisingly inefficient, ranging from about 7 to 67% of the road victims discovered (Table 2). The efficiency of foot monitoring was highest for *P. fuscus* and *B. bufo* — species that are believed to stay on the road for some time after getting killed due to their relatively tough skin and unpalatability, while only about one third of the brown frogs (*R. temporaria* and *R. arvalis*), and about 7% of the salamanders were discovered by foot.

3.4. Impact of road deaths on populations

In 1996, anuran adult population sizes in the area were estimated to be 1075 *Rana temporaria*, 3309 *Rana arvalis*, and 265 *Pelobates fuscus*. In 1997, the figures were 425 *R. temporaria*, 1,680 *R. arvalis*, and 439 *P. fuscus*.

The estimated total number of adult amphibians killed was found by extrapolating the results from the period of road kill monitoring (April, May, and August) to the assumed whole active season (1 April–15 October), assuming that the 3 months of monitoring are representative (Table 3). Finally, the estimated fraction of road-killed adults in 1996 and 1997 was calculated.

4. Discussion

4.1. Probability of getting killed on the road

Formally expressing the probability for an animal to get killed by a single road crossing has been attempted before (Heine, 1987). However, Heine's equation suffers from the logic shortcoming that high vehicle intensities and/or slow moving animals result in negative values of survival probability- values that are then truncated at zero. van Langevelde and Jaarsma (1997) overcome this by turning the equation (very similar to that of Heine (1987)), into an exponential expression, allowing the probability of getting killed by road crossing to approach 1 asymptotically for high traffic intensities and/or slow moving animals. Their equation is very similar to ours, except that van Langevelde and Jaarsma consider the entire paved width to be effective in killing

Table 3
The number of road victims and the estimated fraction of the adult populations killed on the road, found by foot-monitoring in 1996 (85 days) and 1997 (102 days), extrapolated to whole active seasons (1 April–15 October)[a]

	T. vulgaris and *T. cristatus*	*P. fuscus*	*B. bufo*	*R. temporaria* and *R. arvalis*
1996				
Observed victims	17	8	20	91
Estimated victims[b]	86.29	7.61–28.27	25.28–72.73	223.04–399.13
Total estimate for active season	201.02	17.73–65.85	58.90–169.42	519.55–929.73
Fraction of adult population	–	0.07–0.25	–	0.11–0.21
1997				
Observed victims	11	13	14	30
Estimated victims[b]	55.88	12.37–45.94	17.70–50.91	73.53–131.58
Total estimate for active season	108.47	24.01–89.17	34.36–98.82	142.73–255.42
Fraction of adult population	–	0.05–0.20	–	0.07–0.12

[a] The ranges of the total number killed are calculated from estimates of monitoring efficiency (E^*) $\pm$ 2 times S.E. (cf. Table 2). As $E^* - 2 \times$ S.E. for *Tritutus vulgaris* and *T. cristatus* is below zero, only minimum values of total number killed are given. Population estimates for *T. vulgaris* and *T.cristatus* and for *Bufo bufo* are incomplete, and therefore the fraction of adult populations killed is not estimated for these three species.

[b] $\frac{1}{E^* \pm 2 \text{S.E.}} \times$ number of victims found.

whereas we operate with a narrower killing width of vehicles (α). Since van Langevelde and Jaarsma mainly consider large animals (roe deer (*Capreolus capreolus*), foxes (*Vulpes vulpes*), mustelids) their assumption is a realistic approximation, but this does not apply to small animals which may remain still under a passing vehicle without getting hurt. It is also clear from our study that the actual distribution of crossing angles at a site has a large effect on the probability of getting killed; the effect is most pronounced for fast moving animals, and for intermediate values of probabilities of getting killed. The actual distribution of crossing angles at a site is expected to vary considerably between sites, and in this work, we did not record crossing angles in a systematic way. Therefore, we mainly considered perpendicular road crossing, and consequently it needs to be stressed that our calculations of probabilities of getting killed by road crossing must be considered minimum values. Where amphibians have a fixed route to and from spawning sites they may be undeterred by low to medium traffic intensity (i.e. below 12000 vehicles per 24 h). Mortality on this type of road may therefore be higher than predicted from traffic intensity alone. However, this is only speculative, and we recommend investigations on actual crossing angles.

The width (*a*) of vehicles that kill, was calculated as a weighted average of the vehicles on this particular road. The proportion of vehicles is likely to vary somewhat diurnally, seasonally, and with the day of the week. Because there is no existing data on this variation, we did not include it in our model. We did, however, tentatively increase and decrease the proportion of trucks by 5% and changed the proportion of cars accordingly. The resulting probability of getting killed was increased and decreased by up to 5%, respectively. The change in probability was largest on roads with low traffic intensity, and for species with low overall probability of getting killed. Thus, it seems that in situations where traffic is intense, the results of the model are most reliable; for busy roads (15 000+ vehicles per 24 h), with a 5% change in proportion of vehicles as described above, the change in model results for *T. vulgaris*, *T. cristatus*, *B. bufo*, *R. temporaria*, and *R. arvalis* was 1% or less.

Clearly, the three most important factors determining species vulnerability to road mortality are velocity of the species and diurnal movement pattern of the species and the vehicles. As a logical consequence of this, the most vulnerable species are day-active, slow-moving species. Velocity as an important factor has been stressed by several authors (e.g. Heine, 1987; Rosen and Lowe, 1994; Schlupp and Podloucky, 1994; van Langevelde and Jaarsma, 1997), but none considers the diurnal movement pattern of the animals and the vehicles (movement patterns are discussed by Rosen and Lowe (1994), but on a seasonal basis only).

The road investigated has a large diurnal variation in traffic intensity (high traffic intensity in the daytime dropping to almost zero at night), and this pattern reduces the vulnerability of nocturnal amphibians considerably. Other types of roads (e.g. motorways) may have diurnal variation in traffic intensity quite different from this one. In assessing the overall vulnerability of a species to traffic, the frequency of road crossing has to be included as well. *P. fuscus* may have a low frequency of road crossing whereas the badger (*Meles meles*), for example, is vulnerable to traffic mortality because of its frequent road crossings (Verboom, pers. commun.).

4.2. Assessing the number of road kills

Despite earlier attempts to quantify road killed amphibians and reptiles, none of the authors have quantified the efficiency of their estimated number of road

kills. Göransson et al. (1978) developed an expression to calculate the efficiency of foot monitoring. Their equation calibrates the efficiency of routine and control monitorings against all victims found. In contrast with our approach, Göransson et al. do not consider the unknown total number of victims killed on the road, i.e. the ones found plus the ones missed, and they thereby tend to overestimate monitoring efficiency by underestimating the total number of animals killed on the road.

Road-killed amphibians do not remain on the road for long; they are eaten by scavengers or are, especially in rainy weather, obliterated by being repeatedly run over by cars. They presumably have a shorter duration than mammals, for example, whose size and furry skin make them visible for a longer time. Our calculations confirm that many amphibians are missed even when patrolling the road by foot once every 24 h: only 7% (*Triturus vulgaris* and *T. cristatus*) to 67% (*Pelobates fuscus*) of the total number of road victims are found. Patrolling by car, which is done by most authors, is far less efficient. Thus, uncorrected road kill estimates are highly unreliable.

One basic assumption of estimating the size of a population using a Lincoln index is that the population is closed. This assumption is clearly violated in the case of estimating the total number of road-killed amphibians. On the road, new victims are continuously added to the 'population', and others are removed by scavengers. Violation of this assumption tends to underestimate the victims found both at the routine and the control monitoring, and thereby overestimate the total number of amphibians killed. Another basic assumption is the one of independence in observing/missing a road victim during routine and control monitorings, respectively. There may be a slight bias in that very obvious roadkills are more likely to be recorded, but to all intents and purposes, the assumption is met.

4.3. Population size estimates

Our estimates of the population size of *P. fuscus* in the five fenced ponds are fairly accurate since they are based on marked individuals. The estimate of the population size of the two *Rana* species is not as accurate as the one for *P. fuscus*; partly because the brown frogs were not individually marked and partly because a larger fraction of the population bred in the ponds that were not fenced, compared to the *P. fuscus* population. The population estimates of *B. bufo* are very inaccurate, since the main part of the population bred in other ponds than the five fenced ones. They are therefore omitted from the following calculations together with *Triturus vulgaris* and *T. cristatus* and all data from 1995, where population sizes were estimated in the five fenced ponds only and thus do not form a basis of a total population estimate.

Our calculation of the fraction of adult amphibians killed on the road is based on the assumption that we have monitored the entire (meta)populations affected by the highway. We chose 1000 m from the highway to be the upper limit of movement (in the sense that all populations within 1000 m from the highway are believed to be affected by its presence. In the literature, exact data on amphibian movement range are scarce). This assumption is in reasonable accordance with existing data, as *P. fuscus* is recorded to move a maximum of 1200 m between hibernation site and breeding pond (Nöllert, 1990). Moreover, *P. fuscus* seems to be philopatric to its native pond with few adults changing breeding pond from year to year, which makes it reasonable to assume that we have monitored the entire metapopulation affected by road mortality. The two *Rana* species were pooled when estimating the fraction of adults killed on the road, partly because they are difficult to distinguish as road victims and their egg-clumps cannot be distinguished with certainty (Fog et al., 1997). Haapanen (1970) found that the maximum distance moved between years by *R. arvalis* and *R. temporaria* was 350 and 600 m, respectively. Despite the accordance between our assumptions and existing data on amphibian movement range, it is clear that more data on the subject are needed until a firm fraction of amphibians killed can be established. Results should therefore be regarded as preliminary, although within the right range.

4.4. The impact of road kills on the populations

The road mortality estimates from this study cannot be extrapolated to other populations, but the equation, relating probability of getting killed for one individual on the road to the crossing angle, the velocity of the animal and the traffic intensity, is directly applicable to other populations, other geographical areas, and even to other species. The use of the equation is restricted, however, to species that do not behave intelligently towards traffic (e.g. stay on the side of the road until no vehicles are present). It is still useful to consider whether an annual mortality of up to 25 and 21% of the reproductively active adult population of *P. fuscus* and *R. temporaria/R. arvalis*, respectively, would have a significant effect on the population size (note that the annual mortality range is underestimated since it does not take into account the standard errors of the population estimates). That is, does road mortality constitute an additive or a compensatory mortality effect? For anuran adults in general, density independent mortality factors seem to be most important whereas for larvae, both density dependent and density independent mortality factors seem to be important (Duellman and Trueb, 1994, and references therein). If the population in question is mainly regulated by density-independent

mechanisms, such as climatic variability, road mortality will be an additive effect and is thus important as a population regulating factor. If, however, the population is regulated by density dependent factors (mainly intraspecific competition among the larvae, cf. e.g. Wilbur (1972,1977)), road mortality will be compensated for by higher larval survival and the impact on the population will not be very large. This particular *P. fuscus* population is probably regulated in the larval state by density-dependent mechanisms (Hels, unpublished), and the road mortality is therefore expected to have no large regulating effect. If traffic intensity continues to increase, however, increased road mortality may eventually reduce the population to a level where its reproductive output is too small to reach the carrying capacities of the breeding ponds. This in turn may drive the population down to a level where demographic stochastic processes become important for the survival of the population. Finally, it should be noted that road mortality may be even more serious to the juveniles in the population since they are slow movers. This is a field where more investigations are needed, since very little is known about the movement ranges of juvenile amphibians.

Acknowledgements

Appendix A

The probability of an amphibian surviving t time units on the road is denoted p. The change in p during one time step (dt) becomes:

$$dp = -\lambda p dt, \tag{6}$$

where λ is a positive constant depending on: N: mean number of vehicles passing per time unit (the actual number is assumed to be Poisson distributed with mean N), $\frac{a}{L}$: the probability of getting hit, where a is the width of vehicles that actually kills, and L = width of the road. The change in p thus becomes:

$$dp = -\frac{Na}{L} p dt \tag{7}$$

Integration of Eq. (6) yields:

$$p = e^{-\lambda t}. \tag{8}$$

Since $t = \frac{s}{v}$, where s = distance moved to cross the road and v = velocity of the animal in question, Eq. (8) can be rewritten as:

$$p = e^{-\frac{\lambda}{v}s} = e^{-\frac{Na}{Lv}s}. \tag{9}$$

s depends on the angle of crossing the road. Crossing angle is denoted α, $\alpha = 0$ corresponds to perpendicular road crossing, which implies that the following condition must be satisfied for the animal to cross the road: $-\frac{\pi}{2} < \alpha < \frac{\pi}{2}$. Consequently, the distance moved by crossing the road becomes $s = \frac{L}{\cos\alpha}$ (note that for perpendicular road crossing: $s = L$). Mean probability of surviving one road crossing ($P(\text{surv})$), including all possible crossing angles, becomes:

$$P(\text{surv}) = \frac{1}{\pi} \int_{\alpha=-\pi/2}^{\alpha=\pi/2} e^{-\frac{Na}{v\cos\alpha}} d\alpha \tag{10}$$

and the mean probability of getting killed ($P(\text{death})$) consequently becomes:

$$P(\text{death}) = 1 - \frac{1}{\pi} \int_{\alpha=-\pi/2}^{\alpha=\pi/2} e^{-\frac{Na}{v\cos\alpha}} d\alpha, \tag{11}$$

which can be extended to include variation in animal velocity by weighting Eq. (11) with the density function of velocities ($p(v)$), i.e.

$$P_{(\text{death})} = 1 - \frac{1}{\pi} \int_{v=0}^{\infty} p(v) \int_{\alpha=-\pi/2}^{\pi/2} e^{-\frac{Na}{v\cos\alpha}} d\alpha dv. \tag{12}$$

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