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ORIGINAL PAPER

Amphibian road mortality in Europe: a meta-analysis with new data from Poland

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Abstract While the increasing vehicular traffic is widely suspected to play a role in the worldwide amphibian population decline, the research of amphibian road mortality is scarce, fragmented, fraught with methodological problems, and largely inconclusive. As the first attempt at a synthesis, we analyzed all available data on amphibian mortality in Europe and combined them with four previously unpublished surveys conducted by us. Based on our recalculation of road-kill counts in terms of species-specific road-kill recordability, we conclude that, in lowland Central Europe, the common toads, *Bufo bufo*, are the most common victims of vehicular traffic in suburban landscapes, while the common frogs, *Rana temporaria* and *Triturus* newts, prevail in rural landscapes. The green frogs also tend to be more frequent in rural areas. Common tree frogs, *Hyla arborea*, are unexpectedly rare in the road-kill record despite their terrestrial and migratory habits. In consideration of problems with obtaining accurate amphibian population estimates, we further propose the road kills-to-spawners ratio (*R*/*S*) as a working measure of the impact of road mortality on a local population. While the *R*/*S* ratio may not reflect the losses to an entire local amphibian population, it is free of the errors of whole-population estimates, which are notoriously difficult for amphibians. When corrected for species-specific road-kill recordability, most results suggest that the impact of roads on newts may have been underestimated and that the impact on common frog populations may be higher than on those of common toads.

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Introduction

The negative impact of road mortality on local populations of at least some amphibian species (van Gelder 1973; Fahrig et al. 1995; Hels and Buchwald 2001; Cooke and Sparks 2004; Mazerolle 2004; Pellet et al. 2004; Gibbs and Shriver 2005) implicates the rapid increase of traffic intensity in many parts of the World as a factor of the global amphibian population decline (Puky 2006). However, the quantification of this impact on populations of any particular species is a complex task that requires substantial research effort far beyond road-kill counts and taking into account the relative roles of natural mortality, especially its density-dependent mechanisms (Berthoud and Müller 1986; Hels and Buchwald 2001; Harper and Semlitsch 2007). This is probably why there are very few, only three in Europe (van Gelder 1973; Hels and Buchwald 2001; Cooke and Sparks 2004), conclusive studies specifically of the impact road-crossing mortality (rather than roads in general) on amphibian populations.

In this paper, we provide new data on amphibian road mortality from four widely different habitats of Lower Silesia, a southwestern province of Poland, and review the published data on amphibian road mortality in Europe with an attempt to make them better comparable and thus more useful to assess the impact of road mortality on amphibian populations. Having performed breeding censuses in all four study sites, we calculated the populational impact of road mortality in terms of a road kills-to-spawners ratio (*R*/*S*). Our work points to the need of methodological improvements in amphibian road mortality studies and additional basic research in amphibian population biology.

Materials and methods

We analyzed all available (the total of 14) published reports with any usable quantitative information on amphibian road mortality in Europe (Table 1), the majority of them coming from Central Europe. A literature search on Zoological Record did not reveal other reports except for several qualitative and more or less casual observations.

As far as warranted by the monitoring methods, we recalculated both others' and our own road-kill counts using species-specific correction factors, that is, the ratios of all casualties to the those found by routine monitoring. Following Hels and Buchwald (2001), we used 1.88 for common toads, *Bufo bufo*, 3.15 for brown frogs, *Rana temporaria* and *Rana arvalis*, 1.5 for common spadefoots, *Pelobates fuscus*, and 15 for the *Triturus* newts. For other species, we used tentative correction factors, 5 for common tree frogs, *Hyla arborea*, 4 for *Bombina* toads, 3 for the green frogs, *Rana lessonae*, *Rana ridibunda*, and *Rana* kl. *esculenta*, and 2 for the green toads, *Bufo viridis*, which were interpolated from Hels and Buchwald's (2001) experimental values by taking into account body size, visibility, and palatability. Although they may prove too conservative, especially for the tree frogs and *Bombina* toads, their use was unavoidable given the variation in methodology of published road mortality studies.

We studied amphibian mortality on four secondary, two-lane roads in four widely different landscapes of Lower Silesia, SW Poland for two consecutive years (including two breeding seasons). All four surveyed road sections were selected because of the known abundance of amphibians in their environs. Two of them cross rural areas, one a mosaic suburban landscape and the other a street in a small town. Vehicular traffic on all four was in the range of 400–500 vehicles/day. All surveys were performed by walking one road side there and the other back. The four surveyed road sections were as follows:

Chelmski Pond (in the Bory Dolnośląskie conifer forest complex, near Chełm Żarski village of 90 inhabitants, Lubsko county, Żary district, Lubuskie province, 51°47′ N, 14°54′ E). The 500-m road section runs between pastures and meadows on one side and a pine forest surrounding a large, 41-ha pond (reaching to 30 m from the road shoulder) on the other. The surveys were performed three to four times per week between 6:00 and 7:00 A.M. for over 1 year (9 March to 9 November 2001 and 1 February to 15 July 2002).

Stobrawa Forest (Kluczbork county, Opole province, 50°56′ N, 18°06′ E). The 500-m road section crosses hydrophilic broad-leaved woodland with the predominance of the alders, *Alnus glutinosa*, and birches, *Betula verrucosa*, and a 0.8-ha pond located some 300 from the road and connected by a creek to a roadside ditch. The surveys were performed three to four times per week at sunrise for over 1 year (1 March 2000 to 15 June 2001).

Wrocław suburb (the valley of Bystrzyca river, 51°07′ N, 17°02′ E). The 1,800-m road section crosses a mosaic landscape of a small river valley with broadleaved woods including fragments of natural riverside woodland *Salici-Populetum*, a park, and interspersed fields (mostly abandoned cropland), eight pools and small ponds (0.16–1.0 ha, jointly 2.1 ha) with lush hydrophilic vegetation, and a narrow creek (1–1.5 m wide) crossing the road. The closest pond is located 200 m from the road, but flood waters come much closer to the road in the spring. The surveys were performed every other day throughout the amphibian migration season (March to May) and one to two times a week in other months between 6:00 and 9:00 A.M. for over 2 years (1 October 2002 to 30 June 2004) including two breeding seasons.

Town of Lubsko (Żary district, Lubuskie province, 51° 46′ N, 14°56′ E). The 200-m street section in the outskirts of a small town (16,000 inhabitants) lies adjacent to a school playing ground with a 25-m^2 fire-emergency concrete reservoir overgrown by water plants (*Schoenoplectus lacustris*, *Typha angustifolia*, *Lemna minor*). Thirty-seven counts of green toad casualties were performed in two breeding seasons (1 May to 17 July), 16 in 2001, and 21 in 2002.

Our censuses of spawning anurans were performed primarily by counting individuals, spawn clumps, and strings and by registering calls of green frog males. Most difficult were the counts of newts breeding in Stobrawa Forest: The newts were captured three times per season by two persons in the pond, but their numbers in the ditch could be only estimated.

Results

Road-kill densities

The recorded absolute road-kill densities (Table S1) are clearly not comparable because of differences in sampling methods and the length of transects and thus can only provide orders of magnitude of amphibian road-crossing mortality. In the amphibian fatality hotspots, primarily in rural areas, road-kill densities amount to thousands per kilometer per year over short road sections and those in suburban areas are in the range of 100–500 km^{-1} $year^{-1}$. The two highest am-

Table 1 European studies of amphibian road mortality (in chronological order) with the four roads surveyed in this study at the bottom

Site/area, road length, traffic density, and authority	Survey period, frequency and method [breeding season (BS)]	Habitats/landscape	Species[a] in the order of decreasing road-kill frequency
Nijmegen area, "Overasseltse en hatertse vennen" nature reserve, Holland, 1.5 km, 336 vehicles/day (9.4 vehicles/h during toad migration) (van Gelder 1973)	1 BS (22.II–15.V), continuous recording every night "until no or hardly any animals were seen"	Woodland (unspecified)	Only *B.b.* studied
Białowieża Forest, E Poland, 17 km, no traffic data (Wołk 1978)	19 counts (13.V–24.IX), mornings, by motorcycle, 30 km/h, after removing or marking older casualties on the preceding morning	Natural mixed forest with 2 creeks	*R.t.*, *B.b.*
Denmark, 15,224 km various roads, from highway to secondary, no traffic data (Hansen 1982: Table 1)	One-time surveys over 3 years, on moped, "very slowly"	Diverse habitats	*B.b*, BF (*R.d.* and *R.a.*)[b], *B.v.*, T.c., *R.e*
Berlin woods, Germany, 4.7 km, max. 380 (at one end) to 2,000 vehicles/day (Miech 1988)	10 years, irregularly, 2–3 times a week at variable day time, by bike or car, occasionally by foot	Broadleaved and conifer forest, 7 pools, one supplied by a creek	*B.b.*, *R.t.*, *T.v.*, GF, *T.c.*, *R.a.*
Osnabrück area, Germany, 8.5 km across woodland with 2,659 vehicles/day and fields with 780 vehicles/day (Fuellhaas et al. 1989)	1 incomplete year, every 5 days, no day time information, by foot	6.1 km across fields, 2.4 km across woodland	*B.b.*, *R.t.*, *S.s.*, *T.a.*, *T.c.*, GF
Pieniny National Park, S Poland, no road and traffic data (Rybacki 1995)	42 days (27 spring, 15 fall), irregular surveys most counts on one road side only, then multiplied by 2, otherwise methods and times unspecified	Various (in part thermophilic) habitats of the Pieniny Klippen Belt and its surroundings	*B.b.*, *R.t.*, *B.v.*, *T.mo.*, *T.a.*, *Bo.v.*, *S.s.*, *T.c.*, *T.v.*
Sromowce Wyżne, Dunajec Valley, Pieniny Mts, S Poland, 2 km, 60–120 vehicles/h in the morning (Zamachowski and Plewa 1996)	2 incomplete BS (IV-V), morning counts (0700–0900 hours) by unspecified methods	Between a new reservoir and an open field with ditches and vernal pools	*R.t.*, *T.a.*, *B.b.*, *T.mo.*, *T.v.*, *B.v.*, *S.s.*
Warta river delta, Słońsk Nature Reserve, W Poland, 11.3 km, no traffic data (Bartoszewicz 1997)	1 year, by bike or car, twice a week, usually on two consecutive (!) work days	A mosaic of mostly open habitats including marshland	BF and GF, *B.b.*, *B.v.*
Western France (Department Vendée), 68.2 km of a new road (opened preceding fall), "200–450 vehicles/km" (Lodé 2000)[c]	1 incomplete season (7.5 months, IV-XI), 33 weekly surveys by car at <40 km/h and by foot	Unspecified	*B.b.* (56.7% of all amphibians) and 4 unspecified anurans, *T.h.* (28.4% of all amphibians) and 3 unspecified salamandrids
Djursland Peninsula, N Denmark, 0.6 km, 3,200 vehicles/day (Hels and Buchwald 2001)	altogether 6 months: incomplete BS (IV-V) and VIII of 2 consecutive years	Farmland with small woods and numerous ponds	BF, *B.b.*, *Tv.* and *T.c.*, *P.f.*[b]
Wielkopolska landscapes, W Poland, ca. 1,500 km, no traffic data (Rybacki and Krupa 2002)	2–3 morning surveys in one spring (IV–V), presumably by car	Various habitats in 11 protected landscape areas	*B.b.*, *B.v.*, *R.a.*, *R.t.*, *P.f.*, and single *Bo.b.* (misnamed as *Bo.v.*), *H.a.*, *R.e.*, *R.r.*
Oleśnica fish farm, Chodzież county, Wielkopolska Province, W Poland, 1,137 m,	1 BS (16.III–16.VI), by unspecified means, every 2 days afternoon (1500–1600 hours)	420 m across mixed woodland with some ponds and an inn; 700 m across gardening lots and	*T.v.*, *B.b.*, *R.t.*, *R.a.*, *R.e.*, *Bo.b.*, *P.f.*, *T,c.*, *R.l.*, *B.v.*

Table 1 (continued)

Site/area, road length, traffic density, and authority	Survey period, frequency and method [breeding season (BS)]	Habitats/landscape	Species[a] in the order of decreasing road-kill frequency
around 500 vehicles/day (36 vehicles/h between 1400 and 1800 hours) (Rybacki and Domańska 2004)		fields with many ponds; a creek crossing the road and flowing to the ponds	
Zielona Góra woods, W Poland, 5.8 km, 7,000–8,500 vehicles/day (Najbar et al. 2006)	2 years (altogether 1,900 surveys on 437 days), 2–10 (mean 4.3) times a day, regularly morning (0600–0800, 1400–1600, and 1700–2300 hours); mostly by car, occasionally by foot	Pine and mixed forests, 4 creeks expanding into ponds	*B.b.*, *R.t.*, *B.v.*, *P.f.*, *T.v.*, *R.e.*, *T.a.*, *T.c.*, and *R.a*
Wrocław Plain ca. 55 km^2 around Wrocław, Dolny Śląsk (Lower Silesia) Province, 48.8 km, 350–10,500 (mostly 350–479) vehicles/day (Orłowski 2007)	Over 2 years including 2 BS, thrice a week 15.III-30.IX, twice in the remaining periods, by car (20–50 km/h) and occasionally (through migration season) by foot on rain-free afternoons	Arable land (92%) with very little forest (1.6%) and some built-up areas, and 47 pools and ponds (total area 6.7 ha) within 200 m of the road	Only *B.b.* studied
Portalegre District, S Portugal, 26 km, 5,000 vehicles/d (Ascensao and Mira 2006)[c]	2 years, 54 surveys every 2 weeks, by car 20 km/h	Mostly agro-forestry (montado), some pastures, meadows fields and olive groves	*B.c.* 36%, *P.c.* 25%, *B.b.* 14%, *S.s.* 12.5%, *P.w.* 8%, *D.g.* 1.4%, *T.ma.* 0.9%, *H.m.* 0.4%, *R.p.* 0.4%, *A.c.* 0.2%
Chełmski Pond, SW Poland, 0.5 km, 450 vehicles/day (this study)	Over 1 year including 2 BS, 3–4 per week, 6–7 a.m., by foot, there on one road side and back on the other; see also "Material and methods"	Between pastures and meadows on one side and a pine forest surrounding a large pond on the other; see also "Material and methods"	*R.t.*, *B.b.*, *R.a.*, GF (*R.e* and *R.l.*), *T.c*, *P.f.*, *Bo.b.*, *H.a.*
Stobrawa Forest, SW Poland, 0.5 km, 400 vehicles/day (this study)	Over 1 year including 2 BS, 3–4 per week starting at sunrise, by foot, there on one road side and back on the other; see also "Material and methods"	Hydrophilic broad-leaved woodland, a pond some 600 from the road, a creek connecting the pond to the roadside ditch; see also "Material and methods"	*R.t.*, *B.b.*, *T.v.*, GF (*R.e* and *R.l*)
Wrocław suburbs, SW Poland, 1.8 km, 450 vehicles/day (this study). See Ciesiołkiewicz et al. (2006) for a map	Over 2 years including 2 BS, every other day in BS, 1–2 times a week in remaining periods, 0600–0900 hours, by foot, there on one road side and back on the other; see also "Material and methods"	Mosaic landscape of a small river valley, with broadleaved woods, 8 small ponds and a creek; see also "Material and methods"	*B.b.*, *T.t.*, GF, *R.a.*, *H.a.*
Town of Lubsko, SW Poland, 0.2 km, 500 vehicles/day (this study)	2 BS, altogether 37 counts by foot, there on one road side and back on the other; see also "Material and methods"	A small town street adjacent to a school playing ground with a pool	*B.v*

[a] Species abbreviations: A.c. *Alytes cisternasii*, B.b. *Bufo bufo*, B.c. *Bufo calamita*, BF brown frogs, Bo.b. *Bombina bombina*, Bo.v. *B. variegata*, B.v. *Bufo viridis*, D.g. *Discoglossus galganoi*, GF *green frogs*, H.a. *Hyla arborea*, H.m *Hyla meridionalis*, P.c. *Pelobates cultripes*, P.f. *Pelobates fuscus*, P.w. *Pleurodeles walti*, R.a. *Rana arvalis*, R.d. *Rana dalmatina*, R.e. *Rana* kl. *esculenta*, R.l. *Rana lessonae*, R.p. *Rana perezi*, R.r. *Rana ridibunda*, R.t. *Rana temporaria*, S.s. *Salamandra salamandra*, T.a. *Triturus alpestris*, T.c. *Triturus. cristatus*, T.h, *Triturus helveticus*, T.ma. *Triturus marmoratus*, T.mo. *Triturus montandoni*, T.v. *Triturus vulgaris*

[b] The distribution of frogs in Denmark is very patchy (E. Buchwald, pers. comm.). *Rana dalmatina* and, to a lesser extent, *Rana arvalis*, replace *R. temporaria* in some parts of Denmark such the Isle of Lolland, which was surveyed by Hansen (1982). By contrast, *R.. temporaria* is common in Djursland Peninsula but green frogs are absent there (Hels and Buchwald 2001).

[c] Studies were not included in further quantitative comparisons because of the monitoring methods (especially too low frequency) and incomparable species composition (largely unspecified for Western France).

phibian road mortality records, at Sromowce Wyżne and the Oleśnica fish farm (Table S1), are at the expense of single taxa, common frogs and *Triturus* newts, respectively. The mass mortality at Sromowce Wyżne may have been a composite result of setting an ecological trap by separation of the wintering from spawning sites (Zamachowski and Plewa 1996) and disorientation of amphibians following the flooding of a part of the Dunajec river valley (Rybacki 2002). In addition, in upland areas, the common frogs may be more prone to daytime migration than other species commonly observed on European roads (Berthoud and Müller 1986). Mass mortality of *Triturus* newts at the Oleśnica fish farm is apparently caused by their mass migration along a creek (Rybacki and Domańska 2004), as was the case in a location in England (Evans 1989). A similar situation occurs at Stobrawa Forest, where the newts enter the road from a roadside ditch that receives a creek flowing from a pond. The third highest mortality figure comes from a 0.5-km stretch of road at Chelmski Pond where amphibians come to breed in a pond surrounded by a pine forest while their feeding habitat is across the road. This is a typical ecological trap as most amphibians that breed in the pond have to cross the surveyed road, which separates them from feeding habitats and runs very close to the pond.

Species composition

Twenty-six amphibian species have been recorded dead on European roads (Table 1), including 18 out of some 20 amphibian species with ranges across the continental Europe and eight endemic Iberian species from Portugal (Ascensao and Mira 2006). Most of published records come from Central Europe and prove fairly consistent in terms of relative species frequencies (Table 2): The most frequent are common toads, common frogs (as the main or only component of brown frogs), and, after the correction for road-kill recordability, the *Triturus* newts (of various species, depending on the habitat and geographic area). Common toad road kills are abundant in most landscapes, although their numbers show considerable variation as do their populations (Günther and Geiger 1996). They prevail in suburban areas and the only two studied mountainous locations, the Pieniny National Park (Table 1) and the Sudetes in SW Poland (Baldy 2002). In contrast, the common frogs and, after corrections for recordability, the *Triturus* newts prevail in rural areas (including seminatural wilderness) where they may outnumber both brown frogs and common toads (three sites) or at least the toads (one site). In suburban sites, the newts and brown frogs are by an order of magnitude less frequent than in rural areas. The absence of newts in the record from Bialowieża forest, Warta river delta, and Wielkopolska landscapes is probably due to fragmentary sampling (Table 1).

The green frog road kills are more frequent in rural than in suburban sites (Table 2, Fig. 1). The green frogs are absent or rare over large parts of Denmark including the Djursland Peninsula, and the pool frog (*R. lessonae*), the most migratory of European green frogs (Günther 1996a), does not occur there at all. In contrast, their absence in the Białowieża Forest record is due to the lack a nearby pond and/or fragmentary sampling.

Other species including green toads, common spadefoots, *Bombina* toads, and common tree frogs occurred only in some habitats but not in others, the tree frogs being clearly the least frequent among road kills. The only site where the tree frogs perished on road in appreciable numbers is Chełmski Pond, where the top numbers of other amphibian also were killed.

Road kills-to-spawners ratios

The road kills-to-spawners (*R*/*S*) ratios obtained in our study are fairly consistent (Table 3) considering that the estimates they are based on were obtained by a different person in each of the three major sites. The *R*/*S* ratios for common toads (0.23–0.40) are comparable to that projected from van Gelder's data (0.39) in Holland if the whole stretch of road were used by traffic (Table 3). However, those for common frogs (0.40–0.66) are three to four times higher than those recorded in Denmark (Hels and Buchwald 2001). The highest is the *R*/*S* ratio obtained for common newts in Stobrawa Forest after the correction of road-kill numbers. At this site, the number of spawners must have been more than halved even if the actual population size were twice our estimate. Local green frog and *Bombina* toad populations were affected only by the ecological trap at Chełmski Pond, which may also be the case at Oleśnica fish farm (no population estimates are available from this site). Not unexpectedly, a small town (Lubsko) population of green toads incurred heavy losses and may have been nearly halved by moderate street traffic.

Discussion

One approach is to establish the mortality of road-crossing migrants (henceforth referred to as the road-crossing mortality) and determine the fraction of an entire population that crosses the road. The road-crossing mortality has been recorded either by continuous counting of all individuals on a road, both dead and alive (van Gelder 1973), or by a combination of continuous counting and road fencing (Kuhn 1987; Gibbs and Shriver 2005). The road-crossing mortality may equal or approach the road mortality of the entire local breeding population only if all or most breeding adults have to cross a road. This is the case when a breeding site is

Table 2 Species shares (in %) in the European record of amphibian road kills including three of the four roads surveyed in this study (the town of Lubsko and other single-species sites excluded)

Site (R, rural; S, suburban)	Totals		%UN	%NS		%*B.b.*		%BF		%GF		%*B.v.*		%*P.f.*		%*Bo.*		%*H.a.*	
	A	C		A	C	A	C	A	C	A	C	A	C	A	C	A	C	A	C
Oleśnica fish farm (R)	903	6,832	15	34	67	16	4.0	18	7.5	7.4	3.0	0.3	0.1	4.2	0.8	5.5	2.9	0.0	
Chełmski Pond (R)	820	3,114	14	8	30.3	21	10	36	30	12	9.3	0.0		7.0	2.6	1.8	1.9	1.3	1.8
Stobrawa Forest (R)	363	1322	27	5	22	19	10	45	39	3.0	2.0	0.0		0.0		0.0		0.0	
Bialowieża Forest[a] (R)	919	2714	nd	0.0		15.5	10	84.5	90	0.0		0.0		0.0		0.0		0.0	
Djursland Peninsula (R)	204	900	0.0	14	47	17	7.0	59	42	0.0		0.0		10	4.0	0.0		0.0	
Wrocław suburbs (S)	465	938	8	0.0		81	76	9	14	1.3	1,9	0.0		0.0		0.0		0.2	0.4
Zielona Góra woods (S)	3,017	5,967[b]	1.2	0.5	3.5	91	87	2.9	4.6	0.2	0.4	2.3	2.3	1.7	1.3	0.0		0.0	
Osnabrück area (S)	298	678	nd	2.3	15.5	91	75	6.4	8.9	0.3	0.4	0.0		0.0		0.0		0.0	
Berlin woods (S)	2,478	5,828	9	1.6	11	73	58	16	21	1.1	1.4	0.0		0.0		0.0		0.0	
Wielkopolska landscapes	2,009	4,044	41	0.0		42	39	7.4	11.5	+[c]		6.2	6.0	3.3	2.5	+[c]		+[c]	
Pieniny Natn. Park	1,485	3,901	nd	3.7	21	63	45	17	21	0.0		15	12	0.0		1.0	1.6	0.0	
Sromowce Wyżne	16,688	61,344	nd	4.5	18.5	1.0	0.5	94.5	81	0.0		0.02	0.01	0.0		0.0		0.0	
Denmark	1,463	3,349	1.7	1.8	12	81	66.5	12.5	17	0.6	0.8	2.3	2.0	0.0		0.0		0.0	

Actual figures (A) have been corrected (C) using road-kill recordability conversion factors (see "Materials and methods"). Column abbreviations as in Table 1 footnote except UN unidentified, NS Salamandridae

[a] The mean from 19 days was used for a 6-month season on the assumption that higher mortality at the peak of breeding season is approximately compensated by lower mortality in the early spring and late autumn. This is most probably an underestimate (and so is the corrected figure) as the observer may have missed other amphibian species (at least newts). This study was excluded from the species percentage comparisons.

[b] The correction factors may possibly be too high for this study because of frequent monitoring which, however, started hours after sunrise and was done mostly by car.

[c] A few individuals (unspecified number)

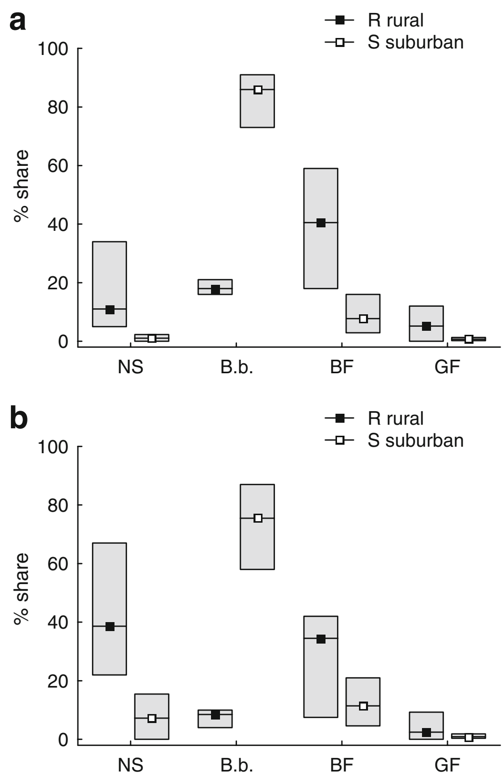

Fig. 1 The median shares (%) of newts and salamanders (*NS*), common toads (*B.b.*), brown frogs (*BF*), and green frogs (*GF*) in all amphibian roadkills from four rural (Oleśnica fish farm, Chełmski Pond, Stobrawa Forest, and Djursland Peninsula) and four suburban (Wrocław suburbs, Zielona Góra woods, Osnabrück area, and Berlin woods) areas: **a** the actual counts; **b** estimates corrected for recordability. The median values for GF in **b** are 2.5 for rural and 0.9 for suburban areas

completely encircled by roads with lethal traffic (probably a rare situation) or when the hospitable terrestrial habitats lie across the road to a body of water that is encircled by inhospitable habitat but provides the only breeding site in the area. In most cases, only a fraction of the population crosses the surveyed section of the road, and thus the road-crossing mortality (i.e., mortality calculated for this fraction only) is higher than the road mortality of the entire population, which can be estimated by complex modeling as employed by Gibbs and Shriver (2005).

Another most common and easier practicable approach in assessing the impact of road-crossing mortality on a local population is through comparing annual estimates of road-kill numbers and the entire local population. However, obtaining these two realistic estimates from raw counts is anything but straightforward, an issue that only begins to be addressed in the literature. The numbers of road kills recorded in the majority of studies, including ours, constitute only a fraction of the actual road kills because cadavers quickly disappear from the road as a result of scavenging and mechanical destruction by vehicles (Hansen 1982; Hels and Buchwald 2001; Slater 2002; Najbar et al. 2006; Langen et al. 2007) and because a fraction of those that remain on the road is overlooked both in surveys by foot (Hels and Buchwald 2001) and from motor vehicles, the latter technique being grossly inaccurate specifically for amphibians (Slater 2002; Langen et al. 2007; see also Puky 2006). Therefore, short of continuous counting of all individuals crossing a road, the actual numbers of road-kills must be estimated using appropriate correction factors for their recordability (i.e., the ratios of actual to recorded numbers of road kills). Road-kill recordability is the product of cadaver's chances to be preserved (for a certain time) and its chances to be noticed by the observer using an appropriate survey technique. Since it clearly depends on body size, mechanical properties, coloration, and palatability, it is clearly species-specific and so must be correction factors as experimentally demonstrated by Hels and Buchwald (2001) for *Triturus* newts, common spadefoots, common toads, and brown frogs. Unfortunately, no experimental correction factors are available for frequent traffic victims from other species. As a result, it remains largely unknown what species are actually most affected by road mortality rather than best represented in road-kill counts except that sedentary species that live in or close to their breeding waters all year round are expectedly less vulnerable than mobile, migratory species (Carr and Fahrig 2001).

Hels and Buchwald's (2001) recordability corrections factors, which were obtained for routine monitoring by foot every day at dawn, are conservative for both our and the majority of published studies that employed much less accurate road-kill counting methods (Table 1). All our surveys were done on foot in the morning hours (although only in Stobrawa forest really at dawn), by walking on one road side there and on the other back, but only every 2–3 days, which substantially increased the chance of removal and destruction of road kills prior to our monitoring. The road-kill recordability must be much lower (if at all calculable) for afternoon surveys, since most amphibians are killed at night, and for monitoring from a motor vehicle, which seems grossly inaccurate even if conducted by two persons in a car, an observer and a driver (Slater 2002; Langen et al. 2007).

Species differences

The common toads and common frogs are the most abundant and ecologically versatile anurans, and both species often breed in the same ponds (Schlüpmann and Günther 1996; Babik and Rafiński 2001; Carrier and Beebee 2003; Cooke and Sparks 2004). Both species undertake relatively long migrations (up to 2 km). However, common toads are much slower than common frogs (Hels and Buchwald 2001), which should make them more vulnerable to road death. And yet, the common frog populations are at least as much affected as, and, after corrections for recordability, probably even more

Table 3 Impact of road mortality on European amphibian populations in terms of road kills-to-spawners ratios as based on actual (A) and corrected (C) road-kill numbers, with spawning aggregation estimates below

Site/area	Newts		*B.b.*		*R.t.*		GF		*B.v.*		*P.f.*		*Bo.*	
	A	C	A	C	A	C	A	C	A	C	A	C	A	C
Chełmski Pond (this study)	No data		0.21 400	0.40	0.22 700	0.66	0.08 600	0.24	–		–		0.09 70	0.34
Stobrawa Forest (this study)	0.09 110 *T.v.*	1.35	0.13 350	0.23	0.13 650	0.40	0.02 280	0.06	–		–		–	
Wrocław suburbs (this study)	–		0.15 1610	0.29	0.19 180	0.61	0.003 910	0.01	–		–		–	
Djursland Pen.[a] (Hels and Buchwald 2001)	no data		–		0.04 3245	0.13	–		–		0.06 352	0.09	–	
Nijmegen area[b] (van Gelder 1973)	–		0.18 280 ♀		–		–		–		–		–	
Wrocław Plain[c] (Orlowski 2007)	–		0.10 5500	0.19	–		–		–		–		–	
Town of Lubsko (this study)	–		–		–		–		>0.4 80	>0.8	–		–	

[a] After corrections for recordability, the fractions of adult brown frogs and spadefoots killed annually by traffic were each about 10% (or, respectively, 7–21% and 5–25%).
[b] Because of continuous registering of all toads there is no need to apply a correction factor. The fraction of the entire female population of 310 killed on the road section used by vehicles was 15.8%. However, if the entire road encircling the spawning site were used, the annual loss to the entire population would be 31.3% and the *R/S* ratio 0.39.
[c] Two to three counts per season by unspecified methods in 46 bodies of water within 200 m from a road

affected by traffic than common toad populations (Table 3). This result agrees with observations that common frog populations have been decimated in the urban areas of Germany (Schlüpmann and Günther 1996) and reduced in the built-up areas with high road densities in the Alps (Landmann et al. 1999), although specifically the role of traffic alone has not been determined.

The moor frogs are much less frequent than common frogs in most road-kill records, except for the results of two to three surveys across the Wielkopolska landscapes (Rybacki and Krupa 2002). The moor frogs as a species are clearly less abundant than are common frogs, although this may not explain the entire difference, as moor frogs were moderately abundant in the surrounding habitats in Stobrawa Forest and Wrocław suburbs (at least 100 in a pond approximately 130 m from the road) and yet nearly absent from the road-kill record. Intriguingly, road density has had less than expected effect on moor frog populations in The Netherlands (Vos and Chardon 1998) in contrast to a strong negative impact on common frogs (Reh and Seitz 1990, Landmann et al. 1999). As compared to moor frogs (Günther and Nabrowsky 1996), common frogs disperse to a wider spectrum of terrestrial feeding habitats, which, in combination with the strong philopatry with respect to the spawning sites (Schlüpmann and Günther 1996), may account for their higher traffic vulnerability.

The rarity of European tree frogs in the road-kill record is somewhat unexpected because this species is widespread and locally abundant throughout most of continental Europe and considered fairly common in Poland (Głowaciński and Rafiński 2003). Pellet et al. (2004) showed some impact of both road density and traffic intensity on their populations in Switzerland, and a related species, *Hyla meridionalis*, has been recorded in small numbers on the roads of Portugal (Ascensao and Mira 2006).

Rural vs. suburban landscapes

Our review of road-kill recording methods employed in various studies (Table 1) suggests great and incalculable differences of accuracy. Furthermore, diverse combinations of provided and missing data made various studies comparable in some but not in other respects; hence, usually only subsets of studies listed in Table 1 could be used for our comparisons. However, our comparisons of the relative shares of species in the lowland record (Table 2) show an-order-of-magnitude differences between rural areas with the prevalence of common frogs and newts and suburban areas with the prevalence of common toads (Fig. 1). Unfortunately, the small sample size of four for each suburban and rural areas, which results from the low comparability of published studies, does not warrant the employment of statistical tests.

The differences in absolute road-kill densities between rural and suburban areas (Table S1) are certainly exaggerated by the different average length of surveyed road sections, 5.2 km for the suburban areas but only 0.7 km for the rural areas where more of mortality hot spots have been selected. However, the striking differences in species shares (Table 2) are unlikely to be substantially affected by road-section length. For example, two of the suburban areas, Wrocław suburbs i Zielona Góra woods, also were selected for high amphibian abundance and yet yielded road-kill species shares similar to the other two suburban sites (Table 2). We therefore suggest that an-order-of-magnitude difference in the absolute numbers of green frog road kills (Table S1) to an extent reflects their greater share in the rural compared to suburban areas, which is consistent with their shares being highest in three rural areas (Table 2).

A straightforward explanation for the species differences in amphibian road mortality between rural and suburban landscapes is that it reflects differences in relative species abundance, which is what is assumed in British monitoring studies of amphibian decline (Cooke and Sparks 2004). In a full agreement with this explanation, differences in the colonization rates of pools by three most common amphibian species in The Netherlands are related to their abundance (Laan and Verboom 1990). It follows that monitoring amphibian road mortality may prove to be the most effective method of detecting overall population trends in addition to determining the impact of vehicular traffic.

Impact on local populations

In order to estimate the impact of traffic on a local breeding population, one has to first know the population size. In a model study, Hels and Buchwald (2001) counted all individuals entering and leaving a body of water and thus could precisely calculate losses to the entire populations of brown frogs and common spadefoots. In practice of extensive rather than intensive amphibian road mortality studies, only a count of spawning individuals (usually at the peak of a breeding season) can usually be obtained and used as a proxy for the entire population. However, the number of spawners may provide a fair approximation of the entire local breeding population only for those amphibians, especially for some green frogs, that stay in or close to their breeding waters throughout the breeding season, although natural mortality in spawning aggregations has to be taken into account if the additive impact of another mortality factor (road traffic) is to be estimated. For other amphibian species, such as the common toads and *Bombina* toads (Günther and Schneeweiss 1996) and common tree frogs (Pellet et al. 2007), the number of spawning individuals (or chorus members) is at any time substantially different from the real size of a local population. Even the maximum number of spawners is only a fraction of the breeding population, which varies among species depending on their biology and behavior (Cooke 2000). For example, female common toads do not breed annually, leave water immediately after spawning, and the number of leaving females is much lower than the number of incomers due to their high mortality in breeding aggregations (Günther and Geiger 1996).

If the population structure of an amphibian species were well known, it would be possible to estimate the entire population size from the maximum spawner count by using an appropriate probabilistic model. We thus propose to explicitly acknowledge that all that can be reliably calculated in most studies of the populational impact of road mortality is the road-kills-to-spawners ratio (*R*/*S*), with the number of road-kills per one year in the numerator and the number of spawning individuals in the denominator. Although both figures are usually only estimated in most resource-limited studies, they can be recorded by counts if enough effort is made (e.g., by employing the combined drift-fencing and pitfall-trap technique). By contrast, the censuses of all individuals (including non-breeders) dispersed on land are barely feasible, making the estimates of entire local populations, e.g., by the addition of 10% (Orlowski 2007), arbitrary and thus prone to errors. By avoiding these compounding errors, the *R*/*S* ratios make various estimates of traffic impact on the same or closely related species (with similar biology such the *Triturus* newts and the three members of the *Rana esculenta* hybrid complex) much better comparable between studies. We therefore believe that it is better to use plain *R*/*S* ratios that are comparable for the same or similar species and bear potentially calculable errors rather than as hoc "corrections" for the entire local population.

There are surprisingly few breeding censuses of amphibians in Europe (Table 3). In the Nijmegen area of Holland, van Gelder (1973) registered all breeding common toads coming and leaving the spawning "fens" by continuous counting and counted their spawn strings. In the Djursland Peninsula of Denmark, Hels and Buchwald (2001) performed a precise count of breeding common frogs by complete drift fencing of five ponds and counting spawn clumps and calling males. Our censuses are clearly much less accurate than those used in the model studies by van Gelder (1973) and Hels and Buchwald (2001) and produce only estimates rather than precise figures subject to statistical evaluation. And yet, they seem to provide informative approximations inasmuch as we used the mean values from two breeding seasons, and the *R*/*S* ratios based on our estimates (Table 3) are fairly consistent between the three major multispecies breeding sites (Chełmski Pond, Stobrawa Forest, and Wrocław suburbs), although each was studied by a different person.

The *R*/*S* ratios overestimate the impact of road-crossing mortality on the entire population inasmuch as spawners do not represent entire local populations. However, we use them to assess this impact for two reasons. First, in the absence of probabilistic models for realistic estimates of the entire population, the R/S ratio is the only currently available measure for quantifying this impact and thus allowing for future corrections once such models are available. Second, for road mortality studies of the same species and even closely related species with similar biology (such as *Triturus* newts), the R/S ratios are certainly better comparable than whole-population estimates based on various ad hoc assumptions. In addition, the overestimations of whole-population mortality stemming from the R/S ratios may, to a degree, be compensated by common underestimations of road-crossing mortality resulting from applying too low recordability correction factors.

In terms of R/S ratios, the impact on local common toad populations is roughly comparable in Holland (van Gelder 1973), England (Cooke and Sparks 2004), and Poland (Table 3). In contrast, our figures for common frogs are three to four times higher than those obtained in Denmark (Hels and Buchwald 2001). The common frog populations are more affected than those of common toads in Chelmski Pond, Stobrawa Forest, and Wrocław suburbs, even though in the latter, the number of common frog road kills is only one fourth of the number of common toad road kills.

The impact of road mortality on the local population of common newts in Stobrawa Forest is likely to be devastating. The newts may incur comparable or even higher mortality at Oleśnica fish farm, Djursland Peninsula, and Chełmski Pond where no spawning aggregation estimates are available. In fact, road mortality of newts may be much higher than normally recorded at most sites, as suggested by the 85% share of newts among all amphibians crossing a road in Luxemburg (Proess 2003).

Relatively low losses to green frog populations are certainly related to their more sedentary life around waters as is the case of American green frogs, *Rana clamitans*, which are much more sedentary and thus much less affected by road traffic than leopard frogs, *R. pipiens* (Carr and Fahrig 2001). However, some green frogs, especially juvenile *Rana* kl. *esculenta*, also explore terrestrial habitats (Günther 1996b) and *R. lessonae* undertake regular overland migrations (Günther 1996a). This explains why at least some green frog populations are vulnerable to ecological trap situations, as exemplified by Chełmski Pond where 24% of the spawning population is destroyed by traffic annually (in the absence of another body of water, the spawning population of green frogs may comprise most of the local breeding population). Despite relatively low road mortality, the numbers of their road kills are by an order of magnitude higher in the rural compared to suburban areas (Table 3), suggesting a strong pressure of urban agglomerations on green frog populations.

Future research suggestions

In terms of future research, our results indicate a need for basic and applied studies to lay a foundation for standardized and informative amphibian road mortality surveys. In the way of basic research, the most needed are studies of species-specific population structure and dispersion, which would allow relating the size of spawning aggregations to the entire local populations and thus make realistic conversions of R/S ratios into road mortality figures for entire populations. In terms of applied studies, the most needed is a continuation of work on differential road-crossing mortality (with many basic ramifications into amphibian locomotion) and road-kill recordability, as started by Hels and Buchwald (2001), which would help to develop hitherto nonexistent minimum standards for amphibian road mortality studies. With appropriate standards and accurate recordability coefficients, these studies will also be useful for monitoring population trends, at least among common species.

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References

Ascensao F, Mira A (2006) Spatial patterns of road kills: a case study in Southern Portugal. In: Irwin CL, Garrett P, McDermott KP (eds) Proceedings of the 2005 international conference on ecology and transportation. Center for transportation and the environment. North Carolina State University, Raleigh, NC, pp 641–646

Babik W, Rafiński J (2001) Amphibian breeding sites characteristics in the Western Carpathians, Poland. Herpetol J 11:41–51

Baldy K (2002) Płazy Gór Stołowych i ich ochrona w latach 1998–2001. Przegl Przyr 13:63–76

Bartoszewicz M (1997) Śmiertelność kręgowców na szosie graniczącej z rezerwatem przyrody Słońsk. Parki Nar Rezerw Przyr 16:59–69

Berthoud G, Müller S (1986) Protection des batraciens le long des routes. Eidgenössisches Verkehrs- und Energiewirtschaftsdepartement, Bern

Carr LW, Fahrig L (2001) Effect of road traffic on two amphibian species of differing vagility. Conserv Biol 15:1071–1078 doi:10.1046/j.1523-1739.2001.0150041071.x

Carrier J, Beebee TJ (2003) Recent, substantial, and unexplained declines of the common toad *Bufo bufo* in lowland England. Biol Conserv 111:395–399 doi:10.1016/S0006-3207(02)00308-7

Ciesiołkiewicz J, Orłowski G, Elzanowski A (2006) High juvenile mortality of grass snakes *Natrix natrix* (L.) on a suburban road. Pol J Ecol 54:465–472

Cooke AS (2000) Monitoring a breeding population of common toads (*Bufo bufo*) in a housing development. Herpetol Bull 74:12–15

Cooke AS, Sparks TH (2004) Population declines of Common toads *(Bufo bufo)*: the contribution of road traffic and monitoring value of casualty counts. Herpetol Bull 88:13–26

Evans GM (1989) Observations on *Bufo bufo* and *Triturus cristatus* road fatalities at Yarlet in Stafford. Herptile 14:139–142

Fahrig L, Pedlar J, Pope SE, Taylor PD, Wegner JF (1995) Effect of road traffic on amphibian density. Biol Conserv 73:177–182 doi:10.1016/0006-3207(94)00102-V

Fuellhaas U, Klemp C, Kordes A, Ottersberg H, Pirmann M, Thiessen A et al (1989) Untersuchungen zum Straßentod von Vögeln, Säugetieren, Amphibien und Reptilien. Beitr Naturkd Niedersachs 42:129–147

Gibbs JP, Shriver WG (2005) Can road mortality limit populations of pool-breeding amphibians? Wetlands Ecol Manag 13:281–289 doi:10.1007/s11273-004-7522-9

Głowaciński Z, Rafiński J (2003) Atlas Płazów i Gadów Polski. Główny Inspektorat Ochrony Środowiska, Warszawa

Günther R (1996a) Kleiner Wasserfrosch—*Rana lessonae* Camerano 1882. In: Günther R (ed) Die Amphibien und Reptilien Deutschlands. Gustav Fischer, Jena, pp 475–489

Günther R (1996b) Teichfrosch—*Rana* kl. *esculenta* Linnaeus 1758. In: Günther R (ed) Die Amphibien und Reptilien Deutschlands. Gustav Fischer, Jena, pp 455–475

Günther R, Geiger A (1996) Erdkröte—*Bufo bufo* (Linnaeus, 1758). In: Günther R (ed) Die Amphibien und Reptilien Deutschlands. Gustav Fischer, Jena, pp 274–302

Günther R, Nabrowsky H (1996) Moorfrosch—*Rana arvalis* Nilsson, 1842. In: Günther R (ed) Die Amphibien und Reptilien Deutschlands. Gustav Fischer, Jena, pp 364–388

Günther R, Schneeweiss N (1996) Rotbauchunke—*Bombina bombina* (Linnaeus, 1761). In: Günther R (ed) Die Amphibien und Reptilien Deutschlands. Gustav Fischer, Jena, pp 215–232

Hansen L (1982) Trafikdraebte dyr i Danmark/Road kills in Denmark. Dan Ornithol Foren Tidsskr 76:97–110

Harper EB, Semlitsch RD (2007) Density dependence in the terrestrial life history stage of two anurans. Oecologia 153:879–889 doi:10.1007/s00442-007-0796-x

Hels T, Buchwald E (2001) The effect of road kills on amphibian populations. Biol Conserv 99:331–340 doi:10.1016/S0006-3207(00)00215-9

Kuhn J (1987) Straßentod der Erdkröte *Bufo bufo* L., Verlustquoten und Verkehrsaufkommen, Verhalten auf der Straße. Beih. Veröff. Naturschutz Landschaftspflege Bad. Wurtt 41:175–186

Laan R, Verboom B (1990) Effects of pool size and isolation on amphibian communities. Biol Conserv 54:251–262 doi:10.1016/0006-3207(90)90055-T

Landmann A, Böhm C, Fischler D (1999) Bestandssituation und Gefährdung des Grasfrosches in Talböden der Ostalpen: Beziehungen zwischen der Größe von Laichpopulationen und dem Landschaftscharakter. Z Ökol Nat Schutz 8:71–79

Langen TA, Machniak A, Crowe EK, Mangan C, Marker DF, Liddle N et al (2007) Methodologies for surveying herpetofauna mortality on rural highways. J Wildl Manage 71:1361–1368 doi:10.2193/2006-385

Lodé T (2000) Effect of a motorway on mortality and isolation of wildlife populations. Ambio 29:165–168 doi:10.1639/0044-7447(2000)029[0163:EOAMOM]2.0.CO;2

Mazerolle MJ (2004) Amphibian road mortality in response to nightly variation in traffic intensity. Herpetologica 60:45–53 doi:10.1655/02-109

Miech P (1988) Wirbeltierverluste auf einer Waldstraße im Spandauer Forst. Berl Naturschutzbl. 32:125–135

Najbar B, Najbar A, Maruchniak-Pasiuk M, Szuszkiewicz E (2006) Śmiertelność płazów na odcinku drogi w rejonie Zielonej Góry w latach 2003–2004. Chronmy Przyr Ojczysta 62:64–71

Orłowski G (2007) Spatial distribution and seasonal pattern in road mortality of the common toad *Bufo bufo* in an agricultural landscape of south-western Poland. Amphib-reptil 28:25–31 doi:10.1163/156853807779799045

Pellet J, Guisan A, Perrin N (2004) A concentric analysis of the impact of urbanization on the threatened European tree frog in an agricultural landscape. Conserv Biol 18:1599–1606 doi:10.1111/j.1523-1739.2004.0421a.x

Pellet J, Helfer V, Yannic G (2007) Estimating population size in the European tree frog (*Hyla arborea*) using individual recognition and chorus counts. Amphib-Reptil 28:287–294 doi:10.1163/156853807780202530

Proess R (2003) Die Amphibienwanderung im oberen Abschnitt der Straße Bridel-Steinsel (Luxemburg). Bull Soc Natur Luxemb 103:93–100

Puky M (2006) Amphibian road kills: a global perspective. In: Irwin CL, Garrett P, McDermott KP (eds) Proceedings of the 2005 international conference on ecology and transportation. Center for transportation and the environment. North Carolina State University, Raleigh, NC, pp 325–338

Reh W, Seitz A (1990) The influence of land use on the genetic structure of populations of the common frog *Rana temporaria*. Biol Conserv 54:239–249 doi:10.1016/0006-3207(90)90054-S

Rybacki M (1995) Zagrożenie płazów na drogach Pienińskiego Parku Narodowego. Pieniny Przyr Czlow 4:85–97

Rybacki M (2002) Czynna ochrona płazów w Pienińskim Parku Narodowym. Przegl Przyr 13:77–86

Rybacki M, Domańska E (2004) Intensywność migracji i śmiertelność płazów na drogach gospodarstwa rybackiego Oleśnica (powiat Chodzież, województwo wielkopolskie). In: Zamachowski W (ed) Biologia Płazów i Gadów—Ochrona Herpetofauny/VII Ogólnopolska Konferencja Herpetologiczna. Wydawnictwo Naukowe Akademii Pedagogicznej, Kraków, pp 90–94

Rybacki M, Krupa A (2002) Wstępny raport na temat śmiertelności płazów na drogach parków krajobrazowych Województwa Wielkopolskiego. Przegl Przyr 13:77–86

Schlüpmann M, Günther R (1996) Grasfrosch—*Rana temporaria* Linnaeus, 1758. In: Günther R (ed) Die Amphibien und Reptilien Deutschlands. Gustav Fischer, Jena, pp 412–454

Slater FM (2002) An assessment of wildlife road casualties—the potential discrepancy between numbers counted and numbers killed. Web Ecol 3:33–42

van Gelder JJ (1973) A quantitative approach to the mortality resulting from traffic in a population of *Bufo bufo* L. Oecologia 13:93–95 doi:10.1007/BF00379622

Vos CC, Chardon JP (1998) Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. J Appl Ecol 35:44–56 doi:10.1046/j.1365-2664.1998.00284.x

Wołk K (1978) Zabijanie zwierząt przez pojazdy samochodowe w Rezerwacie Krajobrazowym Puszczy Białowieskiej. Chrońmy Przyr Ojczysta 6:20–28

Zamachowski W, Plewa G (1996) Śmiertelność płazów podczas wędrówek. In: Zamachowski W (ed) Materiały IV Ogólnopolskiej Konferencji Herpetologicznej. Wydawnictwo Naukowe Akademii Pedagogicznej, Kraków, p 89–91