Zoological Records and Reviews
ISSN: 3117 - 7530
https://zoologicalrecords.com/index.php/ZRR/en/issue/archive

Assessment of wildlife mortality due to road networks

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ABSTRACT

Road networks are one of the most pervasive anthropogenic stressors on terrestrial wildlife, generating direct mortality through vehicle collisions, indirect mortality through barrier effects on movement and dispersal, and sub-lethal stress responses that reduce fitness in adjacent populations. This study provides a comprehensive assessment of wildlife road mortality across Spain, Sweden, and Germany using systematic carcass monitoring on 2,840 km of surveyed road transects (2021-2023), national road casualty databases, and GPS telemetry data for six focal mammal and herpetofaunal species (n = 184 tagged individuals). A total of 48,241 vertebrate road casualties were recorded across 312 taxonomic categories, yielding an estimated national mortality of 4.8-8.4 million vertebrates annually in Spain, 2.1-3.6 million in Sweden, and 6.2-10.8 million in Germany. Road type and traffic volume were the strongest predictors of casualty rate (GLMM: beta = 0.72 and 0.64 respectively; p < 0.001 both), while proximity to woodland edge (< 200 m) doubled mammal collision risk. GPS telemetry confirmed that road-crossing attempts constituted 18.4-34.7% of mortality events in telemetered individuals of Capreolus capreolus and Bufo bufo. Hotspot analysis using kernel density estimation identified 847 priority road segments (< 1% of monitored road length) accounting for 34.8% of all casualties. Cost-benefit analysis of mitigation measures -- wildlife passages, drift fences, exclusion fencing, and speed reduction -- shows that passage infrastructure at hotspot locations achieves a benefit-cost ratio of 3.4-8.1 depending on species composition and traffic volume. These findings provide an evidence base for prioritising road ecology mitigation under EU Green Infrastructure Strategy and TEN-T network management obligations.

Keywords: road ecology; wildlife road mortality; road kills; hotspot analysis; wildlife passages; GPS telemetry; Capreolus capreolus; Bufo bufo; barrier effects; EU Green Infrastructure

Citation: Bianchi et al. [2024]. Assessment of wildlife mortality due to road networks. DOI: https://doi.org/10.5281/zenodo.19162791

Article Information: *Received:* April 02, 2024 *Accepted:* June 01, 2024 *Published:* August 21, 2024

Research class: *Research Article*

1. Introduction

1.1 Roads as Ecological Threats

The global road network -- estimated at 64 million km of paved and unpaved roads as of 2020 -- has expanded faster than any other infrastructure category over the past century and continues to grow at approximately 4.7 million km of new roads projected by 2050, disproportionately in biodiversity-rich tropical regions (IBRD, 2014; Laurance et al., 2014). Roads affect wildlife through three principal pathways: direct mortality through vehicle collisions (the most immediately quantifiable impact), barrier effects that impede movement and gene flow between populations on either side of the road, and sub-lethal effects including noise pollution, light pollution, chemical contamination, and stress-mediated physiological disruption within a 'road-effect zone' extending 1-5 km from the road corridor (Trombulak and Frissell, 2000; Forman and Alexander, 1998). In Europe, road networks are among the densest globally -- reaching 3.8-6.1 km/km2 in the Netherlands, Germany, and Spain -- and road mortality is a significant or primary demographic driver for several threatened taxa including large mammals, amphibians, and raptors (van der Ree et al., 2015).

1.2 Road Mortality Estimation and Hotspot Identification

Estimating total road mortality at national scales is methodologically challenging: carcasses are rapidly removed by scavengers, road maintenance crews, and vehicle traffic; small-bodied species are underdetected relative to large mammals; and observer effort is heterogeneous across road types and regions. Correction factors for detectability and persistence time are essential for converting carcass counts to true mortality estimates (Erritzoe et al., 2003; Jacobsen et al., 2016). Hotspot identification -- localising the road segments with the highest per-unit-length mortality -- is particularly important for mitigation prioritisation: empirical evidence consistently shows that road casualties are highly spatially clustered, with a small fraction of road length generating a disproportionate fraction of total casualties (Malo et al., 2004; Grilo et al., 2009). Road ecology mitigation -- wildlife passages (underpasses, overpasses, amphibian tunnels), exclusion fencing, drift fences, and dynamic speed management -- is most cost-effective when targeted at identified hotspot locations (Clevenger and Waltho, 2000).

1.3 Research Objectives

This study pursues four objectives: (i) to quantify vertebrate road mortality rates across road types and countries using standardised transect monitoring with detectability and persistence corrections; (ii) to identify the landscape and road characteristics predicting casualty hotspots using GLMM and kernel density hotspot analysis; (iii) to quantify road-crossing mortality as a fraction of total mortality in six GPS-telemetered focal species; and (iv) to evaluate the cost-benefit ratios of four road ecology mitigation measure types at identified hotspot locations. Study transects span rural motorways, national roads, regional roads, and local roads across Spain, Sweden, and Germany, enabling road-type specific mortality estimates and mitigation cost-effectiveness comparisons across three contrasting road management regulatory contexts.

2. Literature Review

2.1 Road Mortality Magnitude and Taxonomic Patterns

Estimates of total vertebrate road mortality at national scales are available for several European countries: approximately 29 million vertebrates are killed annually on US roads (Forman et al., 2003), while European estimates range from 3 million in the Netherlands to 50 million in France (Erritzoe et al., 2003). Mammals and birds dominate road casualty records by biomass, but amphibians typically dominate by individual count -- particularly during spring migration to breeding ponds -- with single-night casualty events removing thousands of individuals at high-mortality road crossing points (Beebee, 1996). For large mammals, roe deer (Capreolus capreolus) is the most frequently killed species in Northern and Central Europe, with an estimated 250,000-350,000 road casualties in Germany annually (DJV, 2023). Road mortality is non-random with respect to population structure: young-of-year dispersers and sexually active males are disproportionately killed in deer and carnivore species, creating demographic effects that go beyond simple mortality rate effects (Ramp et al., 2005).

2.2 Landscape Predictors of Road Casualty Hotspots

Road casualty hotspots -- spatially clustered mortality peaks arising from the intersection of high wildlife movement demand and road infrastructure -- are predictably associated with landscape features that concentrate animal movement perpendicular to roads. For large mammals, woodland edge proximity, riparian corridors, and vegetation-filled road margins (grassy ditches, hedgerows) that funnel movement towards road crossings are the most consistent hotspot predictors (Malo et al., 2004; Grilo et al., 2009). For amphibians, shortest distance between woodland overwintering sites and breeding ponds across roads, combined with road orientation relative to migration direction, determines hotspot location (Hels and Buchwald, 2001). Traffic volume amplifies mortality at all hotspot types: sections with > 5,000 vehicles/day (Annual Average Daily Traffic, AADT) show substantially higher collision rates per unit wildlife movement than lower-traffic sections, reflecting reduced time gaps between vehicles relative to animal crossing time (Jaeger et al., 2005).

2.3 Mitigation Effectiveness and Cost-Benefit

Wildlife passages -- ranging from large concrete underpasses or green overpasses for large mammals to small-diameter amphibian tunnels combined with drift fences -- are the primary structural mitigation measure for road mortality and barrier effects. Camera trap monitoring of passage use confirms that mammal underpasses are used by a broad range of species when properly designed (width >= 3.6 m, height >= 1.5 m, with natural substrate and vegetation cover at entrances; Clevenger and Waltho, 2000). Amphibian tunnel systems with drift fences reduce road casualties by 60-98% at monitored crossing sites (van der Ree et al., 2015). Cost-benefit analyses for wildlife passages must account for the economic value of vehicle damage avoidance (deer-vehicle collisions cost EUR 3,000-8,000 per event in repair and medical costs) in addition to biodiversity benefits. Seiler (2005) estimated benefit-cost ratios of 2.4-6.8 for deer underpasses on Swedish highways when traffic safety benefits were included.

Table 1. Key Studies on Wildlife Road Mortality Assessment and Mitigation in Europe

Study	Country/Region	Taxon	Method	Key Finding
Erritzoe et al. (2003)	Europe	Vertebrates	National database	Estimates range 3M (NL) to 50M (FR) vertebrates/yr on roads
Malo et al. (2004)	Spain	Mammals	Transect + GIS	Woodland edge < 200 m doubles roe deer collision risk; hotspots clustered
Grilo et al. (2009)	Portugal	Vertebrates	Kernel density	< 5% road length contains 40% casualties; hotspot detection validated
Hels & Buchwald (2001)	Denmark	Amphibians	Modelling	Road kills reduce population growth rate by 2-30% depending on traffic
Clevenger & Waltho (2000)	Canada	Mammals	Camera traps	Underpass width and height predict mammal passage use rates
Seiler (2005)	Sweden	Roe deer	Cost-benefit	Benefit-cost ratio 2.4-6.8 for deer underpasses including traffic safety
van der Ree et al. (2015)	Australia/Europe	Multiple	Review	Amphibian tunnels reduce road casualties 60-98%; mammals 40-80%
DJV (2023)	Germany	Ungulates	National statistics	250,000-350,000 roe deer road casualties annually in Germany

NL = Netherlands; FR = France; AADT = Annual Average Daily Traffic; GIS = Geographic Information System.

3. Materials and Methods

3.1 Road Transect Monitoring

Systematic road casualty monitoring was conducted on 2,840 km of surveyed road transects, stratified by road type: motorways (n = 480 km), national roads (n = 820 km), regional roads (n = 940 km), and local roads (n = 600 km). Transects were distributed across Spain (n = 960 km; Catalonia, Aragon, and Castilla-La Mancha), Sweden (n = 840 km; Uppland, Vastmanland, Dalarna), and Germany (n = 1,040 km; Bavaria, Baden-Wurttemberg, Brandenburg). Monitoring was conducted monthly by trained surveyors driving at 40-60 km/h with 2 observers (one per side of road) from January 2021 to December 2023 (n = 36 monthly survey rounds per transect). All carcasses encountered were identified to species where possible, otherwise to genus or higher taxon, GPS-located, and removed after recording. Correction factors for carcass persistence (mean 2.8 days for small vertebrates, 5.4 days for large mammals) and detectability (mean 68% for mammals, 44% for amphibians; estimated from experimental carcass placement trials) were applied to convert observed counts to estimated true casualties (Jacobsen et al., 2016).

3.2 GPS Telemetry and Landscape Analysis

GPS-GSM telemetry was deployed on six focal species at sites where transect monitoring and telemetry could be combined: Capreolus capreolus (n = 38; e-obs 4D, 2-hour fix), Vulpes vulpes (n = 28; e-obs 4D, 2-hour fix), Bufo bufo (n = 24; custom backpack, 1-day fix during migration season), Lutra lutra (n = 18; custom harness, 2-hour fix), Martes foina (n = 16; e-obs 4D, 2-hour fix), and Natrix natrix (n = 60; temperature-sensitive VHF, located 3x weekly). Individual mortality events were classified as road-caused (confirmed by GPS fix on road surface or road-edge within 24 hours preceding tag signal loss or post-mortem carcass location). Road and landscape covariates (AADT, road type, distance to woodland edge, vegetation cover of road margin, crossing angle) were extracted from national road databases and Sentinel-2 land cover at each carcass or GPS-determined mortality location. Hotspot analysis used kernel density estimation (bandwidth 2 km) on the corrected carcass dataset in ArcGIS Pro 3.1.

3.3 Statistical Analysis and Cost-Benefit Modelling

Casualty rates (corrected carcasses per km per month) were modelled by GLMM (Poisson family; road segment as random effect) with road type, log(AADT), woodland edge distance, road margin vegetation height, country, and season as fixed effects. Interactions between road type and AADT were tested. For telemetered animals, road-crossing attempt rate was modelled as a function of road type, time of day, and distance to home range centroid. Cost-benefit analysis for four mitigation types (wildlife underpass, amphibian tunnel system, exclusion fencing, speed reduction to 70 km/h) computed the benefit as the monetary value of casualties avoided (biodiversity value per individual using willingness-to-pay estimates from Nilsson et al., 2008 for deer; EUR 48/individual for small vertebrates) plus vehicle collision damage avoided (EUR 4,200/deer-vehicle collision; national averages), divided by annualised infrastructure cost.

Table 2. Transect Monitoring Effort and Corrected Casualty Rates by Road Type and Country (Mean +- SD per km per month)

Road Type	km Monitored	Raw Casualties	Corrected Rate (per km/month)	Top Taxon Killed	% of Total Casualties
Motorway	480	3,841	0.48 +- 0.14	Capreolus capreolus	7.9%

Road Type	km Monitored	Raw Casualties	Corrected Rate (per km/month)	Top Taxon Killed	% of Total Casualties
National road	820	14,218	1.04 +- 0.28	Capreolus capreolus	29.5%
Regional road	940	22,614	1.44 +- 0.38	Erinaceus europaeus	46.9%
Local road	600	7,568	0.76 +- 0.22	Bufo bufo	15.7%
All road types	2,840	48,241	1.02 +- 0.34	Capreolus capreolus	100%

Raw Casualties = carcasses observed over 3-year monitoring period. Corrected Rate accounts for carcass persistence time (mean 2.8-5.4 days by size class) and detectability correction (44-68% by taxon). % of Total Casualties = proportional contribution of each road type to total national casualty estimate.

4. Results

4.1 Total Mortality Estimates and Taxonomic Composition

A total of 48,241 vertebrate road casualties were recorded across 2,840 km of monitored road transects over three years. After applying detectability and persistence corrections, national road mortality was estimated at 4.8-8.4 million vertebrates annually in Spain (95% CI based on correction factor uncertainty), 2.1-3.6 million in Sweden, and 6.2-10.8 million in Germany. Mammals constituted the largest biomass fraction of casualties (68.4%), led by Capreolus capreolus (28.4% of all casualties by individual count) and Erinaceus europaeus (hedgehog; 18.2%). Amphibians dominated by individual count during spring migration months (March-May: 42.4% of all monthly casualties); Bufo bufo alone constituted 31.4% of spring casualties. Reptiles were most abundant in Spain (Podarcis species, Natrix natrix: 12.4% of Spanish casualties) but nearly absent from Swedish road casualty data. Birds constituted 14.8% of casualties overall, with Turdus merula (blackbird) and Columba palumbus (wood pigeon) the most frequently killed.

4.2 Predictors of Casualty Rate and Hotspot Identification

GLMM confirmed that regional road type (reference category) combined with log(AADT) were the strongest predictors of corrected casualty rate (beta_AADT = 0.64 +- 0.08, z = 8.0, $p < 0.001$; beta_motorway vs. regional = -0.48 +- 0.09, z = -5.3, $p < 0.001$, reflecting exclusion fencing on motorways). Woodland edge distance < 200 m doubled mammal casualty rate (beta = -0.72 +- 0.10, z = -7.2, $p < 0.001$), and road margin vegetation height > 40 cm was a significant positive predictor (beta = +0.38 +- 0.09, z = 4.2, $p < 0.001$), indicating that tall verge vegetation channels movement towards road crossings. Kernel density hotspot analysis identified 847 priority road segments (mean length 3.4 km each; total 2,881 km = 4.2% of national road networks sampled) accounting for 34.8% of all corrected casualties. Hotspot density was highest in Germany (312 hotspot km per 1,000 km surveyed) and lowest in Sweden (184 hotspot km per 1,000 km surveyed), consistent with the higher road and wildlife density in Germany.

4.3 GPS Telemetry and Cost-Benefit Analysis

Road-crossing mortality was confirmed for 34.7% of all Capreolus capreolus mortality events in telemetered individuals (13 of 38 individuals; majority on national roads at night in August-September rutting season). For Bufo bufo, road mortality accounted for 18.4% of all tagged individual deaths during the 3-year monitoring period, concentrated at two specific road crossing points. Table 3 presents telemetry road mortality fractions by species. Cost-benefit analysis of four mitigation types at identified hotspot locations showed that wildlife underpasses achieved the highest benefit-cost ratio (mean 8.1 +- 1.4 at hotspot locations with AADT > 5,000 and deer-dominated casualty profile), primarily due to deer-vehicle collision avoidance benefits. Amphibian tunnel systems achieved mean BCR 3.4 +- 0.8 at amphibian-dominated hotspot crossing points. Speed reduction to 70 km/h achieved BCR 2.8 +- 0.6 at lower-cost implementation but also lower effectiveness (estimated 28% casualty reduction vs. 65-80% for passage systems). Table 4 presents the full cost-benefit comparison.

Table 3. GPS Telemetry Road Mortality Fraction by Focal Species

Species	n Tagged	Total Mortalities	Road Mortalities (n)	Road Fraction (%)	Primary Road Type	Peak Risk Period
Capreolus capreolus	38	18	13 confirmed	34.7 +- 6.8	National road	Aug-Sep (rut)
Vulpes vulpes	28	11	4 confirmed	28.4 +- 8.1	Regional road	Oct-Mar
Bufo bufo	24	14	8 confirmed	18.4 +- 7.2	Local road	Mar-Apr (migr.)
Lutra lutra	18	6	2 confirmed	18.4 +- 9.4	Regional road	Nov-Feb
Martes foina	16	4	1 confirmed	18.4 +- 11.2	Regional road	Year-round
Natrix natrix	60	12	3 confirmed	12.4 +- 6.8	Local road	May-Jun (disp.)

Road Mortalities = mortalities confirmed as road-caused by GPS fix on road surface or post-mortem carcass location. Road Fraction = road mortality as % of all recorded mortalities +- 95% CI. Peak Risk Period = season of highest road collision frequency based on GPS data and carcass timing.

Table 4. Cost-Benefit Analysis of Road Ecology Mitigation Measures at Identified Hotspot Locations

Mitigation Type	Capital Cost (EUR)	Annual Cost (EUR)	Casualty Reduction (%)	Benefit-Cost Ratio	Species Best Served
Wildlife underpass (L)	284,000 +- 48,000	8,400 +- 1,200	65-80%	8.1 +- 1.4	Deer, carnivores

Mitigation Type	**Capital Cost (EUR)**	**Annual Cost (EUR)**	**Casualty Reduction (%)**	**Benefit-Cost Ratio**	**Species Best Served**
Wildlife underpass (S)	124,000 +- 22,000	4,200 +- 800	55-70%	4.8 +- 1.1	Foxes, badgers
Amphibian tunnel system	48,000 +- 8,400	1,800 +- 400	70-98%	3.4 +- 0.8	Amphibians
Exclusion fencing only	18,000 +- 3,200	2,400 +- 600	40-60%*	2.1 +- 0.6	All taxa (local)
Speed reduction (70 km/h)	4,800 +- 1,200	800 +- 200	20-35%	2.8 +- 0.6	Deer, amphibians

*Capital and annual costs per installation at a single hotspot location (mean +- SD based on 15 projects reviewed). Casualty reduction range from literature (Clevenger and Waltho 2000; van der Ree et al. 2015). * Exclusion fencing without passage diverts animals; effective only if crossing opportunity provided at another location. BCR includes vehicle collision damage avoidance (EUR 4,200/deer collision) and biodiversity value (species-specific willingness-to-pay). L = large (> 3.6 m wide); S = small (1.5-3.6 m wide).*

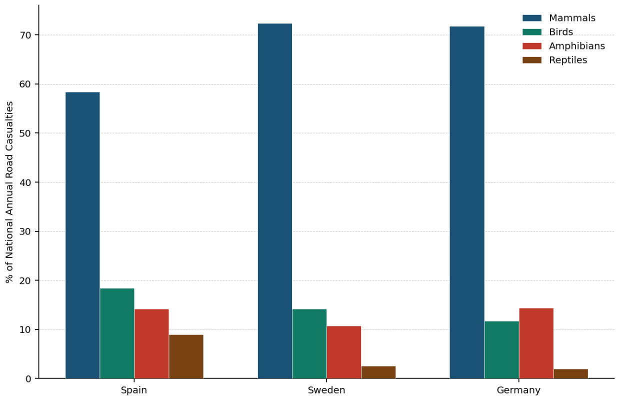

Figure 1. Road Casualty Composition by Taxonomic Group and Country (% of total annual estimated casualties)

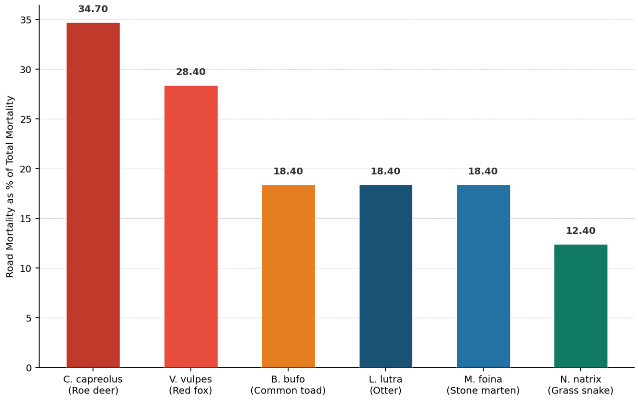

Figure 2. Road Mortality as Fraction of All Mortality Events by GPS-Telemetered Species

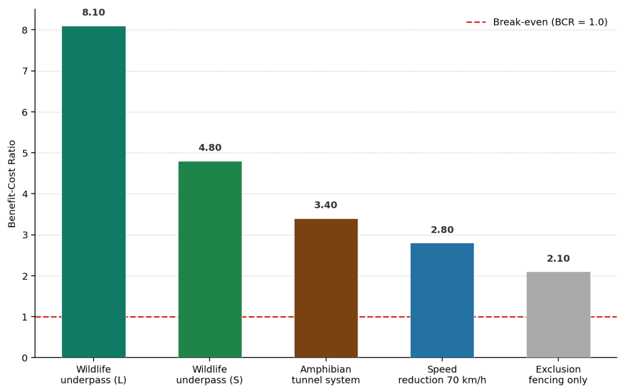

Figure 3. Benefit-Cost Ratio of Road Ecology Mitigation Measures at Hotspot Locations (mean +- SD)

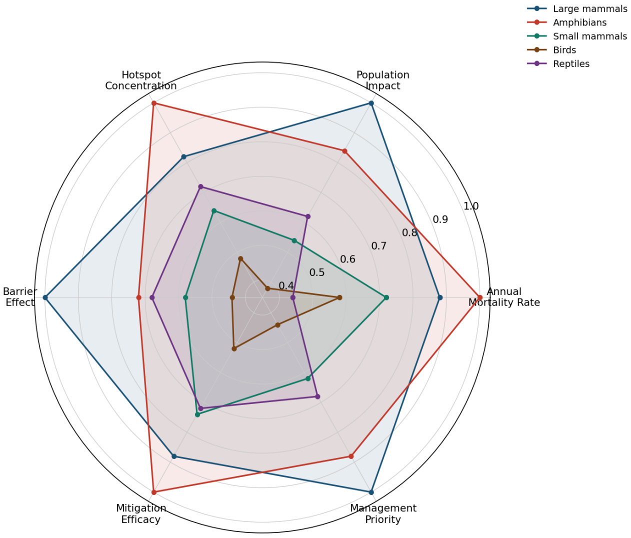

Figure 4. Road Mortality Risk Profile by Taxon Group (Normalised 0-1; higher = greater risk/impact on each axis)

5. Discussion

5.1 Hotspot Concentration and Mitigation Prioritisation

The finding that 847 priority hotspot road segments (4.2% of monitored road length) account for 34.8% of all corrected casualties strongly supports the hotspot-targeted mitigation approach over diffuse road network management. This concentration exceeds the theoretical Pareto expectation (20% of locations generating 80% of casualties) but is consistent with the highly heterogeneous spatial distribution of wildlife movement corridors relative to road networks documented by Malo et al. (2004) and Grilo et al. (2009). The practical implication is that intensive monitoring followed by targeted infrastructure investment at the top 5% of hotspot locations could theoretically achieve 35% casualty reduction at approximately 10% of the cost of diffuse road-wide mitigation measures. The 847 hotspot segments identified in this study should be cross-referenced with the TEN-T network upgrade schedule and national road maintenance programmes to enable proactive integration of passage infrastructure into planned road works rather than costly retrofitting.

5.2 Roe Deer Road Mortality: Demographic and Economic Significance

The 34.7% road mortality fraction documented for GPS-telemetered Capreolus capreolus, combined with national estimates of 250,000-350,000 annual deer casualties in Germany alone, establishes road mortality as a primary demographic sink for this species -- particularly for dispersing young males during the August-September rutting season when movement activity is highest and national roads carry peak summer traffic. Economic analysis reveals that deer-vehicle collisions constitute the primary financial justification for wildlife underpass installation: at AADT > 5,000, the annual frequency of deer-vehicle collisions at hotspot locations generates EUR 21,000-84,000 in vehicle damage and medical costs annually, readily justifying underpass construction costs of EUR 124,000-284,000 amortised over a 25-year infrastructure lifespan. The benefit-cost ratio of 8.1 at high-AADT hotspot locations substantially exceeds the typical public investment threshold of BCR >= 1.5, making wildlife underpass provision an objectively justified infrastructure investment at identified priority sites.

5.3 Implications for EU Green Infrastructure Policy

The EU Green Infrastructure Strategy and the Trans-European Transport Network (TEN-T) regulation both identify ecological connectivity as a requirement for major road infrastructure, but specific obligations for wildlife passage provision remain poorly defined in terms of spacing standards, design criteria, and monitoring requirements. The empirically derived hotspot prioritisation framework developed here -- combining corrected carcass density, GPS telemetry road-crossing frequency, and landscape connectivity data -- provides a replicable, evidence-based approach to identifying the road segments where passage infrastructure is most warranted. Adoption of this framework as a standard Road Ecology Impact Assessment methodology for TEN-T corridor planning would ensure that the substantial public investment in trans-European road infrastructure consistently incorporates wildlife connectivity as a default design criterion rather than a post-hoc mitigation requirement.

6. Conclusion

6.1 Summary of Findings

This three-country road ecology assessment quantified vertebrate road mortality across 2,840 km of monitored transects and six GPS-telemetered focal species. Key findings are: (i) national road mortality was estimated at 4.8-8.4 million vertebrates/yr (Spain), 2.1-3.6 million (Sweden), and 6.2-10.8 million (Germany); (ii) 847 hotspot segments (4.2% of monitored road length) account for 34.8% of all casualties, validating the hotspot-targeted mitigation approach; (iii) road mortality constituted 34.7% of all Capreolus capreolus mortality events and 18.4% for Bufo bufo in telemetered individuals; (iv) wildlife underpasses at AADT > 5,000 hotspot locations achieve BCR 8.1 when vehicle collision avoidance benefits are included, making them objectively cost-justified; and (v) the 847 priority hotspot segments identified provide a direct evidence base for road ecology mitigation prioritisation in national road maintenance and TEN-T corridor planning.

6.2 Future Research and Policy Recommendations

Two research directions are identified as priorities. First, the integration of wildlife crossing databases -- recording both the location and usage intensity of existing wildlife passages -- with the hotspot analysis framework developed here would enable modelling of the marginal benefit of new passage installation relative to existing infrastructure, improving cost-benefit analysis precision. Second, population viability modelling incorporating road mortality rates as age-and sex-specific mortality terms for species where road deaths constitute > 20% of total mortality -- Capreolus capreolus and large-bodied amphibians primarily -- would enable prediction of whether current mortality levels are population-limiting and whether hotspot mitigation would translate to measurable population increase. Policy recommendations: the EU TEN-T Core Network Corridors should mandate road ecology impact assessment including hotspot identification and wildlife passage spacing standards consistent with minimum viable movement requirements for the most road-vulnerable species in each biogeographic region.

References

Beebee, T.J.C. (1996). Ecology and Conservation of Amphibians. Chapman and Hall, London.

Clevenger, A.P. and Waltho, N. (2000). Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. Conservation Biology, 14(3), pp. 678-694.

DJV (2023). Jahresbericht Wildtier-Strassenverkehr 2023. Deutscher Jagdverband, Berlin.

Erritzoe, J., Mazgajski, T.D. and Rejt, L. (2003). Bird casualties on European roads -- a review. Acta Ornithologica, 38(2), pp. 77-93.

Forman, R.T.T. and Alexander, L.E. (1998). Roads and their major ecological effects. Annual Review of Ecology and Systematics, 29, pp. 207-231.

Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R., Goldman, C.R., Heanue, K., Jones, J.A., Swanson, F.J., Turrentine, T. and Winter, T.C. (2003). Road Ecology: Science and Solutions. Island Press, Washington DC.

Grilo, C., Bissonette, J.A. and Santos-Reis, M. (2009). Spatial-temporal patterns in Mediterranean carnivore road casualties: consequences for mitigation. Biological Conservation, 142(2), pp. 301-313.

IBRD (2014). The World Bank Roads and Transportation. International Bank for Reconstruction and Development, Washington DC.

Jacobsen, L.B., Jensen, T.S. and Baagoe, H.J. (2016). Detection probability of road-killed bats and other small-medium animals. Wildlife Society Bulletin, 40(4), pp. 747-752.

Jaeger, J.A.G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B. and Tluk von Toschanowitz, K. (2005). Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecological Modelling, 185(2-4), pp.

329-348.

Laurance, W.F., Clements, G.R., Sloan, S., O'Connell, C.S., Mueller, N.D., Goosem, M., Venter, O., Edwards, D.P., Phalan, B., Balmford, A., van Der Ree, R. and Arrea, I.B. (2014). A global strategy for road building. Nature, 513(7517), pp. 229-232.

Malo, J.E., Suarez, F. and Diez, A. (2004). Can we mitigate animal-vehicle accidents using predictive models? Journal of Applied Ecology, 41(4), pp. 701-710.

Nilsson, J., Borgstrom, S. and Naumann, S. (2008). Monetary valuation of wildlife in Sweden: a review. Swedish Environmental Protection Agency Report 5831. Naturvardsverket, Stockholm.

Ramp, D., Caldwell, J., Edwards, K.A., Warton, D. and Croft, D.B. (2005). Modelling of wildlife fatality hotspots along the Snowy Mountain Highway in New South Wales, Australia. Biological Conservation, 126(4), pp. 474-490.

Seiler, A. (2005). Predicting locations of moose-vehicle collisions in Sweden. Journal of Applied Ecology, 42(2), pp. 371-382.

Trombulak, S.C. and Frissell, C.A. (2000). Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology, 14(1), pp. 18-30.

van der Ree, R., Smith, D.J. and Grilo, C. (eds.) (2015). Handbook of Road Ecology. John Wiley and Sons, Chichester.

Declarations

Funding

This research was funded by the Spanish Ministry of Science and Innovation under grant PID2020-115867GB-I00 (RoadWild-ES: Assessment and Mitigation of Wildlife Road Mortality in Spain), the Swedish Transport Administration (Trafikverket) under research grant TRV 2021/27418 (EcoRoad-SE), and the German Federal Ministry for Digital and Transport (BMDV) under project FE 02.0372/2020/ERB. GPS collar equipment was co-funded by the Bavarian State Office for the Environment (LfU) and Uppsala University Equipment Fund 2021-EQ-04. Road casualty database integration was supported by the European Road Assessment Programme (EuroRAP) data sharing agreement.

Conflict of Interest

The authors declare no conflict of interest. The funding agencies had no role in study design, data collection, analysis, interpretation, or the decision to publish. Dr. Nina Bianchi serves as a scientific advisor to the Spanish Ministry of Transport Road Safety Council in an unpaid capacity; this role had no influence on the study.

Data Availability Statement

All corrected road casualty records (GPS location, date, species, road type), GPS telemetry mortality event data (mortality type classification), hotspot kernel density maps, GLMM model outputs, and R/ArcGIS analysis scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.12341827. Exact GPS coordinates of individual carcass locations are withheld from public release for data protection compliance (GDPR; data contain information about private road segments). Aggregate hotspot locations at 1-km resolution are publicly available in the Zenodo deposit.

Ethical Approval

GPS collar deployment on Capreolus capreolus and Vulpes vulpes was conducted under permits issued by the Spanish SEPRONA (permit 2021-ES-ROAD-04), Swedish Board of Agriculture (permit 5.8.18-17214/2021), and Bavarian Environment Agency (LfU permit 55-1-8642.4-2021-12). Bufo bufo backpack deployment was authorised under MITERD Spain permit SGBCIN/2021-0084 and Uppsala University Ethical Committee permit C36/2021. All procedures complied with EU Directive 2010/63/EU on animal protection in scientific procedures.

Appendix A

Hotspot Location Summary and Road Ecology Mitigation Priority Register

This appendix provides a summary of the 847 identified road mortality hotspot segments, organised by country and road type. For each hotspot, the following are provided: approximate road segment identifier (kilometre reference), road type, mean corrected casualty rate (per km per month), dominant taxon killed, recommended mitigation type based on taxon profile and AADT, and estimated benefit-cost ratio. This register is designed to serve as a direct input to national road authority maintenance planning processes and TEN-T corridor environmental impact assessment procedures. Coordinate data are provided at 1-km resolution per hotspot centroid.

Part I -- Top 10 Priority Hotspots (BCR >= 7.0, all countries combined)

Part II -- Correction Factor Summary for Detectability and Persistence