

Road Mortality for Hedgehogs

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Transport infrastructure is a pervasive element in modern landscapes and continues to expand to meet the demands of a growing human population and its associated resource consumption. Road-induced mortality is often thought to be a major contributor to the marked declines of European hedgehog populations. This review synthesizes available evidence on the population-level impacts of road mortality and the threat to population viability for the five hedgehog species in Europe. Local and national studies suggest that road mortality can cause significant depletions in population sizes, predominantly removing adult males. Traffic collisions are a probable cause of fragmentation effects, subsequently undermining ecological processes such as dispersal, as well as the genetic variance and fitness of isolated populations. Further studies are necessary to improve population estimates and explicitly examine the consequences of sex- and age-specific mortality rates. Hedgehogs have been reported to use crossing structures, such as road tunnels, yet evaluations of mitigation measures for population survival probability are largely absent. This highlights the need for robust studies that consider population dynamics and genetics in response to mitigation. In light of ongoing declines of hedgehog populations, it is paramount that applied research is prioritised and integrated into a holistic spatial planning process.

road mortality

collision

fragmentation

movement

demography

population viability

mitigation

road ecology

hedgehogs

1. Introduction

The last century has been characterised by intense modification of the natural landscape, and road networks are now pervasive in most landscapes on Earth. Perhaps the most conspicuous impact of roads are wildlife–vehicle collisions (WVCs) that result in the death of billions of animals worldwide every year. The growing literature on road ecology has been largely motivated by WVCs that are of legislative or conservation concern and/or which give rise to economic or human safety issues, such as collisions with deer. In comparison, fewer studies have examined smaller mammal species, such as hedgehogs. There are five species of hedgehog with all or part of their range in Europe; *Erinaceus europaeus*, *Atelerix algirus*, *Erinaceus roumanicus*, *Erinaceus concolor* and *Hemiechinus auritus*.

Although hedgehog density has been reported to be up to 35% lower near roads, road-killed hedgehogs are a very familiar sight across Europe and are frequently the main mammal roadkill recorded in citizen science projects and expert multi-species roadkill surveys. For example, an estimated 113,000–340,000 *E. europaeus* individuals are

killed on roads every year in the UK and The Netherlands, and 230,000–350,000 individuals every year in Belgium. This level of road mortality is repeatedly raised as an important driver of the marked declines over the past two decades of *E. europaeus* in several countries across Europe. *A. algirus* has also shown reduced abundance and local extinctions in its introduced range in Europe. In recent times, the field has used nationwide monitoring schemes such as “Project Splatter”, a citizen science study in the UK that collates such data. Studies using nationwide data have demonstrated broad spatiotemporal patterns; hedgehog roadkill hotspots are associated with suburban areas and grassland, as well as the breeding season in late spring and early summer. Records of hedgehog road mortality have also been used to estimate annual road mortality, track epizootics and have the potential to estimate population abundance. Substantial gaps in knowledge remain, however, about whether roads affect long-term population persistence. Likewise, the use of appropriate techniques to evaluate the complexity of the impact (e.g., population modelling using collected demographic data) have received little attention.

Investigating the population-level impacts of road mortality is of both theoretical and applied importance. It is likely that Europe is already the most fragmented continent due to transport infrastructure and road networks continue to expand rapidly. As several European hedgehog species are declining and disproportionately represented in roadkill records, understanding how important road mortality is for population trends is a necessary step for hedgehog conservation.

2. Population-level impacts of road mortality on hedgehogs in Europe

2.1. Does road Mortality Really Reflect Population Persistence?

It is difficult to confirm or refute the impact of road mortality on population trends because survival probabilities depend on a complex set of inter-related factors. Several criteria exist to evaluate the ecological effects of road mortality:

- **Proportion of a population killed on roads annually.** Previous studies of *E. europaeus* have calculated that traffic casualties amount to 9–26% of the total (nationwide) population size in The Netherlands and 10–30% in the UK, assuming the population estimates are accurate. At the local scale, previous studies have used capture–mark–recapture methods to identify an annual loss of 3–22% of local *E. europaeus* populations on roads in Sweden and 24% in Poland.
- **Comparison of road mortality with mortality from other sources and its contribution to cumulative annual mortality.** This can be used to assess the impact of traffic collisions on the mortality–recruitment ratio. Studies suggest that road traffic is consistently in the top three most common causes of death for hedgehogs, alongside illness and natural predation, supporting the narrative that traffic mortality potentially places substantial pressure on population dynamics. The magnitude of this effect will depend on the ability of populations to compensate for additional mortality by increased survival and/or reproduction, for example, with second litters.

Other criteria to evaluate the impact of road mortality include the reproductive output of the affected population, immigration and emigration rates and investigating whether WVCs are compensatory or additive to other forms of mortality.

2.2. The Risk of Road Mortality is Not Equal. Which are the Risk-Prone Individuals?

The risk of road mortality over time varies spatially and between individuals in a population. Differential risk is a function of risk per crossing multiplied by the frequency of crossing. Although research into the road mortality of different sexes and age groups of hedgehogs is sparse, the majority of studies indicate that reproductively active male hedgehogs are most commonly killed on roads. Male hedgehogs have larger home ranges and nightly movements than females, particularly during the breeding season. This would, all other conditions being equal, increase the number of roads that males must cross each night. Conversely, females are most likely to be involved in traffic collisions in autumn after intensive natal care as their net-movement increases to build fat reserves for hibernation. The removal of reproductively active individuals carries a greater threat to hedgehog population viability because it can skew the age ratio and cause a decline in recruitment. However, the disproportionate loss of adult males may not be as consequential for population growth as adult female deaths.

2.3 The Role of Road Mortality in Fragmentation Effects

Road mortality is likely to act as a filter to movement for many species, rather than an absolute barrier, as animals may be able to make successful journeys across the road, even across large roads and bridges. For hedgehogs, road mortality is considered a more severe restriction to dispersal on smaller roads. For example, *E. roumanicus* in Bulgaria and *E. concolor* in Turkey were shown to have greater casualty rates on quieter, regional roads than highways. In severe cases, increased road mortality could lead to death rates exceeding birth rates, which may change a local population to a sink. Both physical barriers and road avoidance behaviour are particularly common on roads with higher traffic volumes and speeds. For example, Rondinini and Doncaster compared observed *E. europaeus* movements in Southampton, UK, with “random walks” and identified clear road avoidance behaviour that increased with road width (and associated higher traffic).

The weak correlation between genetic structure and geographical distance in several hedgehog studies indicates that linear infrastructure restricts gene flow enough to affect genetic heterozygosity. However, the hedgehog's promiscuous mating system and ability for heteropaternal superfecundity (a litter fertilised by different males) may partly counteract the genetic effects of isolation. The reality of this, however, remains untested, and Barthel reported potentially early signs of inbreeding in *E. europaeus* subpopulations in Berlin.

3. Potential Road Mitigation Measures for Hedgehog Populations

As road construction and traffic volumes continue to grow, accommodating the increase in human activity without jeopardising the viability of wild populations remains a major challenge. Approaches for sustainable infrastructure development should tackle both the local (mortality and habitat degradation) and landscape (fragmentation and

population viability) impacts of roads, yet there is no simple solution or decision-making framework. The range of mitigation measures can be classified using four main criteria; road crossing structures, traffic calming measures, habitat management and configuration of the road network.

3.1. Road Crossing Structures

Exclusionary fencing is a dominant strategy to impede an animal's attempt to cross a road. However, fencing was shown to cause a 30% reduction in *E. europaeus* population viability in The Netherlands by intensifying population isolation. Instead, combining fencing with road tunnels or green bridges such as overpasses is widely advocated for many species. Several studies have documented varied levels of crossing structure use by *E. concolor* in Greece, *E. europaeus* in Spain, Portugal, the UK and Poland, and *Erinaceinae* sp. in Spain (see review by De Vries). Hedgehogs have been shown to frequent tunnels with a greater openness ratio (short in length, high and wide) nearer urban areas. Moreover, previous studies demonstrate that hedgehogs avoid areas with predator (badger *Meles meles*) odour, although the avoidance did not always persist. Badgers are known to utilise road tunnels, sometimes very regularly, and whether this negatively influences hedgehog use of road mitigation structures remains unknown.

3.2. Traffic Calming Measures

Smaller-scale traffic calming measures that increase driver awareness may be equally effective and substantially cheaper than road-crossing structures. These aim to enhance preferred crossing sites, which do not necessarily correspond with roadkill hotspots, in order to dissuade the use of riskier crossing locations. Traffic calming measures adopted in the past include speed bumps, speed restrictions and warning signs. These initiatives may be particularly effective for hedgehogs given that they frequently attempt to cross quieter roads. Whilst a reduction in speed would be expected to result in a substantial reduction in roadkill, the realised effect depends on whether drivers adhere to the speed regulations, which can be difficult to govern, and whether, even at a slower speed, a driver can see and avoid a small animal at night.

3.3. Habitat Management

Additional mitigation possibilities include managing roadside habitats by increasing habitat quality, local connectivity and changing road verge management. These improve the core habitat and allow individuals to locate sufficient resources whilst crossing fewer roads. Several authors recommend removing or reducing shrubbery in central medians to reduce road mortality. Modifying hedgerows, which act as conduits of hedgehog movements, near roads is also likely to be an important action. For example, Huijser identified that, out of 942 traffic victims, 20–27% and 140% more *E. europaeus* road casualties were found in areas where hedgerows and railroads, respectively, were perpendicular to roads rather than parallel. Therefore, how roads and local landscape features are orientated in relation to one another warrants consideration.

3.4. Road Configuration

In Western Europe, many major roads were built more than 40 years ago with little consideration for wildlife. Retrofitting crossing structures can be an expensive undertaking and their construction is often logistically challenging. It is therefore essential to consider how landscape configuration can be designed to meet the needs of human settlements, associated road systems and habitat networks simultaneously. Previous multi-species simulation studies have reported that road mortality rates and population persistence were improved when traffic volume was concentrated on fewer roads. Surprisingly, van Strien and Grêt-Regamey reported opposite results for hedgehogs. These studies reinforce the significance of whole landscape planning; the high rates of new road development in Central and Eastern Europe provide the opportunity to consider road configuration and maintain suitable habitat matrices for *E. roumanicus* and *E. concolor*.

4. Conclusions

As hedgehogs remain a prominent victim of WVCs and road infrastructure continues to expand in Europe, evaluating whether hedgehog populations are vulnerable to the long-term negative impacts of roads is urgently needed. Previous studies are in general agreement that adult males are more prone to road mortality and that hedgehog–vehicle collisions can disrupt population dynamics, for example, by fragmentation. However, barriers exist to understanding whether this translates to population decline and to disentangling the relative impact of road mortality on population viability compared to other factors. Future research should prioritise the inclusion of sex- and age-specific fecundity and survival rates in population models and analyses. Moreover, considerations of wildlife must be integrated into the early planning stages of road construction to meet the goals of sustainable development. Collaboration between ecologists, engineers and spatial planners is not only good practice, but likely to be indispensable in achieving a reduction in the conflict for space that characterises the 21st century.

Published Findings	Gaps in Understanding as Revealed by This Review	Directions for Future Research as Recommended by This Review
<ul style="list-style-type: none"> Traffic collisions may cause an annual loss of 3–24% of a local hedgehog population, and 9–30% of a nationwide population [1][2][3][4]. Road mortality is consistently in the top three contributors to total mortality [5][6][7]. 	<ul style="list-style-type: none"> The accuracy of current local and total population estimates. Whether populations can compensate for road mortality with increased survival and/or fecundity. 	<ul style="list-style-type: none"> Establishing standardised surveys for improved population estimates. Long-term population studies to evaluate road mortality in the context of population growth.
<ul style="list-style-type: none"> Hedgehog roadkill is disproportionately clustered in suburban areas and consists 	<ul style="list-style-type: none"> Whether carcass detectability and persistence vary between age groups. 	<ul style="list-style-type: none"> Studies into the road crossing behaviour of different demographic groups.

Published Findings	Gaps in Understanding as Revealed by This Review	Directions for Future Research as Recommended by This Review
predominately of males and adults [8] [9] [10] [11] .	<ul style="list-style-type: none"> How road and habitat characteristics influence road mortality risks between demographic groups over time. 	<ul style="list-style-type: none"> Evaluating the consequences of sex- and age-specific road mortality on hedgehog population trends.
<ul style="list-style-type: none"> Hedgehog populations appear particularly vulnerable to fragmentation effects [9][12]. Hedgehog populations exhibit distinct genetic substructure, often in relation to linear infrastructure [13][14][15]. 	<ul style="list-style-type: none"> Whether the hedgehog's promiscuity and heteropaternal superfecundity can lessen the impacts of isolation on genetic structure. 	<ul style="list-style-type: none"> Establishing isolation effects from roads, such as using inbreeding coefficients or genetic pedigree analysis.
<ul style="list-style-type: none"> Exclusionary fences alone are not an appropriate mitigation measure for hedgehog road mortality [16]. Hedgehogs infrequently use crossing structures [16][17][18]. 	<ul style="list-style-type: none"> The population-level responses to mitigation measures. Whether the use of crossing structures by badgers impacts their efficacy for hedgehogs. Whether traffic-calming methods are an effective and cheaper option for road mitigation. 	<ul style="list-style-type: none"> Quantification of population viability in relation to mitigation using BACI or control/impact studies, such as using roadkill counts, population density and gene flow. Integration of ecological and socioeconomic perspectives on road mitigation and construction.

nowadays mainly found in urban areas, possibly due to the negative effects of badgers *Meles meles*. *Wildl. Biol.* 2015, 21, 51–55.

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