Road Impacts on the Demography and Movement of Animal Populations; Optimising Study Designs and Understanding the Long-Term Consequences

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Copyright statement

Application of research

- Findings included in the data collation report for the England definition of the Favourable Conservation Status of hedgehogs – 2022
- Findings applied in the development of the National Conservation Strategy for hedgehogs in Britain – 2023

Dissemination of research (including, but not limited to)

Publications:

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Documentary film:

- A segment in *Nature's Big Year* – part of the Nature of Things series – Canadian Broadcast Company documentary – 2021

TV News:

- *Channel 5 News* segment on hedgehog road mortality – 2020
- *Notts TV* segment on hedgehog road mortality – 2020

Written communications:

- Moore, L. (2022). From genes to populations: the multi-faceted impacts of road mortality on European hedgehogs and potential mitigation solutions. TransportEcology.info. Accessed at: https://transportecology.info/research/european-hedgehogs-road-mortality-mitigation
- Multiple pieces for The Conversation, including Moore, L. (2023). Roadkill: vehicle collisions may be threatening the survival of some mammal populations. The Conversation. Accessed at https://theconversation.com/roadkill-vehicle-collisions-may-be-threatening-the-survival-of-some-mammal-populations-201886

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Contribution statement

Data collection for all chapters was undertaken by L. Moore. Members of the public assisted with recording hedgehog road mortality. Data for Chapter 6 was collected with the aid of four field assistants and several volunteers around Great Britain.

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CHAPTER 6: Life in the Danger Zone: Understanding Road Avoidance, Barrier Effects and Road Mortality Impacts on Hedgehogs using Multisite Animal Telemetry

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CHAPTER 7: Discussion

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Abstract

Given the extent of the global road network, roads are considered one of the most pressing contemporary conservation issues. However, explicit understanding about *how* roads affect population dynamics, and so how to mitigate these effects, is limited. This thesis aimed to identify the optimal study designs for assessing population-level impacts of roads as well as to understand both animal survival and movements near roads. The west European hedgehog (*Erinaceus europaeus*), a priority species for conservation in the UK, is used as a case study.

Between May 2020 and November 2021, vertebrate road mortality was recorded using repeat, standardised road surveys in Nottinghamshire, UK, and analysed using novel equations, Generalised Linear Models (GLM), and Generalised Additive Models (GAM). Along the road survey route, four sites were repeatedly studied using spotlight surveys to quantify hedgehog population dynamics. Simultaneously, GPS-tracking of 127 hedgehogs across the Nottinghamshire sites and seven additional UK-wide sites took place. Road avoidance behaviour was analysed using GLMs and the 'true' risk of road mortality was analysed using a Resource Selection Function.

Average carcass persistence rates ranged between 0.69 and 6.00 days (average 3.10 days ±4.61 SD) and were driven by body mass and road type. Road mortality patterns tracked life history events and were predicted by a combination of road design, urbanity, and traffic volume. With greater densities, survival probabilities and reproductive rates, more urbanised local hedgehog populations appeared to compensate for road mortality. Eighty-four percent (n = 107) of hedgehogs exhibited significant road avoidance behaviour and road crossings showed variation by sex, road type, time of night, and season. Traffic volume and vehicle speed, especially on the outskirts of residential areas, were key components of the 'true' risk of road mortality, whilst intermediate roads produced the greatest annual road mortality probability.

This thesis provides researchers with robust methodology for the accurate interpretation of road mortality rates and their population-level impacts. In addition, this is the first study to establish local population differences in road mortality impacts in hedgehogs and that road mitigation should consider the potential presence of meta-population dynamics. The GPS data suggest that hedgehogs may be perceiving the risks and rewards of traversing road networks and adjusting their behaviour accordingly. Combining insight from the population and movement ecology, as adopted in this thesis, can ease the constraints surrounding decision-making for conservation planning and road mitigation.

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CHAPTER 1: Introduction 1

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List of abbreviations

AADT	Annual Average Daily Traffic
BACI	Before-After-Control-Impact
GAM	Generalised Additive Model
GLM	Generalised Linear Model
GPS	Geographical Positioning System
MCP	Minimum Convex Polygon
RSF	Resource Selection Function
SCR	Spatial Capture Recapture
VHF	Very High Frequency
WVC	Wildlife-Vehicle Collision

CHAPTER 1: Introduction

1.1 Road ecology: past and present

Transportation activity directly contributes to the growth of the global economy and improvements for both society and human quality of life (Polasky et al., 2005). Central to these benefits are road networks and the associated vehicles. Globally, there are over 36 million kilometres of road and more than half of the remaining roadless areas are less than 1 km^2 in size (Ibisch et al., 2016). Road-related environmental problems were brought to light in the early 1980s (Walper et al., 1981; Bennett, 1991). Following this, the field of 'road ecology' was formalised by Forman and Alexander in the late 1990s (Forman and Alexander, 1998); a field that strives to understand and improve the relationship between the natural environment and road systems. Early work in road ecology focused on the atmospheric pollutants from vehicles, habitat loss and alteration, counts of road mortality, erosion, and sedimentation from road development (Forman et al., 2003). More recently, improved technologies such as satellite imagery and camera traps have enabled more sophisticated quantification of road impacts. This includes traffic noise, light pollution, changes in animal movements, and the genetic-level effects of road mortality and fragmentation (van der Ree, Smith and Grilo, 2015; Johnson et al., 2022).

From the growing literature base, the effects of roads on wild populations are considered to be one of the most pressing contemporary conservation issues (Ibisch et al., 2016; Barrientos et al., 2021). Perhaps the most conspicuous impact of roads are wildlife-vehicle collisions (WVCs). Globally, millions of animals are killed in WVCs every year, such that WVCs are implicated in the depletion and local extinction of populations when not offset by increased per-capita recruitment (Seiler and Helldin, 2006; Borda-de-Água, Grilo and Pereira, 2014). Beyond this, WVCs compromise driver safety around the world, especially when involving large mammals (e.g., deer and antelope), and cause more than 400 human deaths, 59,000 injuries, and up to €900 million in economic losses per year in both the United States of America (USA) and Europe (Schwabe and Schuhmann, 2002; Conover, 2019). Similar issues occur in Africa and Asia (Gebru, 2017; Aga, Woldeamanuel and Tadesse, 2021). In addition, the unnatural and often premature mortality of animals from collisions is considered ethically unacceptable as it contradicts a human's perceived duty of care towards the environment (Englefield et al., 2020; Moore et al., 2021). For these ecological, ethical, and socio-economic reasons, coupled with an expected 25 million kilometres of additional road to be built globally by 2050, road management has become a priority for conservation and landscape planning (Meijer et al., 2018).

Despite the growing demand for ecologically-sensitive road practices, shifting focus to the production of robust evidence that can directly inform mitigation options has been limited. Relatively few systematic studies have been conducted on roadkill and there is a lack of clear guidance on the appropriate study designs that can achieve maximum evidential output at the least cost (Hayward et al., 2015). For example, it is thought that several biases exist that may affect the accuracy of road mortality rate estimates, such as carcass persistence (the time a carcass remains on the road and identifiable) and carcass detectability (the probability of a carcass being detected by an observed if present during a survey; Henry et al., 2021). However, understanding of how to appropriately correct for these biases remains limited, so that study designs vary widely and data remain largely incomparable. The range of existing study designs and lack of corrections for biases also prohibit the separation of the effects of sampling and the factors that truly affect road mortality rates, inhibiting the identification of priorities for road mitigation (Lima Santos et al., 2016).

Financial and logistical challenges limit empirical data collection on the demography and movement ecology of roadside populations that is needed to understand fully the mechanisms affecting population growth and persistence. This hinders understanding of whether local populations can cope with additional mortality from wildlife-vehicle collisions, which local populations are a priority for roadside management, and how best to mitigate the impacts. Without robust evidence of road effects, mitigation largely relies on sporadic, indirect, and inadequate ecological knowledge that can risk wasted resources, sub-optimal or even harmful action (Ascensão et al., 2019).

Calls for research on the persistence of populations near roads was first published 15 years ago by Roedenbeck et al. (2007). However, research commitments around the world are still considered insufficient to support major mitigation initiatives, such as COST 341 (European Co-operation in the Field of Scientific and Technical Research; Luell et al., 2022). Road ecology needs more integrated population and movement ecology approaches, as adopted in this thesis, to strengthen current understanding of the intrinsic and extrinsic factors affecting populations near roads (Shilling et al., 2020).

1.2 The west European hedgehog: a case study

Both in relation to roads and general biology, the west European hedgehog (*Erinaceus europaeus*, hereafter termed ‘hedgehog’) in Great Britain is probably the most studied nationwide hedgehog population around the world. Research has covered, but is not limited to, habitat preferences (Schaus-Calderón, 2021), predator interactions (Lee, 2022), feeding behaviour (Scott et al., 2023), nesting behaviour and hibernation (Bearman-Brown et al., 2020), reproduction (Jackson, 2006), genetics (Rasmussen et al., 2020), and dispersal (Doncaster, Rondinini and Johnson, 2001). Due to an estimated 66% decline in UK population size since 1950 (Roos, Johnston and Noble, 2012), hedgehogs are now listed as a species of principal importance in the UK (Department for Environment, Food and Rural Affairs [DEFRA], 2022) and considered to be Vulnerable on the Red List for Mammals in Great Britain (Mathews et al., 2018).

Roads are often implicated in the decline of hedgehogs in the UK, both via road mortality and road avoidance behaviour (i.e., where animals are deterred from going near or crossing a road; Wembridge et al., 2016; Mathews et al., 2018). Early insight into population-level outcomes of roadkill was developed for this species in The Netherlands (Huijser, 2000). For example, Huijser, Bergers and De Vries (1998) reported that hedgehog density was up to 35% lower near roads. However, definitive conclusions could not be drawn as to whether the reduced density was a function of road avoidance behaviour, lower habitat quality, or direct road mortality. Since then, research has showed a complex relationship between hedgehogs and roads. Hedgehogs have been shown to avoid large, but not small, roads (Rondinini and Doncaster, 2002; Dowding et al., 2010), whilst hedgehog presence is positively associated with traffic volume (Turner, Freeman and Carbone, 2021) and road density (Williams, 2018). Research specifically on hedgehog road mortality has largely focused on raw numbers, with estimated mortality levels of up to 335,000 hedgehogs killed on British roads annually (Wembridge et al., 2016), as well as patterns of hedgehog-vehicle collisions (e.g., Haigh, O’Riordan and & Butler, 2014; Müller, 2018; Rasmussen et al., 2023). The general lack of focus on the population-level processes around roads means that key questions about impact of road mortality on the population persistence of hedgehogs remain unanswered across its range. As such, substantial knowledge gaps remain about the contribution of roads to the decline of hedgehogs across Europe, hindering targeted and cost-effective actions to prevent local population extinctions.

Great Britain presents the opportunity for an insightful case study as it has one of the greatest road densities (1.9 km of roads/km^2) and traffic densities in Western Europe (182 million vehicle kms driven/km; Department for Transport, 2022). The last systematic study of roadkill in Great Britain was in the 1960s (Hodson, 1966). Since then, hedgehog populations and road networks have dramatically changed, including a 12-fold increase in vehicle traffic (Roos et al., 2012; Department for Transport, 2022). Importantly, however, the fundamental understanding developed from this thesis can be applied to other countries.

1.3 Thesis aims, objectives, and structure

As a critical frontier of applied scientific research, the progression of road ecology relies on furthering understanding of the multivariate, quantitative, and cumulative effects of roads on wild populations through appropriate study designs. In summary, existing knowledge gaps include how best to robustly estimate road mortality and evaluate its extent and magnitude across different roads and habitats (Henry et al., 2021). That is, there is little guidance on appropriate study design. This risks spurious conclusions on the scale and urgency of conservation action required through mis-matched and unreliable evidence. In a related manner, another knowledge gap extends to if, and if so how, road mortality is affecting the long-term persistence of wild animal populations, including declining and vulnerable species such as hedgehogs. For many species, it remains unknown whether road mortality causes significant changes in vital rates and becomes, like often surmised, a key driver of population decline, if roads change animal movements, or whether any level of behavioural adaptations exist to inhabiting roadside environments (Barrientos et al., 2021). This gap severally limits the application of appropriate and cost-effective mitigation to safeguard roadside populations. To fill existing knowledge gaps, this thesis aimed to (1) assess optimal study designs for accurate and comprehensive road ecology studies and (2) understand the impacts of roads on the survival and movements of animal populations using hedgehogs as a case study. The ultimate goal is that gathering robust and detailed data will enable a better understanding of the risks and impacts of roads for species such as hedgehogs and facilitate prioritisation of impact mitigation actions at the population levels where they are most needed. Specifically, the objectives of the thesis were:

- To ascertain the biases, limitations, and potential advantages of different data collection methods to obtain more insightful data on population-level impacts of road mortality.

- To determine if and how road mortality may affect population dynamics of mammalian species; specifically, the importance of road mortality in the decline of hedgehog populations.
- To determine patterns of hedgehog road crossing behaviour across different road networks and seasons, and how this links to the risks of road mortality.

The thesis is split into two parts to address the aforementioned knowledge gaps; it begins with a focus on study design using multi-species data at the global and then British scale. The global study provides additional insight into the population impacts of road mortality based on a variety of data collection methods. This is followed by a case study on the road mortality of several local hedgehog populations across a rural-suburban spectrum to explore impacts of road mortality on population persistence. The thesis consists of the following chapters:

Chapter 2

Research gap: there is little knowledge about how study design can affect conclusions on road mortality and how road mortality may be affecting population demography.

This chapter conducts a broad systematic literature review to identify the direct and indirect biological parameters affected by road mortality on mammalian populations worldwide. In order to optimise future research, this review also identifies and critically evaluates existing study designs used to explore the demographic impacts of road mortality.

Chapter 3

Research gap: there is a lack of understanding about the biases affecting the accuracy of road mortality rate estimations, as well as the patterns of road mortality based on reliable, fine-scale data.

This chapter uses high-intensity road mortality surveys combined with both novel and traditional data analyses to quantify the rates and spatio-temporal patterns of road mortality for several species. This chapter provides species-specific guidelines for future road mortality surveys and highlights the biases that should be corrected for.

Chapter 4

Research gap: there is no scientific consensus based on existing literature on the impacts and potential mitigation options for road mortality of five hedgehog species in Europe.

This chapter reviews and summarises the literature on the often-cited role of roads in the ongoing population declines of the five hedgehog species in Europe. This chapter also appraises potential mitigation solutions for hedgehogs near roads and outlines key knowledge gaps in order to guide future research and conservation efforts.

Chapter 5

Research gap: to date, no study in the UK has explored how different hedgehog populations, with varying demography across different habitats, may cope with road mortality.

This chapter compares population-wide road mortality with vital rates such as survival probability, reproduction, and non-road mortality causes across four local hedgehog populations in Nottinghamshire, UK. This, in turn, provides unique insight into how demographic variability translates to resilience or vulnerability to long-term impacts of WVCs.

Chapter 6

Research gap: there is little evidence regarding the factors that may affect if and how hedgehogs change their movements around roads (e.g., road avoidance behaviour) and, consequently, if some road sections produce a greater risk of road mortality for hedgehogs.

This chapter uses high-resolution movement models based on GPS data from 127 hedgehogs across 11 study sites in the UK to describe road avoidance behaviour of hedgehogs across sex, season, and road type. This chapter also adopts novel analysis methods that combines road mortality with road crossing data to assess the risk factors of road mortality in the immediate and long-term.

Chapter 7 concludes the thesis by synthesising the findings from the previous chapters in the wider context of existing literature. By doing so, this chapter makes several suggestions for potential roadside conservation and mitigation for at-risk populations, as well as recommendations for future research in road ecology.

1.4 References

Aga, M., Woldeamanuel, B., & Tadeesse, M. (2021). Statistical modeling of numbers of human deaths per road traffic accident in the Oromia region, Ethiopia. *PloSONE, 16*(5), e0251492. https://doi.org/10.1371/journal.pone.0251492

Ascensão, F., Kindel, A., Teixeira, F. Z., Barrientos, R., D'Amico, M., Borda-de-Água, L., & Pereira, H. M. (2019). Beware that the lack of wildlife mortality records can mask a serious impact of linear infrastructures. *Global Ecology and Conservation, 19,* e00661. https://doi.org/10.1016/j.gecco.2019.e00661

Barrientos, R., Ascensão, F., D'Amico, M., Grilo, C., & Pereira, H. M. (2021). The lost road: Do transportation networks imperil wildlife population persistence? *Perspectives in Ecology and Conservation*, *19*(4), 411–416. https://doi.org/10.1016/J.PECON.2021.07.004

Bearman-Brown, L. E., Baker, P. J., Scott, D., Uzal, A., Evans, L., & Yarnell, R. W. (2020). Over-winter survival and nest site selection of the West-European hedgehog (*Erinaceus europaeus*) in arable dominated landscapes. Animals, 10(9). https://doi.org/10.3390/ani10091449

Bennett, A. F. (1991). Roads, roadsides and wildlife conservation: a review. In D. A. Saunders and R. J. Hobbs (Eds.) Nature Conservation 2: The Role of Corridors (pp 99-117). Surrey Beatty & Sons. Australia : New South Wales.

Borda-de-Água, L., Grilo, C., & Pereira, H. M. (2014). Modeling the impact of road mortality on barn owl (*Tyto alba*) populations using age-structured models. *Ecological Modelling, 276,* 29–37. https://doi.org/10.1016/j.ecolmodel.2013.12.022

Conover, M. R. (2019). Numbers of human fatalities, injuries, and illnesses in the United States due to wildlife. *Human-Wildlife Interactions*, *13*(2), 264–276. https://doi.org/10.26077/r59n-bv76

Department for Environment, Food and Rural Affairs, DEFRA. (2022). *Protected sites and species: detailed information.* Retrieved from https://www.gov.uk/topic/planning-development/protected-sites-species

Department for Transport. (2022). *Road traffic estimates in Great Britain: 2021*. Government of the United Kingdom. Retrieved from https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/1107056/road-traffic-estimates-in-great-britain-2021.pdf.

Doncaster, C. P., Rondinini, C., & Johnson, P. C. D. D. (2001). Field test for environmental correlates of dispersal in hedgehogs *Erinaceus europaeus*. *Journal of Animal Ecology*, *70*(1), 33–46. https://doi.org/10.1111/J.1365-2656.2001.00471.X

Dowding, C. V., Harris, S., Poulton, S., & Baker, P. J. (2010). Nocturnal ranging behaviour of urban hedgehogs, *Erinaceus europaeus*, in relation to risk and reward. *Animal Behaviour, 80*(1), 13–21. https://doi.org/10.1016/j.anbehav.2010.04.007

Englefield, B., Starling, M., Wilson, B., Roder, C., & McGreevy, P. (2020). The Australian roadkill reporting project— applying integrated professional research and citizen science to monitor and mitigate roadkill in Australia. *Animals, 10*(7), 1–20. https://doi.org/10.3390/ani10071112

Forman, R. T. T., & Alexander, L. E. (1998). Roads and their major ecological effects. *Annual Review of Ecology and Systematics, 29*(1), 207–231. https://doi.org/10.1146/annurev.ecolsys.29.1.207

Forman, R. T. T., Sperling, D., Bissonette, J., Clevenger, A., Cutshall, C., Dale, V., … Winter, T. (2003). *Road Ecology: Science and Solutions*. Island Press : Washington, D.C.

Gebru, M. (2017). Road traffic accident: Human security perspective. *International Journal of Peace and Development Studies, 8*(2), 15-24. https://doi.org/10.5897/IJPDS2016.0289

Haigh, A., O'Riordan, R. M., & Butler, F. (2014b). Hedgehog *Erinaceus europaeus* mortality on Irish roads. *Wildlife Biology, 20*(3), 155–160. https://doi.org/10.2981/wlb.12126

Hayward, M. W., Boitani, L., Burrows, N. D., Funston, P. J., Karanth, K. U., Mackenzie, D. I., … Yarnell, R. W. (2015). Ecologists need robust survey designs, sampling and analytical methods. *Journal of Applied Ecology, 52*(2), 286–290. https://doi.org/10.1111/1365-2664.12408

Henry, D. A. W., Collinson-Jonker, W. J., Davies-Mostert, H. T., Nicholson, S. K., Roxburgh, L., & Parker, D. M. (2021). Optimising the cost of roadkill surveys based on an analysis of carcass persistence. *Journal of Environmental Management*, *291*. https://doi.org/10.1016/j.jenvman.2021.112664

Hodson, N. L. (1966). A survey of road mortality in mammals (and including data for the Grass snake and Common frog). *Journal of Zoology, 148*(4), 576–579. https://doi.org/10.1111/j.1469-7998.1966.tb02972.x

Huijser, M. P. (2000). *Life on the edge. Hedgehog traffic victims and mitigation strategies in an anthropogenic landscape.* [PhD Thesis, Wageningen University].

Huijser, M. P., Bergers, P. J. M., & De Vries, J. G. (1998). Hedgehog traffic victims: how to quantify effects on the population level and the prospects for mitigation. In *Proceedings of the International Conference on Wildlife Ecology and Transportation.* 10-12 February 1998, Florida Department of Transportation (pp. 171–180). USA: Florida.

Ibisch, P. L., Hoffmann, M. T., Kreft, S., Pe'Er, G., Kati, V., Biber-Freudenberger, L., DellaSala, D. A., Vale, M. M., Hobson, P. R., & Selva, N. (2016). A global map of roadless areas and their conservation status. *Science, 354*(6318), 1423–1427. https://doi.org/10.1126/science.aaf7166

Jackson, D. B. (2006). The breeding biology of introduced hedgehogs (*Erinaceus europaeus*) on a Scottish island: Lessons for population control and bird conservation. *Journal of Zoology, 268*(3), 303–314. https://doi.org/10.1111/j.1469-7998.2005.00035.x

Johnson, C., Jones, D., Matthews, T., & Burke, M. (2022). Advancing avian road ecology research through systematic review. *Transportation Research Part D: Transport and Environment*, *109*. https://doi.org/10.1016/J.TRD.2022.103375

Lee, K. (2022). *Untangling the roles of prey availability, habitat quality and predation as predictors of hedgehog abundance.* [PhD Thesis, Nottingham Trent University].

Lima Santos, R. A., Santos, S. M., Santos-Reis, M., Picanço de Figueiredo, A., Bager, A., Aguiar, L. M. S., & Ascensão, F. (2016). Carcass persistence and detectability: Reducing the uncertainty surrounding wildlife-vehicle collision surveys. *PLOS ONE*, *11*(11), e0165608. https://doi.org/10.1371/journal.pone.0165608

Mathews, F., Kubasiewicz, L. M., Gurnell, J., Harrower, C. A., McDonald, R. A., & Shore, R. F. (2018). *A review of the population and conservation status of British mammals.* The Joint Nature Conservation Committee. Retrieved from http://publications.naturalengland.org.uk/publication/5636785878597632

Meijer, J. R., Huijbregts, M. A. J., Schotten, K. C. G. J., & Schipper, A. M. (2018). Global patterns of current and future road infrastructure. *Environmental Research Letters, 13*(6). https://doi.org/10.1088/1748-9326/aabd42

Moore, L. J., Arietta, A. Z. A., Spencer, D. T., Huijser, M. P., Walder, B. L., & Abra, F. D. (2021). On the road without a map: Why we need an "ethic of road ecology". *Frontiers in Ecology and Evolution*, *9*, 774286. https://doi.org/10.3389/FEVO.2021.774286

Müller, F. (2018). Langzeit-Monitoring der Strassenverkehrsopfer beim Igel (*Erinaceus europaeus* L.) zur Indikation von Populationsdichteveränderungen entlang zweier Teststrecken im Landkreis Fulda. *Beiträge Zur Naturkunde in Osthessen*, *54*, 21–26. https://www.vno-fulda.de/Publikationen.html

Polasky, S., Nelson, E., Lonsdorf, E., Fackler, P., & Starfield, A. (2005). Conserving species in a working landscape: Land use with biological and economic objectives. *Ecological Applications*, *15*(4), 1387–1401. https://doi.org/10.1890/03-5423

Rasmussen, S. L., Berg, T. B., Martens, H. J., & Jones, O. R. (2023). Anyone can get old—all you have to do is live long enough: understanding mortality and life expectancy in European hedgehogs (*Erinaceus europaeus*). *Animals*, *13*(4), 626. https://doi.org/10.3390/ANI13040626

Rasmussen, S., Nielsen, J., Jones, O. R., Berg, T. B., & Pertoldi, C. (2020). Genetic structure of the European hedgehog (*Erinaceus europaeus*) in Denmark. *PLoS One,* 15(1), e0227205. https://doi.org/10.1371/journal.pone.0227205

Roedenbeck, I. A., Fahrig, L., Findlay, C. S., Houlahan, J. E., Jaeger, J. A. G., Klar, N., … van der Grift, E. A. (2007). The Rauischholzhausen agenda for road ecology. *Ecology and Society, 12*(1). http://www.ecologyandsociety.org/vol12/iss1/art11/

Rondinini, C., & Doncaster, C. P. (2002). Roads as barriers to movement for hedgehogs. *Functional Ecology*, *16*(4), 504–509. https://doi.org/10.1046/j.1365-2435.2002.00651.x

Roos, S., Johnston, A., & Noble, D. (2012). *UK hedgehog datasets and their potential for long-term monitoring* (BTO Research Report No. 598). The British Trust for Ornithology, commissioned and funded by People's Trust for Endangered Species and the British Hedgehog Preservation Society. Retrieved from https://www.bto.org/our-science/projects/gbw/publications/papers/monitoring/btorr598

Luell, B., Bekker, G. J., Cuperus, R., Dufek, J., Fry, G., Hicks, C., … Wandall, B. M. (2022). COST 341 Habitat fragmentation due to transportation infrastructure: Wildlife and Traffic. A European handbook for identifying conflicts and designing solutions. European Co-operation in the Field of Scientific and Technical Research. Retrieved from https://handbookwildlifetraffic.info/

Schaus-Calderón, J. S. (2021). *Responses of the West European hedgehog to urbanisation: impact on population dynamics, animal movement and habitat selection.* [PhD Thesis, Nottingham Trent University].

Schwabe, K. A., & Schuhmann, P. W. (2002). Deer-vehicle collisions and deer value: An analysis of competing literatures. Wildlife Society Bulletin, 30(2), 609-615. https://www.jstor.org/stable/3784524

Scott, D. M., Fowler, R., Sanglas, A., & Tolhurst, B. A. (2023). Garden scraps: Agonistic interactions between hedgehogs and sympatric mammals in urban Gardens. *Animals*, *13*(4). https://doi.org/10.3390/ANI13040590

Seiler, A., & Helldin, J. O. (2006). *Mortality in wildlife due to transportation.* In J. Davenport., & J. L. Davenport (Eds) The Ecology of Transportation: Managing Mobility for the Environment (pp. 165–189). Berlin : Springer

Shilling, F., Collinson, W., Bil, M., Vercayie, D., Heigl, F., Perkins, S. E., & MacDougall, S. (2020). Designing wildlife-vehicle conflict observation systems to inform ecology and transportation studies. *Biological Conservation*, *251*. https://doi.org/10.1016/j.biocon.2020.108797

Turner, J., Freeman, R., & Carbone, C. (2021). Using citizen science to understand and map habitat suitability for a synurbic mammal in an urban landscape: the hedgehog *Erinaceus europaeus*. *Mammal Review, 52*(2), 291-303. https://doi.org/10.1111/mam.12278

van der Ree, R., Smith, D. J., & Grilo, C. (2015). The ecological effects of linear infrastructure and traffic: Challenges and opportunities of rapid global growth. In R. van der Ree, D. J. Smith, and C. Grilo (Eds.) *Handbook of Road Ecology* (pp 1-9). New York : John Wiley & Sons Ltd.

Walper, K. H., Ellenberg, H., Mueller, K., & Stottele, T. (1988). Ausgangssituationen - Strassen-Oekologie - Auswirkungen Von Autobahnen Und Strassen Auf Oekosysteme Deutscher

Landschaften. (Report no. 01274473). *Federal Highway Research Institute*. Retrieved from https://trid.trb.org/view/1035583

Wembridge, D. E., Newman, M. R., Bright, P. W., & Morris, P. A. (2016). An estimate of the annual number of hedgehog (*Erinaceus europaeus*) road casualties in Great Britain. *Mammal Communications*, *2*, 8–14. https://www.mammal.org.uk/wp-content/uploads/2016/04/MC1605_HedgehogsRoads_Wembridge.pdf

Williams, B. M. (2018). *An investigation into the factors influencing hedgehog (Erinaceus europaeus) occupancy throughout rural and urban Britain*. (PhD Thesis, University of Reading].

CHAPTER 2: Demographic Effects Of Road Mortality On Mammalian Populations; A Systematic Review

Based on the article in the peer-reviewed journal *Biological Reviews:*

Moore, L. J., Petrovan, S. O., Bates, A. J., Hicks, H. L., Baker, P. J., Perkins, S. E., & Yarnell, R. W. (2020). Demographic effects of road mortality on mammalian populations: a systematic review. *Biological Reviews,* https://doi.org/10.1111/brv.12942.

2.1 Introduction

Recent estimates suggest that there are 21.6 million kilometres of roads globally, with an expected increase of >50% in road length by 2050 (Dulac et al., 2013; Meijer et al., 2018). Consequently, many conservation biologists argue that the effects of roads on wild animal populations are one of the most pressing contemporary conservation issues (Ibisch et al., 2016; Barrientos et al., 2021). Whilst roads cause substantial habitat loss, fragmentation, pollution (light, noise, chemical) and changes in animal movement (Carvalho et al., 2018), the mortality caused by wildlife–vehicle collisions (WVCs) is perhaps the most obvious impact and has therefore received particular attention. Road mortality is considered one of the largest contributors to wild vertebrate mortality globally and, unlike other forms of direct anthropogenic mortality, it affects individuals irrespective of their body size, physical condition, and conservation status (Hill, DeVault and Belant, 2019).

Raw counts of the numbers of animals killed per unit length of road (hereafter ‘roadkill’) have been published for a broad range of vertebrate taxa. However, these raw counts alone provide little information about the impacts of WVCs on populations (Grilo et al., 2021). Instead, roadkill counts need to be considered in relation to population demography. With this context, it is then possible to avoid simplistic or erroneous conclusions that a high roadkill rate is inevitably debilitating for a population or that low levels of road mortality are not negatively impacting populations (Ramp and Ben-Ami, 2006; Grilo et al., 2021). In addition, impacts of road mortality are likely to be confounded by other forms of change around roads, such as habitat modification (Chambers and Bencini, 2010) and road effect zones (Ibisch et al., 2016). To disentangle road mortality from other road impacts, demographic parameters must be quantified to reveal the relative importance of road mortality and if/how road mortality might be responsible for the observed population dynamics. For example, Jaeger and Fahrig (2001) and Ceia-Hasse et al. (2018) used individual-based models of ‘virtual’ species and demonstrated that road mortality is likely to have a greater impact on population persistence than barrier effects because of the cumulative depletion of individuals *and* lower connectivity when roadkill rates were high. Finally, by using population dynamics, studies can identify populations most at risk from roads and the specific threats against those populations, such that conservation strategies and actions can be defined and prioritised.

Approximately 27% of mammalian species are considered to be threatened with extinction (IUCN, 2020). However, most theoretical and empirical studies on the demographic impacts of road mortality to date have focused on reptiles and birds. For example, Borda-de-Água, Grilo and Pereira (2014) developed a stochastic, age-structured model and found that an annual road mortality rate of 5% can reduce barn owl (*Tyto alba*) populations to half their original size in 50 years. Population declines and/or biased population sex ratios resulting from even relatively low rates of female road mortality have been described for black ratsnakes (*Elaphe obsoleta*; Row, Blouin-Demers and Weatherhead, 2007) and freshwater turtles (Aresco, 2005). Like birds and herpetofauna, several mammalian groups, particularly small mammals and generalist carnivores, actively use roads as corridors for dispersal, routine movements and/or scavenging opportunities (Kautz et al., 2021; Galantinho et al., 2022). In doing so, individuals face an increase in the likelihood of vehicle collisions (Serieys et al., 2021). Unlike other taxa however, vehicle collisions with mammals have shown a pronounced increase over time in response to a growing human footprint (Hill et al., 2019). Moreover, hotspots of mammal roadkill are globally widespread (e.g., Fahrig & Rytwinski, 2009 and Grilo et al., 2021) identified several regions where mammalian biodiversity may be lost due to the influence of existing transport infrastructure. Mammalian road mortality therefore remains a crucial area of study for conservationists.

Scientifically rigorous research into the demographic impacts of road mortality is key to influencing road planning decisions (Roedenbeck et al., 2007). Sound research is also essential to justify recent and future mitigation projects, especially for large-scale, expensive measures that are often targeted at medium and large mammalian species (Huijser et al., 2009). Using study designs capable of producing field data with evidential weight, however, can be challenging. The demography of a population can be poorly understood, obtaining roadkill data can be time-consuming and expensive, and accuracy can decline because of low carcass persistence for several taxa (Santos et al., 2016). This particularly applies to taxa with small body sizes, such as small mammals (e.g., mice, voles and bats), which not only have lower detectability on roadkill surveys but have shorter persistence times compared to many taxa due to the ease of being scavenged (Ruiz-Capillas, Mata and Malo, 2015). Small sample sizes further preclude insight into long-term impacts of road mortality on the structure and sustainability of populations. In general, there is a trade-off between spending resources to understand one population thoroughly, or several populations inadequately. As a result, guidance on how to design and maximise outputs from road mortality studies remains an important yet unfulfilled goal.

Although it is generally accepted that road mortality affects populations to some extent (Rytwinski and Fahrig, 2015), the literature is lacking a clear consensus on *how* road mortality affects the persistence of populations. This systematic review aimed to synthesise and categorise the direct and indirect demographic parameters in mammalian populations around the world that are affected by road mortality, as well as identify the study designs with the greatest inferential strength for assessing road mortality impacts at the population scale. By using a standardised systematic review protocol, existing knowledge can be gathered in an unbiased and comprehensive overview. The extent to which a road affects population persistence may depend on the particular circumstances, such as road density, species behaviour, species-specific habitat quality, and other threats (Roedenbeck et al., 2007). Therefore, the scope of the present systematic review was kept global and broad to synthesise the results from studies conducted under a variety of circumstances. A focus on mammals is not only critical for their conservation, given the increasing threat of extinction of many mammalian populations, but the wide range of mammalian life-history strategies provides valuable insight into different, simultaneous mechanisms affecting population resilience or vulnerability to road mortality (Grilo et al., 2021). Recognising the demographic parameters affected by road mortality, or alternatively how populations cope under additional mortality, allows wildlife managers and conservationists to make transparent, quantitative, and informed decisions. Moreover, an understanding of robust study designs is imperative to build a strong evidence base for the targeted and effective actions around roads that are sorely needed.

2.2 Materials and methods

2.2.1 Literature search

Following the identification of a relevant topic, research aims were developed in consultation with external subject experts in the scoping phase of the review. Experts included researchers, ecological consultants, and non-governmental organisations working in mammal conservation, road ecology, and/or road safety, including Mott MacDonald (consultancy: international; https://www.mottmac.com/), Rimba (non-governmental organisation: Asia; https://rimba.ngo/)

and National Highways (government-owned company: England; https://nationalhighways.co.uk/). Following the guidelines proposed by the Collaboration for Environmental Evidence (CEE; Pullin and Stewart, 2006), a systematic literature search was performed for studies around the world that documented mammal–vehicle collisions and that also provided information relevant to population demography. The CEE guidelines were chosen to enable standardised subject-specific identification of evidence to support conservation practice and road management. The literature search was conducted in April 2021, using two electronic databases: *Scopus* and *Web of Science* Core Collection®. Importantly, *Web of Science* incorporates several regional databases that allow searches for non-English-language literature. The search was created using a thorough scoping of the literature and a benchmarking process. The following Boolean search string was used in each database: (roadkill OR road-kill OR “road kill”) OR (mortalit* OR fatalit* OR strike OR collision AND anthropogenic OR vehicle OR road OR highway OR traffic OR motorway OR freeway OR expressway) AND (survival OR population OR viability OR threat OR decline OR extinction OR extirpation OR depletion OR dispers* OR movement OR migrat* OR genet*) AND NOT (vessel OR boat). The search was performed in English, French, Spanish, Portuguese, and Brazilian Portuguese (Appendix I), and no country limitations were applied. To ensure objective and comprehensive coverage, studies published in any print outlet were included, as were multi-taxa studies that may have relevant mammalian demographic data amongst that of other taxa. The search was restricted to publications reporting data from 2000 to 2021, inclusive, to account for the drastic historical increase in global traffic volume (Schafer and Victor, 2000). However, traffic volume has continued to increase annually and no comparisons are made between studies based on the relationship between traffic volume and road mortality impacts.

In addition, the first 400 results of an advanced title search using the same search string on the meta-search engine *Google Scholar* were also checked for relevance to increase grey literature returns (i.e., literature produced outside of traditional academic publishing channels, such as government reports and working papers), particularly in the non-English language literature (Haddaway et al., 2015). Papers, conference proceedings, and technical reports published on additional online platforms were also searched for, including conferences such as the International Conference on Ecology and Transportation (ICOET) and from road ecology centres such as the Western Transportation Institute. Thesis repositories of *Ethos* (UK) and *ProQuest* (worldwide) were used to search for relevant theses.

2.2.2 Screening and inclusion criteria

All selected studies were subject to a stepwise selection process. Before screening for relevance, all studies were screened for duplicate data sets between sources with the most complete sources selected. Studies were then selected for inclusion using the *a priori* criteria based on consultation with experts shown in Table 2.1.

Table 2.1: *A priori* criteria used to select studies for inclusion during the systematic review.

	***A priori* criteria**
Population	Wild mammal population in any country.
Intervention	Road collisions leading to the mortality of a mammalian animal. Any road type was considered.
Comparator	No comparator, gradient, or Before–After–Control–Impact (BACI) methods were necessary for inclusion.
Outcome	Any effect on population biology, including (but not limited to) *per capita* mortality, age/stage/sex-specific mortality, reproductive rates, movement, growth rates, and genetic structure.
Types of study	Any empirical study or simulation using real-world data.

Scientific studies were assessed for inclusion at three successive levels: first on titles (*N* = 11,238), then abstracts (*N* = 1,025), and finally full texts (*N* = 624). If a study investigated more than one taxon, species, or demographic parameter, all mammalian species and parameters were considered and data on each were obtained separately. Table 2.2 lists the inclusion and exclusion criteria applied at the full-text stage. Kappa analysis is a statistical test to measure interrater reliability and so was used to verify the level of reviewer agreement on article inclusion at the third screening stage between two reviewers (L.J.M. and R.W.Y.; Landis and Koch, 1977). A random subsample of 10% of the studies was used (Kappa = 0.63, indicating ‘substantial agreement’ *sensu;* Landis and Koch, 1977). There was 82% agreement between the two reviewers on the random subsample of studies. As appropriate inter-rater agreement for systematic reviews is regarded to be >80%, sufficient comparability between reviewers was achieved for this literature search (McHugh, 2012).

Table 2.2: List of inclusion/exclusion criteria at the full-text stage during the systematic search.

	Criteria
Included in the final set of papers	**Original research –** studies that presented empirical data on road mortality with any demographic data. This included simulation studies if using real data, either collected by the authors or from existing literature post-2000.
	Systematic data collection – road mortality figures collected in a systematic manner or from monitoring wild populations (e.g., *via* radio-collars) to ensure accuracy of collated data. Papers were excluded if they were not explicit about data-collection methods.
	Road mortality only – studies that assessed the impacts caused by roads, excluding other transportation infrastructure such as railways. Data were only included if reports of road mortality were presented separately from other transport collisions.
Excluded from the final set of papers	**Public involvement** – studies using records that were reliant on public involvement, such as from rescue centres, wildlife hospitals or citizen science, because of potential recorder inaccuracies, spatial auto-correlation, and/or non-exhaustive samples due to an unknown, variable, and unbalanced sampling effort.
	Lack of population context – reports of sex- and age-specific roadkill or spatiotemporal roadkill patterns with no population context, such as population size, sex- or age-ratio.
	Outside of desired time period – studies that reported data spanning pre- and post-2000 and that could not be separated for quantitative analyses.
	Opportunistic data – studies that reported on roadkill data collected systematically *and* opportunistically but did not separate the data.
	Literature reviews – including meta-analyses.

2.2.3 Data extraction, qualitative synthesis, and quantitative analyses

Meta-data, such as species, conservation status, and country, were tabulated for each relevant research study found. Relevant information relating to the road mortality and demographic parameters of studied populations was identified and subsequently categorised into direct or indirect parameters based on established demographic theory and further sub-categorised (Krebs, 2009). Categories were formulated once the relevant studies meeting the inclusion criteria for this review had been identified. Study designs were similarly categorised after identifying the relevant studies. A narrative synthesis was undertaken using tables and figures that describe the evidence base itself and the findings of individual studies. To standardise data extraction from the variety of study designs, the proportion of a population killed on roads was calculated per year for each population for which relevant data were provided. As chi-squared tests compare data with expected values (in this case, an even sex or age distribution), this test was used to quantify the presence or absence of sex- or age-biases in the roadkill records relative to the source population.

2.3 Results

2.3.1 Overall results from the scientific literature

The search identified 15,298 studies, totalling 11,238 when duplicates were removed. Of these, 624 studies were assessed at the full text stage and 83 studies (13.3% of the 624 studies) met the inclusion criteria and were retained for analyses. The main reason for the exclusion of studies was that they lacked demographic data to accompany the road mortality figures (259 studies). Details on the search, screening, and quality assessment results are summarised in Figure 2.1.

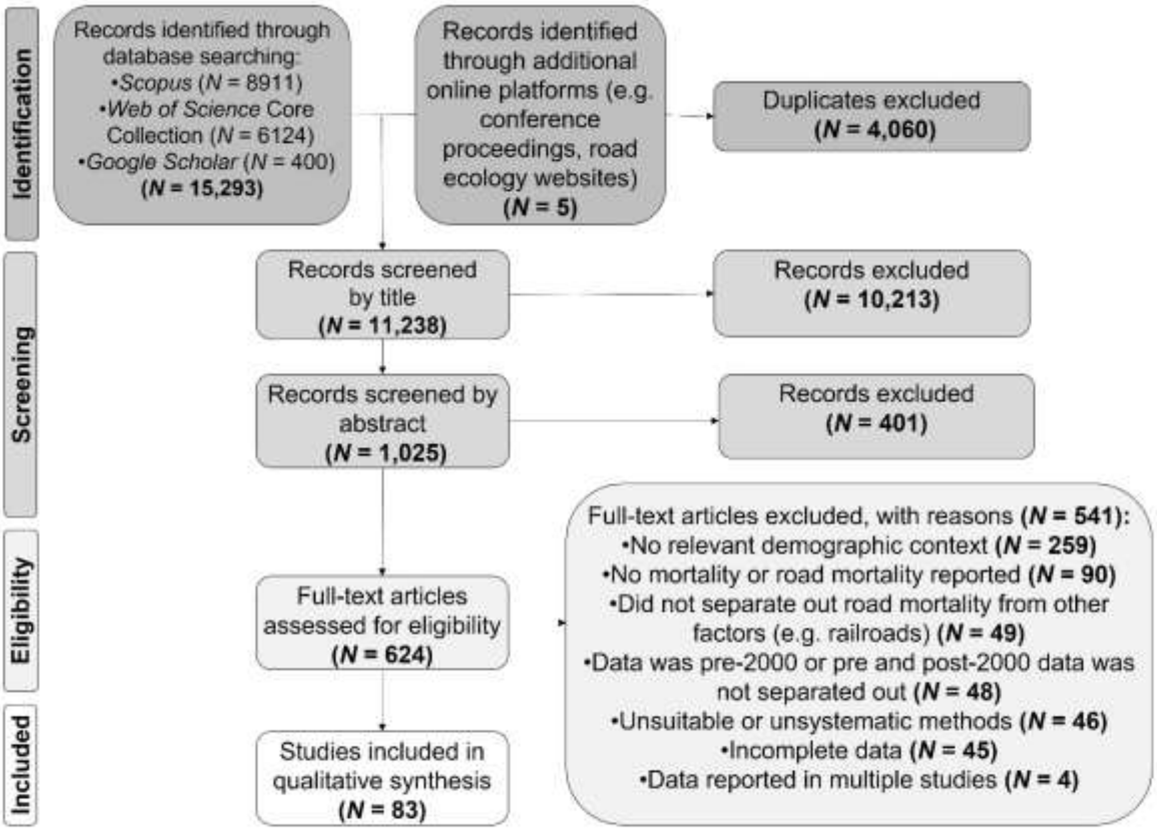


Figure 2.1: Literature search and screening flow diagram of studies included and excluded from the systematic review.

Although the literature search was conducted in five languages, all studies meeting the inclusion criteria were in English. During abstract screening, 5.1% (*N* = 52) of studies or, as a minimum, their abstracts were in non-English languages, including French (*N* = 16), Brazilian Portuguese (*N* = 14), Spanish (*N* = 12), German (*N* = 7), Croatian (*N* = 1), Dutch (*N* = 1), and Russian (*N* = 1). In addition, 2.6% (*N* = 16) of full texts screened had the whole text or abstract in Spanish (*N* = 7), Brazilian Portuguese (*N* = 5) or French (*N* = 4). The reasons for the exclusion of these non-English language studies followed the same pattern as the studies in English (Figure 2.1). The most common type of document was journal article (*N* = 75), followed by PhD Thesis (*N* = 3), technical or government report (*N* = 3), book chapter (*N* = 1), and conference proceeding (*N* = 1). The studies were collated from 22 countries with the majority (57.8%) from North America (Figure 2.2).

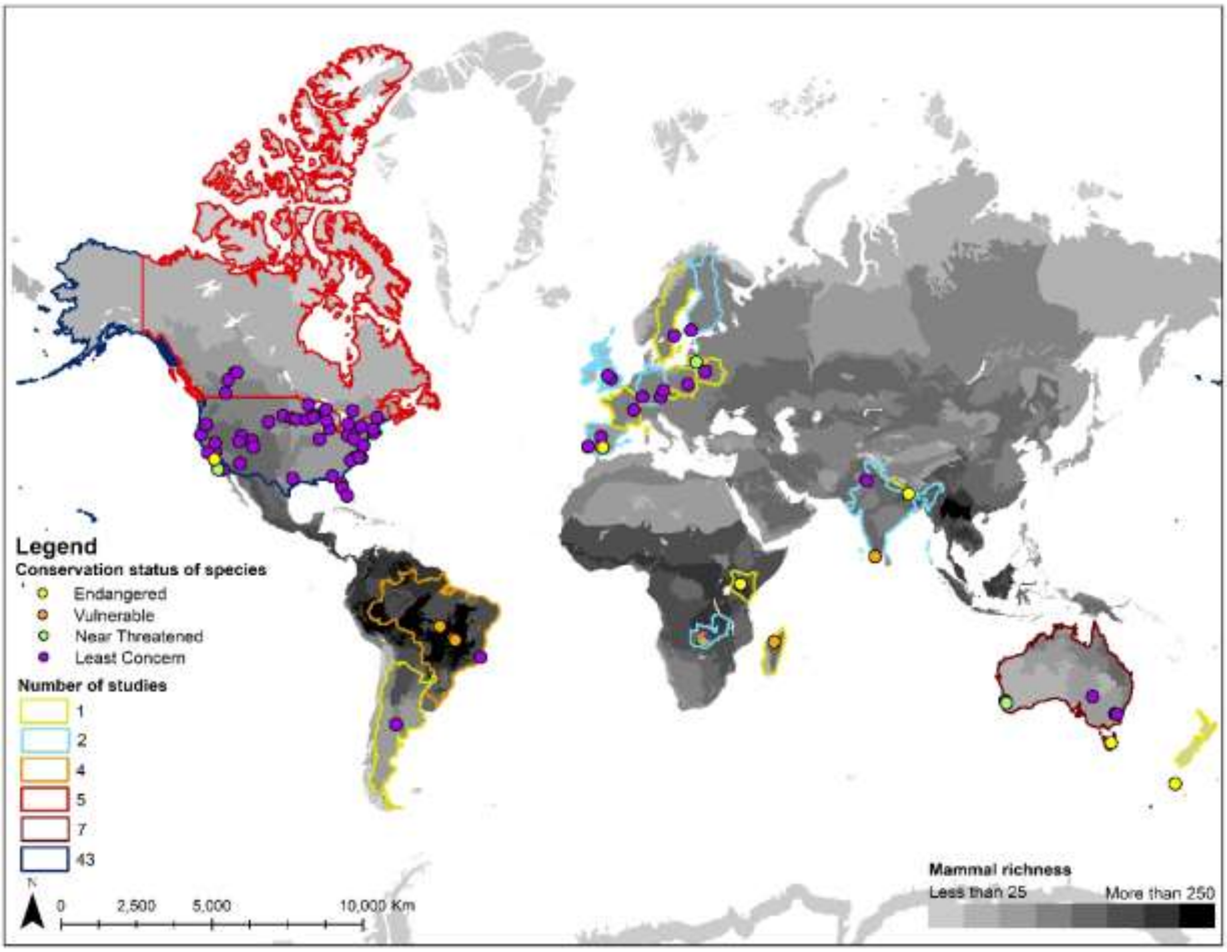


Figure 2.2: Locations of the 83 studies included in the qualitative synthesis. Coloured points represent the centroid location of each study.

The studies retained for analysis reported data on 69 mammalian species from ten taxonomic orders (Figure 2.3). Out of the 69 species identified, 54 are categorised as Least Concern, five are Near Threatened, four are Vulnerable and six are Endangered (IUCN, 2021). The review revealed a variable but overall increasing number of publications reporting mammalian road mortality and demography between 2000 and 2021, ranging between one and nine papers published each year.

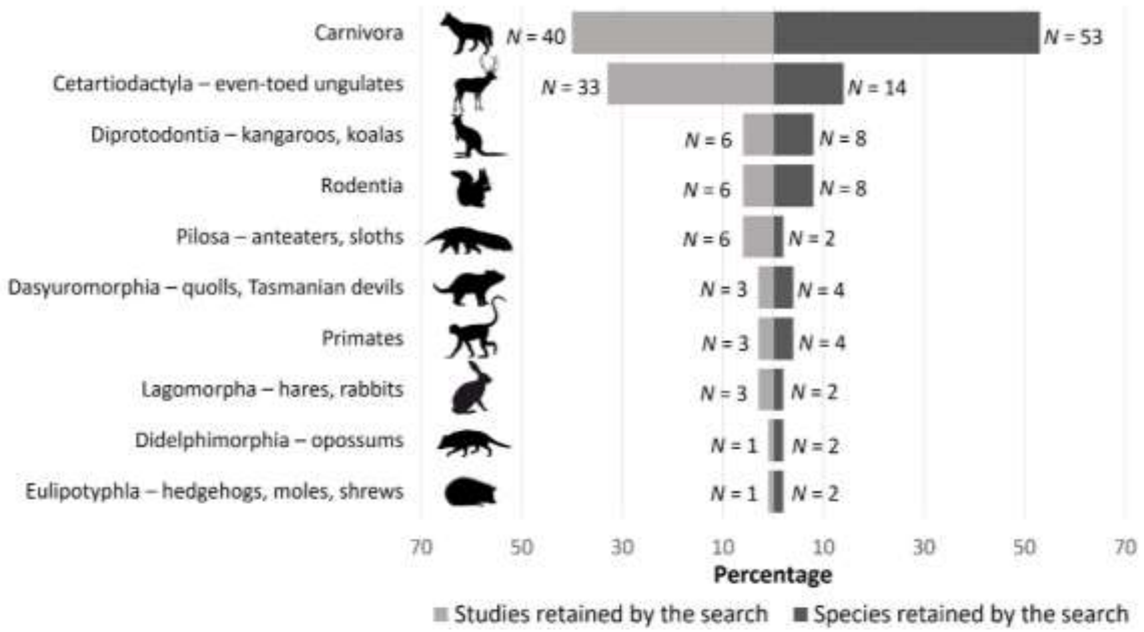


Figure 2.3: Percentage and numbers of studies and species included in the systematic review, by taxon. Note that some studies reported data on several species. Various Artists/Shutterstock.com.

Nine research methods were categorised amongst the identified studies (see Appendix II for identified advantages and disadvantages of these methods). The most common methods were radio-tracking only (*N* = 52) and year-round population monitoring only (*N* = 10). Thirteen studies combined systematic roadkill surveys with another survey method, including (*a*) a one-time population estimate (*N* = 6), (b) secondary population data (i.e., published population size estimates; *N* = 3), (*c*) radio-tracking (*N* = 1), (*d*) population monitoring (*N* = 1), (*e*) both radio-tracking and population estimate (*N* = 1). Two population estimates were conducted using genetic fingerprinting from hairs. Studies also combined population monitoring and radio-tracking (*N* = 3), and utilised simulations (*N* = 6) such as Population Viability Analyses. The average sample size for a radio-tracked population was 93 individuals (range: 2 – 492). Seven studies used Before–After (*N* = 2) and Control–Impact (*N* = 5) experimental designs but none used a Before–After–Control–Impact (BACI) design. Excluding simulation studies, study duration increased over time and ranged between less than one year to 17 years; four studies (5.2%) were less than one year in length, 52 studies (67.5%) were 1–5 years in length, 17 studies (22.1%) were 6–10 years in length, and four studies (5.2%) were 11–17 years in length.

Five direct and three indirect demographic parameters were identified in relation to road mortality (Table 2.3). Overall, 87.2% of the studies identified reported direct demographic effects of road mortality on the focal populations, whilst 12.8% reported indirect demographic effects of road mortality.

Table 2.3: Descriptions of the eight parameters categorised from the 83 papers retrieved during the systematic review. Note that some studies reported data on several species.

	Demographic parameters	**Description**	**Number of studies (percentage of studies)**
Direct	Percentage of a population killed on roads per year	The number of individuals killed on roads as a percentage of the total population per year.	61 (36.1%)
	Contribution to total mortality	The contribution of road mortality deaths relative to the total mortality rate in a set time period, such as a year.	58 (34.3%)
	Sex-biased road mortality	The ratio of males: females found killed on roads relative to the sex ratio in the population (i.e., whether one sex is killed on roads more than expected given their prevalence in the population). A significant chi-squared result was considered to represent a bias.	16 (9.5%)
	Age-biased road mortality	The ratio of adults: sub-adults: juveniles found killed on roads relative to the age ratio in the population. Age class was taken from the study. A significant chi-squared result was considered to represent a bias.	13 (7.7%)
	Roadkill during inter-patch or long-distance movements	Road mortality interfering with the success of movement-related behaviour that is not part of day-to-day activities (e.g., foraging), such as mortality during known dispersal events or migration.	7 (4.1%)
Indirect	Population growth rates	Temporal changes to population growth rate because of animals removed by road mortality.	7 (4.1%)
	Population persistence	The extent to which road mortality impacts the persistence of populations.	5 (3.0%)
	Genetic diversity	Changes to the heterozygosity within/between populations as a result of road mortality.	2 (1.2%)

2.3.2 Description of direct demographic parameters

2.3.2.1 Percentage of a population killed on roads per year

Mortality on roads accounted for 0.02 to 50.0% of the local populations per year based on 61 studies, 40 species, and 85 populations. Twenty-six studies reported an annual loss of up to 1% on roads, 38 studies reported a loss of 1.1–5.0%, 14 studies reported a loss of 5.1–10.0%, four studies reported a loss of 10.1–20.0%, and the remaining three studies reported a loss of 30.0–50.0% from the population. Split by taxon, the percentage of the population killed on roads was greatest for Dasyuromorphia (quolls *Dasyurus* spp., Tasmanian devils *Sarcophilus harrisii*) and lowest for Cetartiodactyla (even-toed ungulates; Figure 2.4A). Intra-specific populations differed in the proportion of the population lost on roads annually. For example, white-tailed deer (*Odocoileus virginianus*) had an 11.5-fold difference in proportional loss across four studies, whilst the annual proportional loss of beech martens (*Martes foina*) ranged from 1.11 to 33.0% between two studies (see online supporting material; https://doi.org/10.1111/brv.12942). In one study of six populations of American black bear (*Ursus americanus*) in Florida, United States of America (USA), annual proportional loss ranged between 0.76 and 11.49% (Simek et al., 2005).

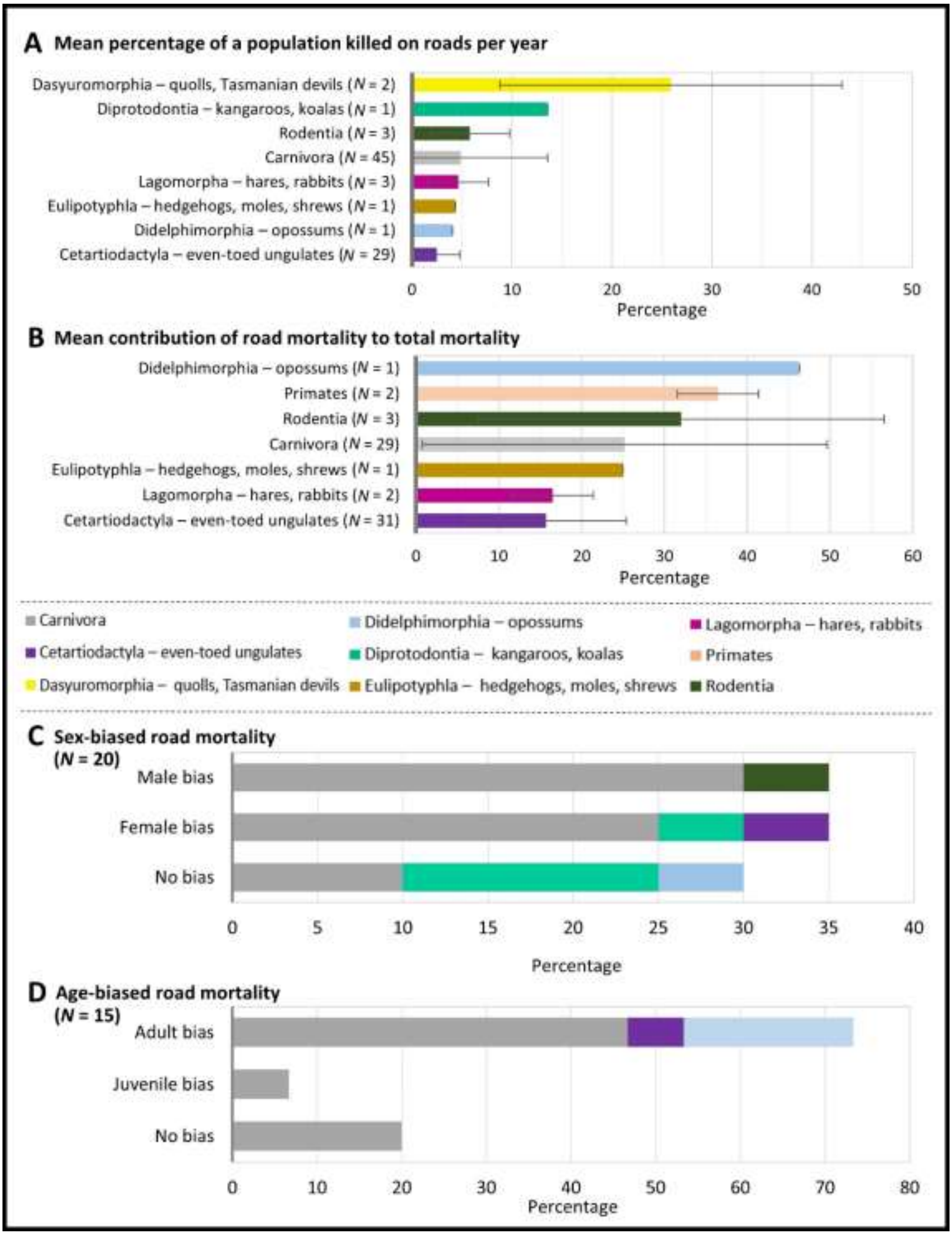


Figure 2.4: Results from four direct demographic parameters identified by the systematic search. The number of studied populations is provided in brackets. (A) Mean percentage of studied populations killed on roads. (B) Mean contribution of road mortality to total mortality for the studied populations. (C) Percentage of populations with male-biased, female-biased and no sex bias to the road mortality records. (D) Percentage of populations with adult-biased, juvenile-biased and no age bias to the road mortality records. Error bars in A and B represent standard deviation.

2.3.2.2 Contribution to total mortality

Between 1.1 and 80.0% of a population's total known mortality was due to roadkill out of 58 studies, 35 species, and 69 populations. Thirty-two studies reported a 1.0–15.0% contribution from road mortality to total mortality, 16 studies reported a 15.1–30.0% contribution, nine studies reported a 30.1–45.0% contribution, six studies reported a 45.1–60.0% contribution, and three studies reported a 60.0–80.0% contribution from road mortality to total known mortality. Split by taxon, the mean contribution from road mortality to total mortality was greatest for Didelphimorphia (opossums) and lowest for Cetartiodactyla (even-toed ungulates; Figure 2.4B). Data on cause-specific mortality was provided for 57 populations. Of these, 28.1% experienced road mortality as the largest contributor to total mortality, with a further 29.8% and 31.5% of populations experiencing road mortality as their second and third largest mortality factor, respectively. Other prevalent causes of mortality were hunting, predation, and disease. Intra-specific population differences were evident for several Cetartiodactyla species such as elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*) and white-tailed deer, and Carnivora such as American black bear and puma (*Puma concolor*). For example, out of four studies, elk populations had a 20-fold difference in the contribution of road mortality to total mortality, whilst the contribution differed between six puma populations by 7.9-fold (see online supporting material; https://doi.org/10.1111/brv.12942).

2.3.2.3 Sex-biased road mortality

Many studies that reported the sex ratio of roadkill (16 papers, 15 species, 20 populations) did so on small sample sizes of roadkill and therefore inference power of the results is low (Fraser *et al*., 2013). Seven populations (35% of studied populations) experienced significantly more female road mortality than would be expected by chance (Figure 2.4C; see online supporting material - https://doi.org/10.1111/brv.12942 - for chi-squared test results). For example, whilst female bobcats (*Lynx rufus*) made up 38% of the radio-collared population, 75% (*N* = 4 WVC) of the roadkill were female (Serieys et al., 2021). Likewise, common wallaroo (*Osphranter robustus*) females were killed more than expected (observed: 9, expected: 2.4) relative to males (observed: 25, expected: 31.6; Klöcker, Croft and Ramp, 2006). Conversely, seven populations (35% of studied populations) showed significantly male-biased road mortality, although again with small sample sizes (Figure 2.4C; see online supporting material; https://doi.org/10.1111/brv.12942). For example, whilst 42% of American fishers (*Pekania pennanti*) in a population in California, USA, were male, 100% of the roadkill was male (*N* = 2 WVC; Sweitzer et al., 2016). Additionally, six populations (30%) identified in this review did not show any sex bias of the roadkill. Intra-specific population comparisons were possible for three species. Whilst two populations of red kangaroo (*Osphranter rufus*) showed the same lack of bias, two populations of both coyote (*Canis latrans*) and common wallaroo showed differing sex biases in their roadkill records (see online supporting material; https://doi.org/10.1111/brv.12942).

2.3.2.4 Age-biased road mortality

Many studies that reported the age ratio of roadkill (13 papers, 9 species, 15 populations) did so on small sample sizes of roadkill and therefore inference power of the results is low (Fraser et al., 2013). Eleven populations (73% of studied populations) experienced significantly more adult road mortality than would be expected by chance (Figure 2.4D; see online supporting material - https://doi.org/10.1111/brv.12942 - for chi-squared test results). For example, whilst 54% of an American black bear population was comprised of adults, 100% (*N* = 11 WVC) of the roadkill was adults (Tri et al., 2017). In comparison, coyote was the only species reported where sub-adults in the population were killed more frequently than would be expected by chance (25% of the population comprised of subadults, 100% of the roadkill was subadults, *N* = 2 WVC; Stevenson et al., 2016). In three populations (20% of studied populations), adults and juveniles were killed on roads in similar proportions to their populations (see online supporting material; https://doi.org/10.1111/brv.12942). Intra-specific population comparisons were possible for four species. Whilst two populations of white-tailed deer showed the same adult bias in road mortality, two populations of both coyote and puma showed differing age biases in their roadkill records. Out of five American black bear populations across two studies, four populations showed an adult bias whilst one population showed no bias in the roadkill records.

2.3.2.5 Roadkill during inter-patch or long-distance movements

Seven studies on six species and 14 populations revealed movement parameters that are directly affected by roadkill. Two studies compared the routine movements of resident animals to the exploratory and migratory movements of translocated animals (Frair et al., 2007; Wright et al., 2020). For both elk and mule deer, authors reported that non-resident animals were more commonly killed on roads compared to residents (Frair et al., 2007; Wright et al., 2020). Moreover, three studies reported road mortality of dispersing animals (i.e., moving out of their natal area; Kanda, 2005; Fey, Hämäläinen and Selonen, 2016; Carvalho et al., 2018). Dispersal movements were shown to correspond to a heightened road mortality rate for young common genets (*Genetta genetta*; N = 38 WVC; Carvalho et al., 2018). Two of the three dispersing rural female Virginia opossums (*Didelphis virginiana*) were killed on roads during dispersal movements (Kanda, 2005). Again, caution is recommended in interpreting these results because of the low inference power derived from small sample sizes. High road mortality of dispersing animals was not universally reported. One (3.2%) of the 32 tracked juvenile red squirrels (*Sciurus vulgaris*) died during dispersal movements in Finland, although three other dispersing individuals disappeared and traffic mortality remains a possible cause (Fey et al., 2016). Migration was discussed in one paper: four (1.1%) out of 359 mule deer were killed in WVCs during migration in south-central Oregon, USA (Coe et al., 2015).

2.3.3 Description of indirect demographic parameters

2.3.3.1 Population growth rates

Population growth rates were examined and reported in seven studies on 20 species and 22 populations. Chambers & Bencini (2010) examined population growth rates for three tammar wallaby (*Notamacropus eugenii*) populations. Road mortality reduced the population growth rate between 2005 and 2007 by 1–6% for a population in the relatively undisturbed southern bushland and 8–16% for populations in a highly developed neighbouring site. Desbiez et al. (2020) used empirical roadkill data for a Population Viability Analysis (PVA) in Brazil and showed that the road mortality of giant anteaters (*Myrmecophaga tridactyla*) decreased the stochastic growth rate of that population by half. While population growth rates remained over 2% per year, the population’s ability to withstand and recover from other anthropogenic threats such as fire and disease outbreaks was considered to be lower. Three studies collected empirical data on both road mortality rates and population growth for 16 populations, including Northern bushbuck (*Tragelaphus scriptus*), oribi (*Ourebia ourebi*), common hippopotamus (*Hippopotamus amphibius*) and common warthog (*Phacochoerus africanus*; Belant, 2007; Ruiz-Capillas et al., 2015; Nyirenda, Namukonde and Fushike, 2017). The road mortality rates of each of the 16 populations appeared sustainable and the population sizes continued to grow over several years. For example, an American marten (*Martes americana*) population experienced 12.5% of its mortality from vehicle collisions, yet the population size continued to increase at a rate of 16% per year over three years (Belant, 2007).

2.3.3.2 Population persistence

Population persistence was reported in five studies on three species and 22 populations. Desbiez et al. (2020) reported that a loss of 18% of the adult giant anteater population due to road mortality in the Brazilian Cerrado resulted in a 47% probability of extinction in 100 years, compared to no extinction risk over 100 years of a baseline population under no significant threats. Desbiez et al. (2020) also reported a difference in effects based on sex-biased road mortality, whereby female-only roadkill produced a 46.1% probability of extinction in 100 years, compared to a 0.1% chance from male-only roadkill. Diniz & Brito (2013) calculated that if 15% of a giant anteater population in Parque Nacional Brasília, Brazil, were killed on roads, the population would reduce in size by 78% (180 to 40 individuals) in 5–6 years, followed by local extinction in <8 years. Finally, Roger, Laffan and Ramp (2011) conducted a sensitivity analysis for common wombats (*Vombatus ursinus*) in New South Wales, Australia. Populations with 40% annual road fatality (26.7 individuals ±13.8 SD) presented a high probability (50%) of decline, even for the largest initial abundance and carrying capacity values.

2.3.3.3 Genetic diversity

Genetic diversity was examined in two studies, each examining a different giant anteater population in Brazil and showing similar results. Diniz & Brito (2013) examined the heterozygosity of giant anteaters in Parque Nacional Brasília in several roadkill scenarios. The simulations showed that with 25 individuals killed per year (15% of the population), most of the original genetic diversity within the population was maintained. For a giant anteater population in the Brazilian Cerrado, Desbiez et al. (2020) showed that the population at year 100 had 95% of its genetic diversity remaining under the present road mortality scenario. However, genetic diversity was more severely reduced in simulated populations experiencing road mortality of both sexes (heterozygosity = 0.798), followed by female-only road mortality (heterozygosity = 0.835), compared to male-only road mortality (heterozygosity = 0.948; Desbiez et al., 2020).

2.4 Discussion

Gathering mammalian demography data is notoriously difficult (Stenglein et al., 2015). During the stepwise selection process, 305 studies were removed because of a lack of demographic data accompanying roadkill counts or the use of unsystematic study design, leading to an incomplete or unreliable data set for population-level assessments. Therefore, despite intensive global research over the past 20 years, many critical questions about long-term impacts of road mortality remain unanswered. The purpose of this review was to explicitly search for and retain studies reporting road mortality impacts on demographic parameters in order to synthesise data on how road mortality affects populations and not the extent of road mortality worldwide. As such, this review draws no conclusions about the number of populations free from the risk of WVCs, although previous studies have indicated that most terrestrial populations are vulnerable to vehicle collisions (Hill et al., 2019; Barrientos et al., 2021). It must be emphasised that several studies identified in this review are based on small roadkill sample sizes. This may be a function of the relatively short duration of many studies and/or the difficulty in identifying sex from decomposed or damaged carcasses. Therefore, it is unclear how well these results represent the wider population.

Despite the systematic literature search being conducted in five languages and studies included from 22 countries, studies that met the inclusion criteria were only in English. This could be a result of a publication bias towards research-intensive and developed countries that have a greater prevalence of English speakers (Nuñez and Amano, 2021) and/or that non-English studies often have less-robust study designs than the English literature (Amano et al., 2021). Consequently, the latter may result in English-language studies being published in higher-impact journals that stipulate articles to be written in English, which also have more thorough indexing procedures for well-known literature search systems compared to non-English journals (Amano et al., 2021).

2.4.1 Direct demographic parameters

2.4.1.1 Depletion effects

Many studies identified in this review revealed that road mortality can remove a large number of animals from the population compared to population size or other mortality factors (e.g., Seiler, 2003; McCleery et al., 2008; Lehrer, Schooley and Whittington, 2012; Grueber et al., 2017). In particular, road mortality was the greatest source of mortality for approximately one-third of populations for which data were provided (N = 16 out of 57 populations). Twelve of these populations were surrounded by urbanised landscapes or anthropogenic development, as opposed to natural forests, savannahs, and national park for example. This highlights the well-cited link between urbanisation and additional anthropogenic mortality (McCleery et al., 2008; Tri et al., 2017; Wright et al., 2020). Large individual losses on roads can directly reduce the effective population size and/or increase mortality rates above recruitment rates, therefore making populations vulnerable to environmental and demographic stochasticity, as shown for many species (Carvalho and Mira, 2011; Roger et al., 2011).

The way in which high roadkill rates shape population persistence is likely to be nuanced, possibly explaining the variation in road mortality impacts on intra-species populations identified in this review. The impacts likely depend on the suitability of the surrounding environment and associated background demographic parameters such as population growth and the potential for compensating mechanisms (Seiler, 2003). Crucially, the relative importance of road mortality is likely to be context specific as the road configuration and habitat quality surrounding a population can vary, for example between core and edge habitats or along the urban–rural gradient (Lehrer et al., 2012). These in turn affect population dynamics, including population densities which are a key factor in determining the level of road mortality that a population can sustain (Wright et al., 2020).

For some populations, roadkill can have a small effect on the persistence of the population (Cypher, Bjurlin and Nelson, 2009; Sidorovich, Novitsky and Solovej, 2020). It is thought that species with fast life histories experiencing high fecundity, large population densities and rapid population growth are more able to replace lost individuals quickly (Rytwinski and Fahrig, 2015). Fifteen populations identified in this review continued to show stable or increased growth rates over three or more years despite relatively high road mortality. Many of the identified species meet some or all elements of fast life histories, such as American martens and 13 ungulate species (Belant, 2007; Ruiz-Capillas et al., 2015; Nyirenda et al., 2017). A knowledge gap remains for small mammals, such as mice, voles, and bats, however. This is because low carcass detectability and persistence of small-bodied animals preclude accurate roadkill rate estimates and therefore conclusions about the extent that roadkill depletes these populations. Of note, 14 of the 15 populations shown to have stable or increased growth rates despite road mortality inhabited National Parks. This suggests that high-quality, protected environments can contribute to the resilience of populations to anthropogenic threats such as roads (Pereira et al., 2010; Nyirenda et al., 2017).

2.4.1.2 Sex- and age-biased road mortality

It is noteworthy that road mortality appeared to be adult-biased in 10 out of 15 studies that provided relevant data, which is likely a consequence of the greater roaming behaviour of adults to find mates and food. Mammalian age-specific survival is typically characterised by low rates in young animals and high rates in adults (Arso Civil et al., 2019). Changes in adult survival can have the greatest effect on population trajectories, particularly for species where adult lifespans are long relative to the time taken to reach maturity (Chambers, 2009). Therefore, adult-biased road mortality is a pertinent concern as it can reduce effective population sizes and reproduction rates. However, whether adults and juveniles have different detection probability (e.g., because of the smaller size of juveniles), which may bias estimates of population structure and therefore any inference from the data, remains unknown.

As sex structure and mortality are central to population stability, a sex bias in road mortality can be used in projections of longer-term impacts (Klöcker et al., 2006). A relatively even spread of male, female and no bias to roadkill was found amongst the retained studies, although the number of studies identified was small. A lack of sex bias in road mortality is unlikely to affect a population's persistence beyond the general depletion of individuals as the population structure is likely to remain unchanged. There is a strong narrative in the literature that males are more vulnerable to roadkill than females (e.g., Miotto et al., 2012; Green-Barber and Old, 2019). However, whilst males are often killed on roads more frequently than females, this review shows that males are not necessarily killed more than would be expected based on their numbers in the population. Variations in sex-specific survival rates moderate population dynamics and the severity of these impacts is likely to depend on the species' social structure and mating systems. Female survival typically exerts a greater effect on population trends than male survival. Low, but consistent, female road mortality may cause a male-skewed population, as similarly shown for reptiles (Mitro, 2011); males become mate limited and female fecundity is reduced, generating Allee effects and increasing population extinction risk (Simmons et al., 2010).

For species that live in family groups, female road mortality has been shown to exert indirect, sublethal effects on the recruitment of populations. The death of a mother by vehicle collisions can lead to the death of dependent juveniles, either by starvation (Snow et al., 2012) or infanticide (Logan and Runge, 2020). Vehicle collisions of male or females were responsible for 2.1% of bond dissolution within a grey wolf (C*anis lupus*) population in Scandinavia, which can destabilise social structure and reduce population growth (Milleret et al., 2017). For solitary and territorial species, the impact of male- or female-biased road mortality may be dependent on territory ownership and whether other reproductively viable individuals are able to fill the vacant breeding territories (Mumme et al., 2000; Riley et al., 2006). Overall, studies identified in this review agreed that adult-biased, and specifically female-biased, road mortality are likely to be critical to population dynamics.

2.4.1.3 Roadkill during inter-patch or long-distance movements

Three out of the four studies reporting information on the road mortality of dispersing animals reported relatively high roadkill rates (Kanda, 2005; Pereira et al., 2010; Carvalho et al., 2018). Risk of road mortality during dispersal or extraterritorial excursions has also been shown for some birds (Mumme et al., 2000; Bujoczek, Ciach and Yosef, 2011) and reptiles (Bonnet, Naulleau and Shine, 1999). A suite of Geographical Positioning System (GPS)/radio-tracking data indicate that the risk could be a function of a greater road crossing frequencies during dispersal than during exploratory or routine movements (Grilo et al., 2012; Fey et al., 2016). When road mortality of dispersing animals is high, patch connectivity is limited and gene flow is restricted (Balkenhol and Waits, 2009; Jackson and Fahrig, 2011). In extreme cases, high road mortality for populations in patchy habitat networks may lead to source–sink dynamics, as speculated by Grilo et al. (2012) for a roadside population of beech martens in Portugal. Collevatti et al. (2007) also suggest that the high inbreeding within a giant anteater population in Emas National Park in Brazil may be, at least in part, a result of extensive roadkill between the park and nearby Cerrado fragments, hence decreasing migration and gene flow. Therefore, it remains possible that road mortality may be influencing the dynamics of subpopulations far from roads. However, a high mortality of dispersers does not necessarily lead to subdivision (Carvalho and Mira, 2011), suggesting that in some cases, even a small number of successful dispersers can ensure sufficient gene flow and prevent the development of spatial genetic structuring.

2.4.2 Indirect demographic parameters

Several authors highlighted the vulnerability of growth rates of some, but not all, populations to road mortality in the short term. Changes to growth rates, and hence population persistence, as a result of roadkill may be mediated by lower effective population sizes and/or altered mortality:recruitment ratio. Population persistence may be particularly threatened by roadkill if the (sub)population exhibits site fidelity and/or lives in patchy habitat that may decrease immigration due to increasing patch isolation (Snow et al., 2012). It is possible that under certain conditions, such as areas extensively and/or rapidly modified by humans, individuals select roadside habitats for favourable resource availability. In turn, these populations are subject to ecological trap dynamics following lower survival in roadside habitats (Battin, 2004). These dynamics can shape population structure and sustainability and have previously been reported for Eurasian lynx (*Lynx lynx;* Basille et al., 2013) and several bird species including mourning wheatears (*Oenanthe lugens*; Ben-Aharon, Kapota and Saltz, 2020) and Florida scrub jays (*Aphelocoma coerulescens*; Mumme et al., 2000).

Road mortality may not directly cause local extinctions for all impacted populations, especially if the species-specific habitat quality is high and so populations are relatively resilient to environmental stressors. However, collisions can make populations more vulnerable to environmental and demographic stochasticity, as shown for common wombats (Roger et al., 2011) and giant anteaters (Desbiez et al., 2020). Most animal populations are subject to multiple stressors that operate at various spatial and temporal scales and interact to some degree, either additively or synergistically (Doherty et al., 2015). For example, Roger et al. (2011) showed that intermediate levels of roadkill of common wombat individuals in the Kosciuszko National Park in New South Wales, Australia, caused the population to be more sensitive to variation in juvenile survival and even low roadkill levels increased their vulnerability to fires. For species with slow breeding rates, as is the case for common wombats, populations are less able to offset high mortality rates attributed to roads or other threats. In turn, immigration from the surrounding area will be important for the persistence of these roadside populations (Rytwinski and Fahrig, 2015).

It is possible that road mortality can indirectly impact populations that are otherwise resilient to WVCs by causing the loss of local populations of ecologically functional species, such as apex predators. Trophic cascades and changes to interspecific associations are a well-known result from the decline of key species (Fischer et al., 2012). Road mortality that causes the local extinction of key predator species may incite a mesocarnivore influx, changing ecosystem structure and the vital rates of populations in the wider ecological community (as reported for other mortality causes; Hollings et al., 2014).

2.4.3 Compensatory and additive mechanisms of road mortality

The demographic impacts of road mortality were shown to be highly variable amongst the study species and intra-specific populations identified in this review. This may be a function of the small roadkill sample sizes of several studies retained by the search, which makes the results inherently inconsistent. The variable results also demonstrate that the interplay of roadkill with other context-specific factors, and how that affects the mortality:recruitment ratio, will influence the capacity for populations to persist despite road mortality (Roger et al., 2011). Extrinsic and intrinsic factors can affect whether road mortality is additive to natural mortality, resulting in a net reduction in total survival rates, or is compensated for by a reduction in natural mortality and/or increased reproductive rates (Sparkman, Waits and Murray, 2011). Studies identified in this review report both additive and compensatory mechanisms of road mortality. For example, Burroughs et al. (2006), Tri et al. (2017), and Logan and Runge (2020) found that white-tailed deer, pumas and American black bears had a greater level of road mortality in conditions with lower mortality from other anthropogenic causes (e.g., harvesting, humane lethal control). However, Chambers and Bencini (2010) found both compensatory and additive mechanisms for the road mortality of tammar wallaby populations in Australia, suggesting that road mortality impacts depend on other factors that also affect vital rates. Additive road mortality has also been reported in red wolves (*Canis rufus;* Sparkman et al., 2011) and, in addition to mammals, in several bird species (Bujoczek et al., 2011), spotted salamander (*Ambystoma maculatum*; Gibbs and Shriver, 2005) and turtles (Congdon, Dunham and van Loben Sels, 1994). It is likely that, in many cases, road mortality is neither completely additive nor compensatory. This is because road mortality is, to some extent, influenced by density-dependent mechanisms and its consequences on population dynamics can also depend on which individuals are killed on roads and when (Desbiez et al., 2020). This is corroborated by Lehnert, Bissonette and Haefner (1998) who demonstrated that for a mule deer population in the USA, 50% of all animals killed on the highway would have died from non-road causes before the next breeding season. Nevertheless, mechanisms underlying either compensatory or additive effects of road mortality remain poorly understood and warrant further investigation to improve the accuracy of road mortality assessments.

Of great concern is that rare and threatened species often have (sometimes naturally) small population sizes and/or a population growth rate that is close to zero or negative (Desbiez et al., 2020). As such, even a low but uncompensated road mortality rate can remove a significant percentage of the population, thereby constraining annual survival and inducing or exacerbating population decline (Sparkman et al., 2011). This has important implications for conservation because when road mortality is additive, mitigation efforts around roads are a more pressing requirement than if compensatory mortality is assumed.

2.5 Considerations for road ecology study design

It can be argued that population growth is a fundamental parameter of interest in studies of anthropogenic mortality and quantifying it should be prioritised. Although population size and raw roadkill counts are useful, they are a stationary snapshot and unlike population growth, they do not consider the impact of demographic variability and its role in any compensatory processes (Seiler, 2003).

The methods used and sample sizes collected can drastically alter the conclusions of road mortality impacts. There are typically three methods to obtain roadkill data: (1) systematic road surveys; (2) radio-tracking (and associated telemetry technologies such as GPS and satellite tracking) or constant population monitoring; and (3) opportunistic records (often *via* unstructured citizen science; Appendix II). Radio-tracking tailored to the focal species provides a less-biased sample because most road mortalities are usually detected. However, data from radio-tracking can often only be based on a small sample of individuals due to financial and logistical challenges. Such studies might not be free of bias nor be representative of the wider population depending on the method used for capture (Stenglein et al., 2015), meaning mortality data should also be interpreted cautiously. Roadkill surveys, whether systematic or not, are more targeted and can detect a large proportion, but rarely all, of the roadkill present. However, efficiency of the surveys and carcass detectability can be low depending on survey frequency and carcass size. Non-systematic surveys such as from citizen science participants have additional issues of bias across the survey area depending on the geographic spread of surveyor effort. Moreover, opportunistic records such as *ad hoc* observations from park wardens or tourists could bias the significance of mortality factors because death events are detected differently (Stenglein et al., 2015). For example, Pereira et al. (2010) reported that 18% (seven individuals) of a Geoffroy’s cat (*Leopardus geoffroyi*) population in central Argentina was killed on roads when using opportunistic sampling and ranger interviews to record carcasses, yet only 5% (one individual) of a radio-tracked subset of the same population was killed on roads.

2.5.1 Improving study design

Replicated, manipulative study designs such as BACI are considered the highest standard of study design in road ecology (Rytwinski and Fahrig, 2015). These studies can be used to detect demographic changes, particularly at the genetic level, and to separate confounding factors (Figure

2.5). Of the 83 studies included in this review, seven studies used experimental designs – two studies used Before–After and five used Control–Impact, often comparing urban or high-density road networks to rural or low-density areas. Collecting sufficiently long-term data both pre- and post-road construction, as per BACI protocol, is usually difficult to achieve because many roads have already been built or their construction is imminent at the research conception stage. The majority (72.7%) of studies identified in this review were less than 5 years in duration. The length of a study on road mortality should be species appropriate and cover more than one generation. Longer-term studies can overcome the challenges of small roadkill sample sizes and of quantifying population demographics and their variability, particularly for long-lived species and when combined with individual-based methods such as marking individuals (Desbiez et al., 2020). The large costs associated with long-term, manipulative studies can be shared with collaborative research action (see below; Fraser et al., 2013).

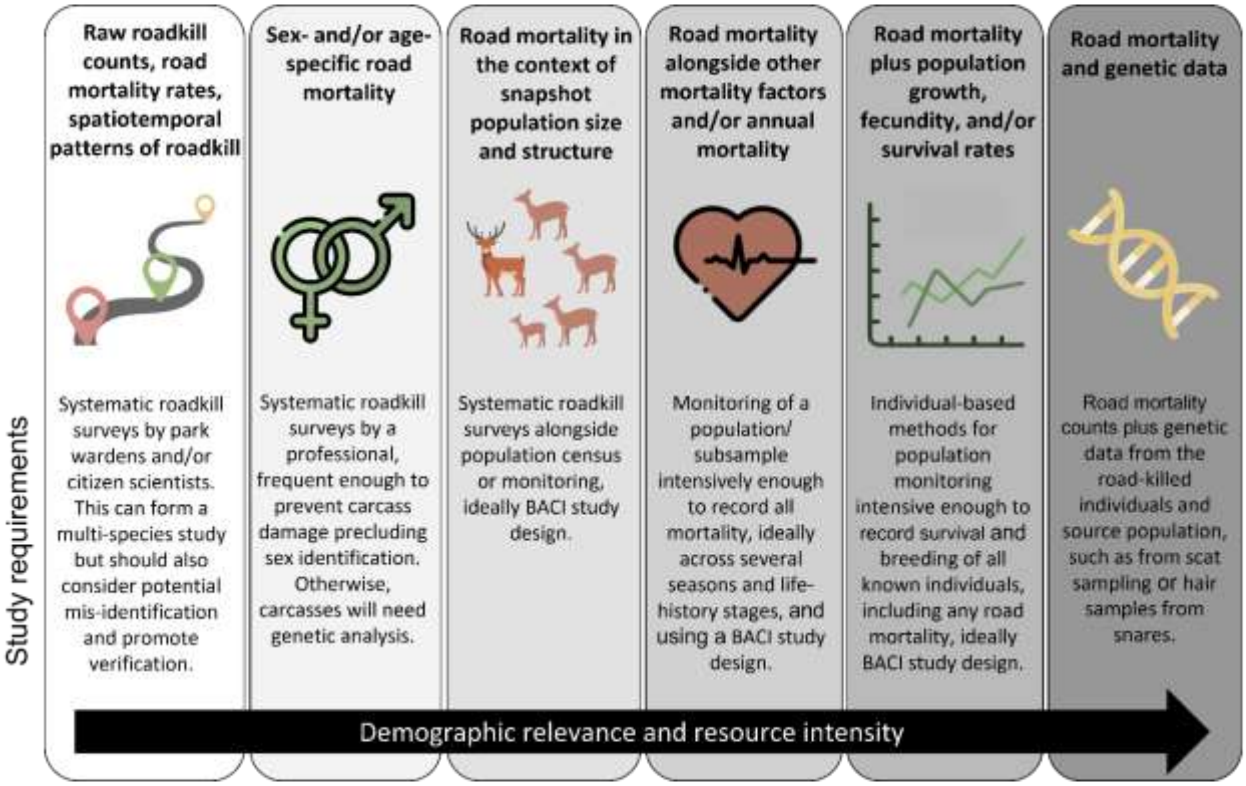


Figure 2.5: Suggested hierarchy and requirements of study designs relevant to examining the impacts of road mortality on population persistence. BACI, Before–After–Control–Impact. Various Artists/Flaticon.com

Genetic studies are a critical component of examining the long-term viability of roadside populations. However, neither of the two retained studies that reported the effects of road mortality on genetic diversity used empirical genetic data (Diniz and Brito, 2013; Desbiez et al., 2020). The development of genotypic approaches (analyses based on the genotypes of individuals) and high-resolution molecular markers (e.g., single nucleotide polymorphisms; SNPs) offer powerful methods to examine fitness-related genetic effects, such as population genetic structure, fragmentation, and diversity (Balkenhol and Waits, 2009; Simmons et al., 2010; Jackson and Fahrig, 2011). For example, genotypic approaches such as genetic pedigree, spatial-autocorrelation and parentage analysis can identify important within-population processes, including demographic history and sex-biased dispersal (e.g., across roads; Balkenhol and Waits, 2009). Such approaches can be informative at fine spatial and temporal scales, can be readily scaled up, are complementary to the other field-based approaches, and are becoming less expensive over time (Corlett, 2017). Moreover, advances in laboratory protocols, such as Polymerase Chain Reaction (PCR) from tissues of road-killed animals, can improve sex identification of badly decomposed or damaged roadkills, or roadkills of monomorphic species (Barragán-Ruiz et al., 2021).

Population viability can depend on the extent and nature of dispersal and immigration between road and non-road habitats (Mumme *et al*., 2000). Therefore, studies that combine radio-tracking data, or radio-frequency identification (RFID) tags and related transponders (Testud et al., 2019), with roadkill data can incorporate explicit assumptions about successful and unsuccessful road crossings (Riley et al., 2006; Fahrig and Rytwinski, 2009). Ultimately, a blend of genetic and field-based approaches with appropriate statistical modelling, as shown by Carvalho et al. (2018), is needed to assemble the suite of relevant data for accurate road mortality assessments (Figure 2.5). Importantly, cost analyses should be integrated into study planning to enable efficient resource allocation for research, and likewise for any subsequent mitigation, in turn improving returns for investment (White et al., 2022). Sharing the monetary costs associated with robust study design will likely require collaborative experimental research at an international scale. Collaborations can pool resources more easily, including expertise, money, and equipment, across several road networks, simultaneously improving the quality of study design and sample sizes (Fraser et al., 2013; Rytwinski and Fahrig, 2015).

2.6 Future research directions

Despite the increasing interest and research focus over recent decades, more detailed road mortality studies are needed to ensure a robust understanding of demographic impacts on mammalian populations and that efforts to reduce such impacts are focussed on the most at-risk populations. The interaction between road mortality and movement behaviours, such as dispersal and migration, remains relatively under-studied. Future research should investigate the replacement rate following the death of a breeder in areas intersected by roads and the success rate of individuals dispersing across roads. Appropriate context will be essential in interpreting these results, considering that road crossings by dispersing subadults do not necessarily translate into gene flow (Riley et al., 2006). How often road mortality contributes to the reduction in genetic integrity and the shape of that decline over time (e.g., linear, exponential) should also receive research attention. To understand a population's capabilities to sustain ongoing road mortality, investigations into whether road mortality is compensated for, even partially, by increased survival, reproduction or migration should be prioritised.

2.7 Conclusion

The conservation of wildlife populations impacted by roads has gained recognition as an issue of worldwide concern. This work found that studies collecting data on the demographic effects of road mortality are relatively rare, but some generalities emerge from the existing literature. The 83 retained studies from the systematic search demonstrate that road mortality can place substantial pressure on population size and/or background mortality rates. Female-biased road mortality appears more frequent than previously recognised in the literature and is likely to be a critical element in negative population trajectories. Due to a common occurrence of adult-biased road mortality, wildlife–vehicle collisions (WVCs) place a heavy toll on species that naturally experience high adult survival. It is evident that the demographic effects of road mortality are not limited to the immediate location or time period of the WVCs. Long-term (meta-)population dynamics and populations far from roads may be affected by lower survival and unsuccessful dispersal inciting source–sink dynamics. However, some populations can tolerate additional mortality and maintain population growth over several years, most likely a result of high reproductive rates. Understanding how road mortality shapes the structure and sustainability of wildlife populations is challenged by the complexity of underlying processes. Road mortality interacts with demographic and environmental variability in populations, causing context-specific responses to road mortality.

This review stresses that conservation strategies that seek to address the impact of roads must collect data on relevant demographic parameters, such as population growth and survival rates, as well as the concurrent threats to the target population(s). Studies that use rigorous study design, ideally with a combination of methods and/or using an experimental design, will hold the greatest inferential strength for assessing population-level impacts of WVCs. Examining the link between road mortality and movement behaviours, as well as additive or compensating mechanisms to road mortality, should be research priorities for more accurate insight into long-term consequences. The knowledge gathered from this review is a step towards sustainable road development and maintenance amidst growing road networks, particularly in megadiverse and developing countries that hold some of the world's most threatened species and last remaining wilderness areas. Moving forward, quantifying the demographic impacts of road mortality should become an established process within comprehensive road mortality assessments and the planning of impact mitigation. Crucially, this will enable proactive conservation action of populations at risk.

2.8 References

Amano, T., Berdejo-Espinola, V., Christie, A. P., Willott, K., Akasaka, M., Báldi, A., … Sutherland, W. J. (2021). Tapping into non-English-language science for the conservation of global biodiversity. *PLOS Biology, 19*(10), e3001296. https://doi.org/10.1371/journal.pbio.3001296

Aresco, M. J. (2005). The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. *Biological Conservation, 123*(1), 37–44. https://doi.org/10.1016/j.biocon.2004.10.006

Arso Civil, M., Cheney, B., Quick, N. J., Islas-Villanueva, V., Graves, J. A., Janik, V. M., … Hammond, P. S. (2019). Variations in age- and sex-specific survival rates help explain population trend in a discrete marine mammal population. *Ecology and Evolution, 9*(1), 533–544. https://doi.org/10.1002/ECE3.4772

Balkenhol, N., & Waits, L. P. (2009). Molecular road ecology: Exploring the potential of genetics for investigating transportation impacts on wildlife. *Molecular Ecology, 18*(20), 4151–4164. https://doi.org/10.1111/j.1365-294X.2009.04322.x

Barragán-Ruiz, C. E., Paviotti-Fischer, E., Rodríguez-Castro, K. G., Desbiez, A. L. J., & Galetti, P. M. (2021). Molecular sexing of Xenarthra: a tool for genetic and ecological studies. *Conservation Genetics Resources, 13*(1), 41–45. https://doi.org/10.1007/s12686-020-01168-2

Barrientos, R., Ascensão, F., D'Amico, M., Grilo, C., & Pereira, H. M. (2021). The lost road: Do transportation networks imperil wildlife population persistence? *Perspectives in Ecology and Conservation, 19*(4), 411–416. https://doi.org/10.1016/J.PECON.2021.07.004

Basille, M., van Moorter, B., Herfindal, I., Martin, J., Linnell, J. D. C., Odden, J., … Gaillard, J. M. (2013). Selecting habitat to survive: the impact of road density on survival in a large carnivore. *PLOS ONE*, *8*(7), e65493. https://doi.org/10.1371/JOURNAL.PONE.0065493

Belant, J. L. (2007). Human-caused mortality and population trends of American marten and fisher in a U.S. national park. *Natural Areas Journal*, *27*(2), 155–160. https://doi.org/10.3375/0885-8608(2007)27[155:HMAPTO]2.0.CO;2

Ben-Aharon, N., Kapota, D., & Saltz, D. (2020). Roads and road-posts as an ecological trap for cavity nesting desert birds. *Frontiers in Conservation Science*, *1*, 614899. https://doi.org/10.3389/fcosc.2020.614899

Bonnet, X., Naulleau, G., & Shine, R. (1999). The dangers of leaving home: Dispersal and mortality in snakes. *Biological Conservation*, *89*(1), 39–50. https://doi.org/10.1016/S0006-3207(98)00140-2

Borda-de-Água, L., Grilo, C., & Pereira, H. M. (2014). Modeling the impact of road mortality on barn owl (Tyto alba) populations using age-structured models. *Ecological Modelling*, *276*, 29–37. https://doi.org/10.1016/j.ecolmodel.2013.12.022

Bujoczek, M., Ciach, M., & Yosef, R. (2011). Road-kills affect avian population quality. *Biological Conservation*, *144*(3), 1036–1039. https://doi.org/10.1016/J.BIOCON.2010.12.022

Burroughs, J. P., Campa, H., Winterstein, S. R., Rudolph, B. A., & Moritz, W. E. (2006). Cause-specific mortality and survival of white-tailed deer fawns in southwestern lower Michigan. *Journal of Wildlife Management*, *70*(3), 743–751. https://doi.org/10.2193/0022-541X(2006)70[743:CMASOW]2.0.CO;2

Carvalho, F., Lourenço, A., Carvalho, R., Alves, P. C., Mira, A., & Beja, P. (2018). The effects of a motorway on movement behaviour and gene flow in a forest carnivore: Joint evidence from road mortality, radio tracking and genetics. *Landscape and Urban Planning*, *178*, 217–227. https://doi.org/10.1016/j.landurbplan.2018.06.007

Carvalho, F., & Mira, A. (2011). Comparing annual vertebrate road kills over two time periods, 9 years apart: a case study in Mediterranean farmland. *European Journal of Wildlife Research*, *57*(1), 157–174. https://doi.org/10.1007/s10344-010-0410-0

Ceia-Hasse, A., Navarro, L. M., Borda-de-Água, L., & Pereira, H. M. (2018). Population persistence in landscapes fragmented by roads: Disentangling isolation, mortality, and the effect of dispersal. *Ecological Modelling*, *375*, 45–53. https://doi.org/10.1016/j.ecolmodel.2018.01.021

Chambers, B., & Bencini, R. (2010). Road mortality reduces survival and population growth rates of tammar wallabies on Garden Island, Western Australia. *Wildlife Research*, *37*(7), 588–596. https://doi.org/10.1071/WR10080

Chambers, B. K. (2009). *Human disturbance affects the ecology and population dynamics of the tammar wallaby, Macropus eugenii, on Garden Island, Western Australia*. [PhD Thesis, University of Western Australia].

Coe, P. K., Nielson, R. M., Jackson, D. H., Cupples, J. B., Seidel, N. E., Johnson, B. K., Gregory, … Speten, D. A. (2015). Identifying migration corridors of mule deer threatened by highway development. *Wildlife Society Bulletin*, *39*(2), 256–267. https://doi.org/10.1002/wsb.544

Collevatti, R. G., Leite, K. C. E., de Miranda, G. H. B., & Rodrigues, F. H. G. (2007). Evidence of high inbreeding in a population of the endangered giant anteater, *Myrmecophaga tridactyla* (Myrmecophagidae), from Emas National Park, Brazil. *Genetics and Molecular Biology*, *30*(1), 112–120. https://doi.org/10.1590/S1415-47572007000100020

Congdon, J., Dunham, A., & van Loben Sels, R. (1994). Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. *American Zoologist*, *34*(3), 397–408. https://doi.org/10.1093/icb/34.3.397

Corlett, R. T. (2017). A bigger toolbox: Biotechnology in biodiversity conservation. *Trends in Biotechnology*, *35*(1), 55–65. https://doi.org/10.1016/J.TIBTECH.2016.06.009

Cypher, B. L., Bjurlin, C. D., & Nelson, J. L. (2009). Effects of roads on endangered San Joaquin kit foxes. *Journal of Wildlife Management*, *73*(6), 885–893. https://doi.org/10.2193/2007-576

Desbiez, A. L. J., Bertassoni, A., & Traylor-Holzer, K. (2020). Population viability analysis as a tool for giant anteater conservation. *Perspectives in Ecology and Conservation*, *18*(2), 124–131. https://doi.org/10.1016/j.pecon.2020.04.004

Diniz, M. F., & Brito, D. (2013). Threats to and viability of the giant anteater, *Myrmecophaga tridactyla* (Pilosa: Myrmecophagidae), in a protected Cerrado remnant encroached by urban expansion in central Brazil. *Zoologia (Curitiba)*, *30*(2), 151–156. https://doi.org/10.1590/S1984-46702013000200005

Doherty, T. S., Dickman, C. R., Nimmo, D. G., & Ritchie, E. G. (2015). Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. *Biological Conservation*, *190*, 60–68. https://doi.org/10.1016/j.biocon.2015.05.013

Dulac, J. (2013). *Global land transport infrastructure requirements. Estimating road and railway infrastructure capacity and costs to 2050.* International Energy Agency. Retrieved from https://www.iea.org/reports/global-land-transport-infrastructure-requirements

Fahrig, L., & Rytwinski, T. (2009). Effects of roads on animal abundance: An empirical review and synthesis. *Ecology and Society*, *14*(1). https://doi.org/10.5751/ES-02815-140121

Fey, K., Hämäläinen, S., & Selonen, V. (2016). Roads are no barrier for dispersing red squirrels in an urban environment. *Behavioral Ecology*, *27*(3), 741–747. https://doi.org/10.1093/beheco/arv215

Fischer, J. D., Cleeton, S. H., Lyons, T. P., & Miller, J. R. (2012). Urbanization and the predation paradox: The role of trophic dynamics in structuring vertebrate communities. *BioScience*, *62*(9), 809–818. https://doi.org/10.1525/bio.2012.62.9.6

Frair, J. L., Merrill, E. H., Allen, J. R., & Boyce, M. S. (2007). Know thy enemy: experience affects elk translocation success in risky landscapes. *Journal of Wildlife Management*, *71*(2), 541–554. https://doi.org/10.2193/2006-141

Fraser, L. H., Henry, H. al, Carlyle, C. N., White, S. R., Beierkuhnlein, C., Cahill, J. F., … Turkington, R. (2013). Coordinated distributed experiments: an emerging tool for testing global hypotheses in ecology and environmental science. *Frontiers in Ecology and the Environment*, *11*(3), 147–155. https://doi.org/10.1890/110279

Galantinho, A., Santos, S., Eufrázio, S., Silva, C., Carvalho, F., Alpizar-Jara, R., & Mira, A. (2022). Effects of roads on small-mammal movements: Opportunities and risks of vegetation management on roadsides. *Journal of Environmental Management*, *316*. https://doi.org/10.1016/j.jenvman.2022.115272

Gibbs, J. P., & Shriver, W. G. (2005). Can road mortality limit populations of pool-breeding amphibians? *Wetlands Ecology and Management*, *13*(3), 281–289. https://doi.org/10.1007/s11273-004-7522-9

Green-Barber, J. M., & Old, J. M. (2019). What influences road mortality rates of eastern grey kangaroos in a semi-rural area? *BMC Zoology*, *4*(11), 1–10. https://doi.org/10.1186/s40850-019-0047-8

Grilo, C., Borda-de-Água, L., Beja, P., Goolsby, E., Soanes, K., le Roux, A., Koroleva, E., Ferreira, F. Z., Gagné, S. A., Wang, Y., & González-Suárez, M. (2021). Conservation threats from roadkill in the global road network. *Global Ecology and Biogeography*, *30*(11), 2200–2210. https://doi.org/10.1111/GEB.13375

Grilo, C., Sousa, J., Ascensão, F., Matos, H., Leitão, I., Pinheiro, P., Costa, M., Bernardo, J., Reto, D., Lourenço, R., Santos-Reis, M., & Revilla, E. (2012). Individual spatial responses towards roads: implications for mortality risk. *PLOS ONE*, *7*(9), 1–11. https://doi.org/10.1371/journal.pone.0043811

Grueber, C. E., Reid-Wainscoat, E. E., Fox, S., Belov, K., Shier, D. M., Hogg, C. J., & Pemberton, D. (2017). Increasing generations in captivity is associated with increased vulnerability of Tasmanian devils to vehicle strike following release to the wild. *Scientific Reports*, *7*(1). https://doi.org/10.1038/s41598-017-02273-3

Haddaway, N. R., Collins, A. M., Coughlin, D., & Kirk, S. (2015). The role of Google Scholar in evidence reviews and its applicability to grey literature searching. *PLOS ONE*, *10*(9), e0138237. https://doi.org/10.1371/journal.pone.0138237

Hill, J. E., DeVault, T. L., & Belant, J. L. (2019). Cause-specific mortality of the world's terrestrial vertebrates. *Global Ecology and Biogeography*, *28*(5), 680–689. https://doi.org/10.1111/geb.12881

Hollings, T., Jones, M., Mooney, N., & Mccallum, H. (2014). Trophic cascades following the disease-induced decline of an apex predator, the Tasmanian Devil. *Conservation Biology*, *28*(1), 63–75. https://doi.org/10.1111/cobi.12152

Huijser, M. P., Duffield, J. W., Clevenger, A. P., Ament, R. J., & McGowen, P. T. (2009). Cost-benefit analyses of mitigation measures aimed at reducing collisions with large ungulates in the United States and Canada: A decision support tool. *Ecology and Society*, *14*(2). http://www.ecologyandsociety.org/vol14/iss2/art15/

Ibisch, P. L., Hoffmann, M. T., Kreft, S., Pe'Er, G., Kati, V., Biber-Freudenberger, L., … Selva, N. (2016). A global map of roadless areas and their conservation status. *Science*, *354*(6318), 1423–1427. https://doi.org/10.1126/science.aaf7166

IUCN. (2020). *IUCN Red List 2017-2020 Report*. Retrieved from https://nc.iucnredlist.org/redlist/resources/files/1630480997-iucn_red_list_quadrennial_report_2017-2020.pdf

IUCN. (2021). *IUCN Red List of Threatened Species*. Retrieved from https://www.iucnredlist.org/

Jackson, N. D., & Fahrig, L. (2011). Relative effects of road mortality and decreased connectivity on population genetic diversity. *Biological Conservation*, *144*(12), 3143–3148. https://doi.org/10.1016/j.biocon.2011.09.010

Jaeger, J. A. G., & Fahrig, L. (2001). Modeling the effects of road networks patterns on population persistence: relative importance of traffic mortality and 'fence effect'. In *Proceedings of the 2001 International Conference on Ecology and Transportation*, 24 – 29 September 2001, North Carolina State University (pp. 298 – 312). USA : Colorado.

Kanda. (2005). *Factors influencing survival and reproduction of Virginia opossums (Didelphis virginiana) at their northern distributional limit.* [PhD Thesis, University of Massachusetts Amherst].

Kautz, T. M., Fowler, N. L., Petroelje, T. R., Beyer, D. E., Svoboda, N. J., & Belant, J. L. (2021). Large carnivore response to human road use suggests a landscape of coexistence. *Global Ecology and Conservation*, *30*, e01772. https://doi.org/10.1016/J.GECCO.2021.E01772

Klöcker, U., Croft, D. B., & Ramp, D. (2006). Frequency and causes of kangaroo-vehicle collisions on an Australian outback highway. *Wildlife Research*, *33*(1), 5–15. https://doi.org/10.1071/WR04066

Krebs, C. J. (2009). *Ecology: The Experimental Analysis of Distribution and Abundance* (6th ed.). London : Pearson.

Landis, J. R., & Koch, G. G. (1977). The measurement of observer agreement for categorical data. *Biometrics*, *33*(1), 159. https://doi.org/10.2307/2529310

Lehnert, M. E., Bissonette, J. A., & Haefner, J. W. (1998). Deer (Cervidae) highway mortality: using models to tailor mitigative efforts. In *Proceedings of the XXIIIrd Congress of the International Union of Game Biologists*, Office National de la Chasse (pp 835–841). France : Paris.

Lehrer, E. W., Schooley, R. L., & Whittington, J. K. (2012). Survival and antipredator behavior of woodchucks (*Marmota monax*) along an urban-agricultural gradient. *Canadian Journal of Zoology*, *90*(1), 12–21. https://doi.org/10.1139/Z11-107

Logan, K. A., & Runge, J. P. (2020). Effects of Hunting on a Puma Population in Colorado. *Wildlife Monographs*, *209*(1), 1–35. https://doi.org/10.1002/wmon.1061

McCleery, R. A., Lopez, R. R., Silvy, N. J., & Gallant, D. L. (2008). Fox squirrel survival in urban and rural environments. *Journal of Wildlife Management*, *72*(1), 133–137. https://doi.org/10.2193/2007-138

McHugh, M. L. (2012). Interrater reliability: the kappa statistic. *Biochemia Medica*, *22*(3), 276. https://doi.org/10.11613/bm.2012.031

Meijer, J. R., Huijbregts, M. A. J., Schotten, K. C. G. J., & Schipper, A. M. (2018). Global patterns of current and future road infrastructure. *Environmental Research Letters*, *13*(6), 064006. https://doi.org/10.1088/1748-9326/aabd42

Milleret, C., Wabakken, P., Liberg, O., Åkesson, M., Flagstad, Ø., Andreassen, H. P., & Sand, H. (2017). Let’s stay together? Intrinsic and extrinsic factors involved in pair bond dissolution in a recolonizing wolf population. *Journal of Animal Ecology*, *86*(1), 43–54. https://doi.org/10.1111/1365-2656.12587

Miotto, R. A., Cervini, M., Begotti, R. A., & Galetti, P. M. (2012). Monitoring a puma (*Puma concolor*) population in a fragmented landscape in southeast Brazil. *Biotropica*, *44*(1), 98–104. https://doi.org/10.1111/J.1744-7429.2011.00772.X

Mitro, M. G. (2011). Demography and viability analyses of a diamondback terrapin population. *Canadian Journal of Zoology*, *81*(4), 716–726. https://doi.org/10.1139/Z03-045

Mumme, R. L., Schoech, S. J., Woolfenden, G. E., & Fitzpatrick, J. W. (2000). Life and death in the fast lane: demographic consequences of road mortality in the Florida Scrub-Jay. *Conservation Biology*, *14*(2), 501–512. https://doi.org/10.1046/j.1523-1739.2000.98370

Nuñez, M. A., & Amano, T. (2021). Monolingual searches can limit and bias results in global literature reviews. *Nature Ecology and Evolution*, *5*(3), 264. https://doi.org/10.1038/S41559-020-01369-W

Nyirenda, V. R., Namukonde, N., & Fushike, P. (2017). Road kills of wild vertebrates in Kafue National Park, Zambia, between January 2008 and December 2012. *African Journal of Ecology*, *55*(4), 738–741. https://doi.org/10.1111/aje.12388

Pereira, J. A., Fracassi, N. G., Rago, V., Ferreyra, H., Marull, C. A., McAloose, D., & Uhart, M. M. (2010). Causes of mortality in a Geoffroy’s cat population - a long-term survey using diverse recording methods. *European Journal of Wildlife Research*, *56*(6), 939–942. https://doi.org/10.1007/s10344-010-0423-8

Pullin, A. S., & Stewart, G. B. (2006). Guidelines for systematic review in conservation and environmental management. *Conservation Biology*, *20*(6), 1647–1656. https://doi.org/10.1111/j.1523-1739.2006.00485.x

Ramp, D., & Ben-Ami, D. (2006). The effect of road-based fatalities on the viability of a peri-urban Swamp Wallaby population. *The Journal of Wildlife Management*, *70*(6), 1615–1624. https://doi.org/10.2193/0022-541X(2006)70[1615:TEORFO]2.0.CO;2

Riley, S. P. D., Pollinger, J. P., Sauvajot, R. M., York, E. C., Bromley, C., Fuller, T. K., & Wayne, R. K. (2006). A southern California freeway is a physical and social barrier to gene flow in carnivores. *Molecular Ecology*, *15*(7), 1733–1741. https://doi.org/10.1111/j.1365-294X.2006.02907.x

Roedenbeck, I. A., Fahrig, L., Findlay, C. S., Houlahan, J. E., Jaeger, J. A. G., Klar, N., … van der Grift, E. A. (2007). The Rauischholzhausen agenda for road ecology. *Ecology and Society*, *12*(1). http://www.ecologyandsociety.org/vol12/iss1/art11/

Roger, E., Laffan, S. W., & Ramp, D. (2011). Road impacts a tipping point for wildlife populations in threatened landscapes. *Population Ecology*, *53*(1), 215–227. https://doi.org/10.1007/s10144-010-0209-6

Row, J. R., Blouin-Demers, G., & Weatherhead, P. J. (2007). Demographic effects of road mortality in black ratsnakes (*Elaphe obsoleta*). *Biological Conservation*, *137*(1), 117–124. https://doi.org/10.1016/j.biocon.2007.01.020

Ruiz-Capillas, P., Mata, C., & Malo, J. E. (2015). How many rodents die on the road? Biological and methodological implications from a small mammals' roadkill assessment on a Spanish motorway. *Ecological Research*, *30*(3), 417–427. https://doi.org/10.1007/s11284-014-1235-1

Rytwinski, T., & Fahrig, L. (2015). The impacts of roads and traffic on terrestrial animal populations. In R. van der Ree, D. J. Smith, and C. Grilo (Eds.), *Handbook of Road Ecology* (pp. 237–246). New York : John Wiley & Sons Ltd.

Santos, R. A. L., Santos, S. M., Santos-Reis, M., Picanço de Figueiredo, A., Bager, A., Aguiar, L. M. S., & Ascensão, F. (2016). Carcass persistence and detectability: Reducing the uncertainty surrounding wildlife-vehicle collision surveys. *PLOS ONE*, *11*(11), e0165608. https://doi.org/10.1371/journal.pone.0165608

Schafer, A., & Victor, D. G. (2000). The future mobility of the world population. *Transportation Research Part A: Policy and Practice*, *34*(3), 171–205. https://doi.org/10.1016/S0965-8564(98)00071-8

Seiler, A. (2003). *The toll of the automobile: Wildlife and roads in Sweden.* [PhD Thesis, Swedish University of Agricultural Sciences].

Serieys, L. E. K., Rogan, M. S., Matsushima, S. S., & Wilmers, C. C. (2021). Road-crossings, vegetative cover, land use and poisons interact to influence corridor effectiveness. *Biological Conservation*, *253*. https://doi.org/10.1016/j.biocon.2020.108930

Sidorovich, A. A., Novitsky, R. v., & Solovej, I. A. (2020). Road mortality of carnivores (Mammalia, carnivora) in Belarus. *Zoodiversity*, *54*(3), 211–220. https://doi.org/10.15407/zoo2020.03.211

Simek, S., Jonker, S., Schieck, B., Endries, M., & Eason, T. (2005). *Statewide assessment of road impacts on bears in six study areas in Florida.* Florida Fish and Wildlife Conservation Commission. Retrieved from https://www.worldcat.org/title/874911074

Simmons, J. M., Sunnucks, P., Taylor, A. C., & van der Ree, R. (2010). Beyond roadkill, radiotracking, recapture and Fst-a review of some genetic methods to improve understanding of the influence of roads on wildlife. *Ecology and Society*, *15*(1). https://doi.org/10.5751/ES-03162-150109

Snow, N. P., Andelt, W. F., Stanley, T. R., Resnik, J. R., & Munson, L. (2012). Effects of roads on survival of San Clemente Island foxes. *Journal of Wildlife Management*, *76*(2), 243–252. https://doi.org/10.1002/jwmg.247

Sparkman, A. M., Waits, L. P., & Murray, D. L. (2011). Social and demographic effects of anthropogenic mortality: a test of the compensatory mortality hypothesis in the Red Wolf. *PLOS ONE*, *6*(6), e20868. https://doi.org/10.1371/journal.pone.0020868

Stenglein, J. L., van Deelen, T. R., Wydeven, A. P., Mladenoff, D. J., Wiedenhoeft, J. E., Businga, … Heisey, D. M. (2015). Mortality patterns and detection bias from carcass data: An example from wolf recovery in Wisconsin. *Journal of Wildlife Management*, *79*(7), 1173–1184. https://doi.org/10.1002/jwmg.922

Stevenson, E. R., Colter Chitwood, M., Lashley, M. A., Pollock, K. H., Swingen, M. B., Moorman, C. E., & DePerno, C. S. (2016). Survival and cause-specific mortality of coyotes on a large military installation. *Southeastern Naturalist*, *15*(3), 459–466. https://doi.org/10.1656/058.015.0307

Sweitzer, R. A., Popescu, V. D., Thompson, C. M., Purcell, K. L., Barrett, R. H., Wengert, G. M., … Woods, L. W. (2016). Mortality risks and limits to population growth of fishers. *Journal of Wildlife Management*, *80*(3), 438–451. https://doi.org/10.1002/jwmg.1020

Testud, G., Vergnes, A., Cordier, P., Labarraque, D., & Miaud, C. (2019). Automatic detection of small PIT-tagged animals using wildlife crossings. *Animal Biotelemetry*, *7*(1), 21. https://doi.org/10.1186/s40317-019-0183-5

Tri, A. N., Edwards, J. W., Ryan, C. W., Carpenter, C. P., Carr, P. C., Ternent, M. A., … Petty, J. T. (2017). Harvest rates and cause-specific mortality of American black bears in the wildland–urban interface of the Mid-Atlantic region, USA. *Ursus*, *28*(2), 195–207. https://doi.org/10.2192/ursu-d-16-00033.1

White, T. B., Petrovan, S. O., Christie, A. P., Martin, P. A., & Sutherland, W. J. (2022). What is the price of conservation? A review of the status quo and recommendations for improving cost reporting. *BioScience*, *72*(5), 461–471. https://doi.org/10.1093/biosci/biac007

Wright, C. A., Adams, I. T., Stent, P., & Ford, A. T. (2020). Comparing survival and movements of non-urban and urban translocated mule deer. *The Journal of Wildlife Management*, *84*(8), 1457–1472. https://doi.org/10.1002/jwmg.21935

Appendices I – II

Appendix I: Search strings of the five languages used in the systematic literature search.

Brazilian Portuguese	English	French	Spanish	Portuguese
Matança na estrada	Roadkill	Animaux morts sur la route	Animal atropellado	Estrada da morte / Acidente rodoviário
Mortalidade	Mortality/ mortalities	Mortalité	Mortalidad	Mortalidade
Fatalidade	Fatality/fatalities	Fatalité	Fatalidad	Fatalidade
Greve	Strike	Frappe	Ataque / golpe	Pancada
Colisão	Collision	Collision	Colisión	Colisão
Antropogênico	Anthropogenic	Anthropique	Antropogénico	Antropogénico
Veículo	Vehicle	Véhicule/transporte	Vehículo	Veículo
Estrada	Road	Route	Carretera	Estrada
Rodovia	Highway	Autoroute	Carretera	Auto-estrada
Tráfego	Traffic	Trafic	Tráfico	Trânsito
Autoestrada/ autopista	Motorway	Autoroute	Autopista/estrada	Auto-estrada/ autopista
Autoestrada	Freeway	Autoroute	Autopista	Auto-estrada
Via expressa	Expressway	Voie express	Autopista	Via expressa
Sobrevivência	Survival	Survie	Supervivencia	Sobrevivência
População	Population	Population	Población	População
Viabilidade	Viability	Viabilité	Viabilidad	Viabilidade
Ameaça	Threat	Menace	Amenaza	Perigo
Declínio	Decline	Déclin/régression	Descenso/ disminución	Declínio
Extinção	Extinction	L’extinction	Extinción	Extinção
Extirpação	Extirpation	L’extirpation	Extirpación	Extirpação
Esgotamento	Depletion	Epuisement	Agotamiento	Exaustão
Dispersão	Dispersal	Dispersion	Dispersión	Dispersão
Movimento	Movement	Mouvement	Movimiento	Movimento
Migrando	Migrating	Migration de / migrer	Migrando	Migrando
Migração	Migration	Migration	Migração / migración	Migração
Genético	Genetics	Génétique	Genético	Genético
Navio / embarcação	Vessel	Navire / bateau/vaisseau	Buque / embarcación	Navio / embarcação
Barco	Boat	Bateau	Barco / bote	Barco

Appendix II: Suggested advantages and disadvantages of various study designs identified in the systematic review in relation to their ability to collect data relevant for interpretating population-level impacts of road mortality.

Method	Advantages	Disadvantages	Sensitivity of method (probability of detecting carcass if present)	References
Radio tracking only (and associated telemetry technologies such as GPS* and satellite tracking)	• Detailed information to provide context to road mortality, including survival rates, cause-specific mortality, reproduction, movements (including inter-patch or dispersal movements), and behaviour of individuals and groups. • No bias to the significance of mortality causes as all causes are detected equally. • Suitable for individual recognition and monitoring of individuals without unique marks or colouration. • Can be used in remote areas. • Relatively long life of tracking equipment. • Different equipment is available to suit study design and objectives, such as satellite tracking, GPS tracking, VHF‡ tracking.	• High initial costs (but equipment generally has long life span). • Due to high initial costs, often applied to a small sample of individuals. • High labour and time requirements (although less so for GPS and satellite tracking). • GPS collars/tags are of limited use for small mammals because of collar weight or the inability to produce a recordable signal, although technology continues to advance.	High sensitivity	Tri et al., 2017 ; Benson et al., 2020 ; Serieys et al., 2021
Year-round population monitoring	• Detailed information to provide context to road mortality, including survival rates, cause-specific mortality, reproduction, movements (including inter-patch or dispersal movements), and behaviour of individuals and groups. • Details on individuals and the whole population, rather than a small subsample of the population.	• Can require intensive survey effort and logistics. • Likely restricted to smaller areas due to survey effort needed. • Requires standardisation for robust data collection.	High sensitivity	Arlet et al., 2021 ; Lenting et al., 2019

Radio-tracking and year-round population monitoring	• Detailed information to provide context to road mortality, including survival rates, cause-specific mortality, reproduction, movements (including inter-patch or dispersal movements), and behaviour of individuals and groups. • Comprehensive knowledge on a sub-sample of individuals can give further insight into trends observed in the wider population.	• Different biases in the detection of mortality causes between radio-tracking and year-round monitoring need to be considered when interpreting data. • High labour and time requirements due to intensive survey effort and logistics. • High initial costs for radio-telemetry equipment.	High sensitivity	Snow et al., 2012 ; Pereira et al., 2020
Systematic roadkill surveys and one-time population estimate (capture, mark–recapture/resight, counts along transects or variable plots, genetic data from, for example, hair snares)	• Systematic surveys can detect a large proportion of the roadkill present, increasing accuracy of records compared to opportunistic records. • Population size is context for road mortality rates allowing estimation of proportion of population killed on roads annually.	• Populations can fluctuate over time, therefore comparing road mortality with a single population size estimate provides a snapshot only. • Systematic roadkill surveys can have low searcher efficiency and carcass detectability, especially for small sized carcasses. • Intensive survey effort needed to cover large areas.	Medium sensitivity	Simek et al., 2005 ; Ruiz-Capillas et al., 2015
Systematic roadkill surveys and radio tracking	• Systematic surveys can detect a substantial proportion of the roadkill present, increasing accuracy of records compared to opportunistic records. • Combining these methods provides extensive population context to the road mortality figures, such as cause-specific mortality and reproduction. • No bias to the significance of mortality causes as all causes are detected equally. • Good for validation between the methods for a comprehensive data set.	• Costly. • High labour and time requirements. • Sample sizes of radio-tracked individuals are often small, therefore roadkill may be found of untracked individuals with limited background information (e.g., age, road crossing movements).	High sensitivity	Carvalho et al., 2018

Systematic roadkill surveys and population monitoring	• Systematic surveys can detect a substantial proportion of the roadkill present, increasing accuracy of records compared to opportunistic records. • Combining these methods provides extensive population context to road mortality figures, such as cause-specific mortality and reproduction. • Likely to have known identity or background information for road-killed individuals. • Good for validation between methods for a comprehensive data set.	• Can require intensive survey effort and logistics. • Likely restricted to smaller areas due to survey effort needed.	High sensitivity	Nyirenda et al., 2017
Systematic roadkill surveys and secondary population data	• Systematic surveys can detect a large proportion of the roadkill present, increasing accuracy of records compared to opportunistic records. • Can collect data on roadkill of multiple species simultaneously if secondary data are available for context. • Cheaper and quicker than collecting primary data.	• Systematic roadkill surveys can have low searcher efficiency and carcass detectability, especially for small-sized carcasses. • Secondary population data are not always available for the same time period as the roadkill surveys, leading to a potential mis-match in information. • No control over the quality of secondary population data.	Medium sensitivity	Seiler, 2003 ; Balčiauskas, 2012 ; Roger et al., 2012
Systematic roadkill surveys, radio tracking and population estimate	• Likely to record virtually all roadkill present. • Detailed information to provide context to road mortality, including survival rates, cause-specific mortality, reproduction, movements (including inter-patch or dispersal movements), and behaviour of individuals and groups. • Suitable for individual recognition and monitoring of individuals without unique marks or colouration.	• Costly. • High labour and time requirements.	Very high sensitivity	van Manen *et al.*, 2012

Simulations using real data (e.g., Population Viability Analyses, sensitivity analyses)	• Can assess conservation priorities by forecasting stochastic and deterministic processes governing population growth rates. • Can direct decision-making by comparing a range of alternative management strategies (note that simulations provide better relative than absolute results). • Uncertainties and natural variabilities in a population can be incorporated into models.	• The accuracy of the results relies on a large amount of high-quality data. • The required data and/or a good level of understanding of the focal species is rarely available. • Relative certainty in the results is restricted to a few time intervals only as errors are magnified with each time step. • Many models remain unvalidated.	n/a	Burgman and Possingham 2010
Opportunistic records of road mortality, often by citizen science, rescue centres, wildlife hospitals, *ad hoc* observations by park wardens or tourists.†	• Large amounts of data can be collected. • Can collect data on roadkill of multiple species simultaneously. • Long-term and geographically widespread data can be collected. • Depending on target species, can be undertaken with limited capacity or training.	• Unsystematic roadkill surveys often have low searcher efficiency, carcass detectability, especially for small-sized carcasses, and potential recorder inaccuracies. • Tendency to report charismatic and easily identifiable species more than professional surveys. • Spatial auto-correlation due to potential bias in geographical spread of surveyor effort (i.e. unknown, variable, and unbalanced sampling effort). • Raw roadkill figures only, without population context to aid interpretation.	Low sensitivity	Balčiauskas, 2020 ; Valerio et al., 2021

†These methods were not included in the review due to the potential limitations detailed above but are included here for completeness.

Additional supporting information on the key data collated from the final set of articles identified in the systematic search may be found online at https://doi.org/10.1111/brv.12942 in the Supporting Information section.

CHAPTER 3: Optimising the Study of Multi-Species Road Mortality Rates and Investigating Spatio-Temporal Patterns of Wildlife-Vehicle Collisions

3.1 Introduction

Wildlife-vehicle collisions (WVCs), estimated to kill millions of animals worldwide every year, are of growing ecological, ethical, and socio-economic concern through damage to vehicles and human fatalities (Seiler and Helldin, 2006; Baxter-Gilbert et al., 2015). Coupled with an expected >50% increase in global road length between 2010 and 2050, managing WVCs has become an important step in conservation and landscape planning (Dulac, 2013; Meijer et al., 2018). As road management can be logistically difficult and expensive, achieving reductions in subject WVCs requires evidence-based prioritisation of the road segments with the greatest amount of roadkill. This, in turn, requires sound estimates of road mortality rates (Santos et al., 2016). However, the detection and quantification of road mortality is hampered by a number of substantial difficulties such as, amongst others, factoring in the rate of carcass decomposition and appropriate road survey frequency (Henry et al., 2021). In other words, it is possible that many carcasses are missed on roadkill surveys. Several authors report a 2 to 39-fold underestimation of the true road mortality when influential factors are not corrected for (Santos et al., 2016; Barrientos et al., 2018; Henry et al., 2021). Only recently have concerns over the influence of these difficulties been raised, and the severity and direction of different factors influencing the accuracy of survey data remain understudied. Due to this, many roadkill studies do not correct for these potentially influential factors (e.g., Canal et al. 2018; Akrim et al. 2019), for example with mathematical corrections, whilst others use secondary correction factors from studies in different locations (e.g., González-Suárez et al. 2018; Tejera et al. 2018). The potential inaccuracies in road mortality rate estimations risk spurious conclusions about the population impacts, as well as the required scale, urgency, and subsequent effectiveness of implemented conservation actions.

Among the factors that influence the accuracy of road mortality estimates, carcass detectability (the probability of a carcass being detected by an observer if present during a survey) and carcass persistence rates (the time a carcass remains on the road and identifiable) have been considered the most important factors (Santos, Carvalho and Mira, 2011; Ratton, Secco and da Rosa, 2014; Barrientos et al., 2018). Carcass detectability can be affected by the experience of the observer, survey method (i.e., by foot, bicycle, car surveys of different speed), and size of the carcass (Slater, 2002; Gerow et al., 2010; Teixeira et al., 2013; Collinson et al., 2014). Carcass persistence time appears to be influenced by factors such as weather, body size, and taxonomic group (Henry et al., 2021). Santos et al. (2011) and Lima Santos et al. (2017) reported lower carcass persistence on roads with lower traffic volumes, whilst Slater (2002) and Guinard et al. (2012) found no effect of traffic volume. Smaller body sizes such as those of amphibians have been found to have shorter persistence times than larger animals (Teixeira et al., 2013; Barrientos et al., 2018) and scavenging activity can also play a key role in carcass persistence (Dhiab, D'Amico and Selmi, 2023). In fact, scavengers have been shown to remove 76% of carcasses on roads within 12 hours in Cardiff, UK (Schwartz et al., 2018). Assumptions about carcass persistence on roads are largely based on small samples sizes (Ruiz-Capillas, Mata and Malo, 2015), but also on experiments using intentionally-placed carcasses (e.g., Ruiz-Capillas et al., 2015; Lima Santos et al., 2017; Schwartz et al., 2018). However, the latter can inflate removal rates if the same roads are studied as scavengers congregate and can focus activity along the study transects (known as scavenger swamping; Slater, 2002). As such, some current study designs introduce their own biases and can compromise the reliability of correction estimates.

Optimised study design will balance the logistical and financial costs of surveys with species-specific carcass detection (Henry et al., 2021). Surveying too frequently can waste time and financial resources whilst, at the other end, it has been estimated that 71% of road mortality could remain undetected by weekly, instead of daily, surveys (Burgstahler et al., 2023). Although a few daily surveys have been completed (e.g., Henry et al., 2021; Burgstahler et al., 2023), published literature is largely based on weekly (e.g., Barthelmess and Brooks, 2010; Haigh et al., 2014b), monthly (e.g., Ruiz-Capillas et al., 2015; Canal et al., 2018), or unsystematic schedules (e.g., Underhill, 2002; Brockie, 2007). Critically, it has been shown that different survey frequencies can lead to differences in the identification of road mortality hotspots (Santos et al., 2015), risking expensive yet ecologically-ineffective mitigation. The range of study designs, sampling frequencies, and use of intentionally-placed carcasses prohibit the separation of the effects of sampling and the factors that truly affect road mortality rates. Moreover, they can lead to simplistic study designs (e.g., a lack of testing between taxa) and/or inaccurate and misleading results Ascensão et al., 2019). Accurate approaches for monitoring road mortality are needed to derive robust mortality estimates, to optimise resource use, and to appropriately prioritise mitigation (Collinson et al., 2014). This is considered an essential consideration when extrapolating road mortality rates to regional or nationwide scales. Previous attempts to estimate nationwide road mortality did so without correction factors and only for a few key species (Underhill, 2002).

Instead, accurate (i.e., corrected) road mortality rates can be extrapolated, albeit still with caution and ideally with further future spatial testing and replication, to give an indication of the extent and severity of species-specific threats (Gerow et al., 2010), as well as track population trends over time (George et al., 2011).

The timing and locations of road collisions are not random (Gunson, Mountrakis and Quackenbush, 2011). Instead, spatial and temporal aggregations of road mortality are generally influenced by road (width, presence of road verge) and traffic (vehicle speed and volume) characteristics, adjacent land use, and biological traits of the species (Jaarsma, van Langevelde and Botma, 2006). For example, road mortality is strongly influenced by the life history stages such as migration, dispersal, and breeding (Grilo, Bissonette and Santos-Reis, 2009). The effect of spatial and temporal factors on roadkill can vary by species. For example, responses of bats to artificial streetlights was dependent on the feeding strategy and the flight style of the species (Rydell et al., 2017). Identifying likely spatial and temporal aggregations of road mortality affords decision-makers more informed options for conservation interventions (Lin, 2016). However, research on spatio-temporal patterns has largely been conducted using citizen science data (Raymond et al., 2021; Barg, MacPherson and Caravaggi, 2022), with associated issues of species mis-identification, temporal clustering, spatial bias, and a lower diversity index of road mortality compared to surveys conducted by trained ecologists (Balčiauskas et al., 2020). As such, there is an urgent need to delineate road mortality patterns based on standardised road surveys in order to establish baselines of monitoring across priority areas and species assemblages. Moreover, accurate data on road mortality rates and patterns are not only needed for environmental impact assessments and, if needed, the placement of expensive mitigation, measures should also be monitored to evaluate their effectiveness. To achieve this, further guidelines on study designs in road ecology are needed.

The overall aim of this study was to conduct a systematic road mortality study in Nottinghamshire, UK, to provide guidance for optimal study design, as well as to produce accurate assessments of the magnitude and patterns of multi-species road mortality. Nottinghamshire was chosen as the study area because it allowed for a road survey route that was relatively representative of the British road network in terms of road types and proportions of road type lengths. In addition, the collection of road mortality through COVID-19 related lockdowns enabled comparisons of road mortality through unprecedented changes to traffic (Institute for Government, 2022). Specifically, the study objectives were to (1) quantify the rates and predictors of carcass persistence; (2) calculate robust road mortality rate estimates for all observed species, correcting for bias; (3) quantify the temporal patterns of road mortality by day of the week and month, as well as pre- and during COVID-19 related lockdowns; (4) quantify the predictors of the spatial distribution of road mortality for eight focal species; and (5) estimate annual road mortality counts at the regional (i.e., Nottinghamshire) and national level (i.e., England and Great Britain). Based on literature predominately from mainland Europe, it is hypothesised that carcass persistence will be lower on quieter roads, for smaller species, and during wet conditions (Santos et al., 2011; Lima Santos et al., 2017). Should the spatio-temporal patterns of road mortality be non-random as suggested in the literature (Gunson et al., 2011), it is expected that there will be species-specific peaks in relation to activity levels and optimal habitat (Jaarsma et al., 2006; Grilo et al., 2009). This study can help expand the knowledge base needed for Britain to meet the standards of road mitigation for wildlife already exemplified in other road-dense countries like the Netherlands and North America (Huijser et al., 2009; Dulac et al., 2013).

3.2 Methods and materials

3.2.1 Road mortality surveys

Driving surveys for road mortality were conducted along a 69.7 km route on alternate days (3-4 times a week, including weekends, totalling of 18,749 km) between 14th May 2020 and 30th November 2021, inclusive (Figure 3.1). Driving the road survey route was chosen over cycling or walking to maximise road coverage and survey frequency (Santos et al., 2016), and were independent of weather and temperature. The survey route was designed to include a mixture of road types and surrounding habitat in a way that was representative of Britain’s road network i.e., covering road types in proportion to the wider British road network. The route consisted of A-roads (16%), B-roads (10%), and minor/local roads (74%), compared to 12%, 8% and 79% of these road types within the British road network, respectively (Department for Transport, 2022a). A-roads are main (also known as principal) roads that connect major destinations such as cities, with an annual average daily traffic (AADT) of 19,000 vehicles/day. B-roads are distributor roads often located between towns or villages with an AADT of 7,000 vehicles/day. Minor roads often link residential areas or villages to the rest of the road network, with an AADT of 3,000 vehicles/day, whilst local roads serve short distances within neighbourhoods, such as residential streets, with an AADT of 1,000 vehicles/day (Department for Transport, 2022b). Note that these AADT values are a snapshot and averaged from automatic traffic counters that are strategically placed to record every vehicle travelling along a section of road (Sfyridis and Agnolucci, 2020). To reflect the range in AADT and the road classifications of European road networks, herein A-roads will be referred to as main roads, B-roads as intermediate roads, and both minor and local roads as minor roads. Motorways (the widest and fastest roads, representing 1% of Britain's road network) and dual carriageways (fast roads with two lanes and a central median, representing 2% of Britain's road network; Department for Transport, 2022a) were not in the proximity of the study sites nor were able to be safely surveyed with only one surveyor, and therefore were not surveyed. It is important to note that 24% of the road mortality survey occasions took place during a national lockdown as part of the response to the Covid-19 pandemic, where road traffic was up to 49% lower than the equivalent month the year before (Department for Transport, 2022b).

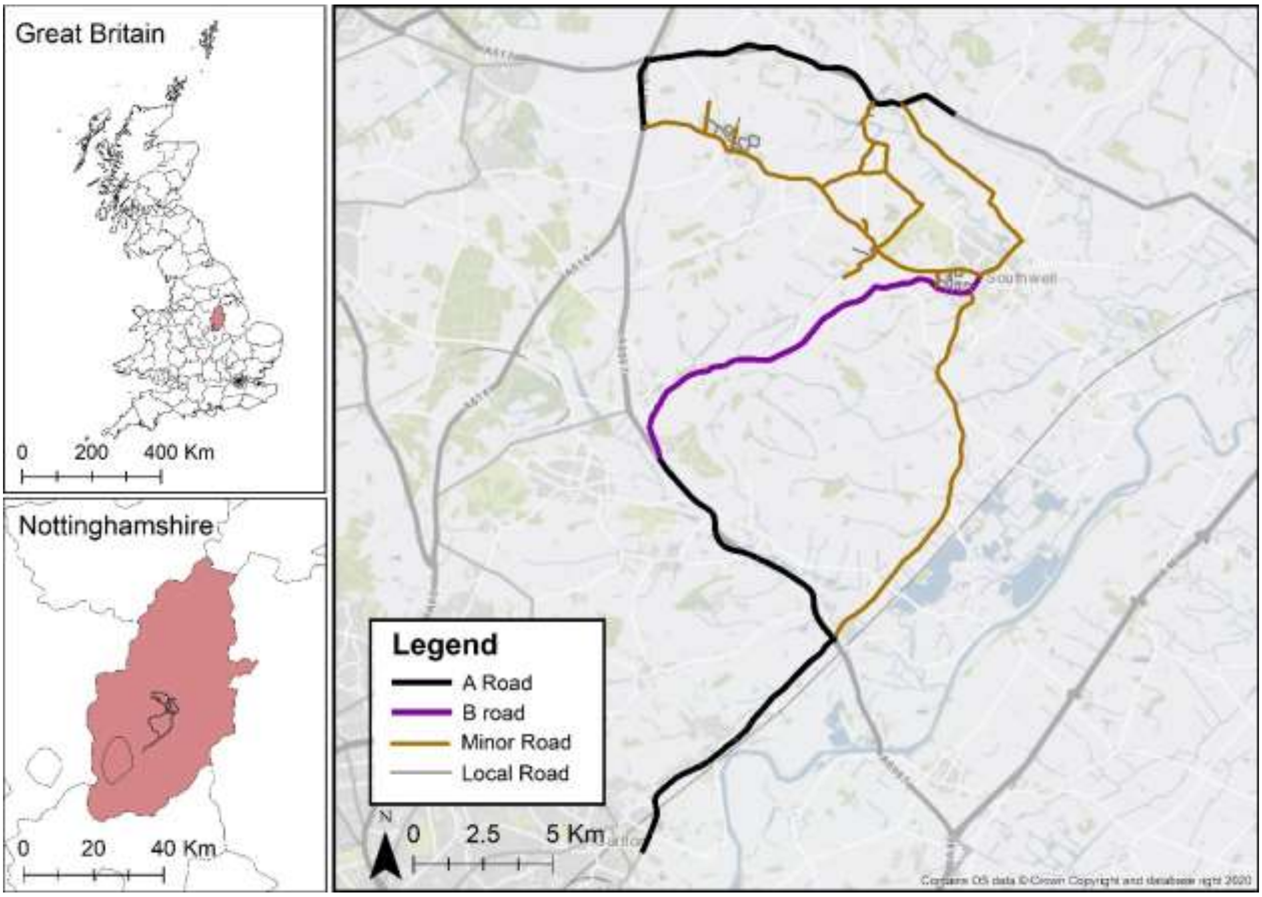


Figure 3.1: Road mortality survey route driven between May 2020 and November 2021. Top left: location of Nottinghamshire (highlighted) within Great Britain. Bottom left: location of the road survey route within Nottinghamshire.

Three pilot road surveys prior to the commencement of the study were used for training in carcass sightings, familiarisation with the survey route, and the removal of existing carcasses for accurate carcass persistence assessments. Surveys started one hour or less after sunrise to reduce carcass removal by diurnal scavengers and humans, as well as damage by morning traffic on the day of the survey. The survey route was driven in the same direction by a single observer travelling between 20-40 mph. This speed range was deemed appropriate to balance reliable detection and driver safety (Collinson et al., 2014). The observer (L.J.M) was the same during every survey.

Immediately following observation by car, road-killed animals were examined on foot when safe to do so and Geographic Positioning System (GPS) coordinates of the carcass were recorded using a handheld GPS device (Garmin 60 GPS unit; mean lateral accuracy 3 m). Of the observed roadkilled animals, 0.9 % (n = 19) of the carcasses could not be assessed directly due to safety concerns and were examined at distance using binoculars. Carcass condition was ranked as being either a whole carcass, having experienced some damage such as missing limbs, or being completely degraded. Where possible, sex was discerned based on the sexual dimorphism of external coat or plumage, or external genital morphology. Based on existing quantifiable criteria, age could be reliably discerned for hedgehogs only. Hind foot length (heel to the base of the middle nail) of roadkilled hedgehogs was deemed the most appropriate aging technique, compared to alternatives such as tooth growth rings, due to its lack of variability in adulthood and suitability for measurements in the field. Juvenile hedgehogs (also known as ‘young of the year’) were classed as individuals with a hind foot length of <3.6 cm (Haigh, 2014a) and defined as individuals found before their first hibernation. Adults were classed as individuals who had survived at least one hibernation.

In order to measure carcass persistence, carcasses were not removed from the road. Therefore, in order to avoid double counting, extensive notes and photographs of the location, appearance, and any discernible features (such as missing limb, colour) of the carcass was noted. During each subsequent survey, the presence or absence of each carcass was noted to give a record of carcass persistence. The GPS waypoint of the carcass was used to find the original location if required. When a carcass disappeared, searches for the carcass over 20 m either side of the original location were made on foot in case it had been moved (e.g., by a scavenger or person; Santos et al., 2016; Dhiab et al., 2023).

3.2.2 Data analysis

3.2.2.1 Road mortality rates and carcass persistence

The average species-specific carcass persistence time across all road surveys and by road type was calculated by fitting an exponential decay curve to the raw carcass persistence times in the software Siriema (Version 2.3; Coelho et al., 2017). A Kruskal-Wallis test was used to test for an association between functional group and average body mass (obtained from the literature) of each observed species, which revealed a strong relationship ($X^2 = 1072.240$, df = 5, p-value <0.001). Therefore, body mass was used in analyses herein as body mass shows greater variability across species, even within the same functional groups (Santos et al., 2016).

A combination of habitat, road, and individual characteristics were chosen based on previous studies to explore correlates of carcass persistence (Table 3.1). Distance to arable, as an index of urbanity, was based on the Ordnance Survey Mastermap Topography Layers and high resolution (<1 metre) Aerial Photography (Ordnance Survey, 2020) and extracted using the 'analysis' toolbox in ArcGIS 10.3.1 (ESRI, 2015). Two environmental variables – average precipitation and average air temperature – were taken from the Brackenhurst Weather Station (53.06277, -0.96068, 2 km from the centre of the road surveys) for the day of each survey

Following Zuur et al. (2010), assumptions of a linear regression were examined. Normality was tested using a normal Q-Q plot because formal statistical tests such as Shapiro-Wilk or Kolmogorov-Smirnov were inappropriate due to their over-sensitivity to sample size effects. Homoscedasticity was visually examined via a scatterplot whilst outliers and influential values were tested using standardised residuals and Cook's distance (Jones, 2019). No outliers in the explanatory or response variables were detected. Raw carcass persistence times were modelled for all species collectively by fitting a Generalised Linear Model (GLM). Due to the use of non-negative count data that was not over-dispersed, a Poisson family error distribution and log link function was used. Models were run in R (version 3.6.1; R Core Development Team, 2022) and fitted using the package '*lme4'* (version 1.21; Bates et al., 2015). The best-fitting model was identified using Akaike's Information Criterion (AICc; corrected for small sample sizes; Burnham & Anderson, 2004). Deviance and the distribution of residuals were used to check model fit.

Table 3.1: *A priori* models for the carcass persistence of all species recorded in the road surveys in Nottinghamshire from May 2020 to November 2021.

	Model	Description	Justification	Reference
M0	Null	Null	-	-
M1	Road type	European classification of road type; main road, intermediate road, minor road, local road (see Section 3.2.1)	Carcass degradation has been shown to be influenced by road classification	Santos et al., 2011 ; Santos et al., 2016
M2	Distance to arable	Distance (metres) to arable land - cropland, horticultural land (for example nurseries, vegetable plots), freshly ploughed land and grassland managed for silage	Index of urbanity; scavenger communities can differ throughout landscapes	Slater, 2002; Schwartz et al., 2018; Dhiab et al., 2023
M3	Body mass	Average body mass of species (grams), taken from the literature	Larger-bodied carcasses have differing carcass persistence to smaller-bodied carcasses	Gerow et al., 2010 ; Ruiz-Capillas et al., 2015 ; Henry et al., 2021
M4	Road type * body mass	Interaction between road type and the average body mass of species (grams, taken from the literature)	The body mass of a carcass may alter how quickly it is degraded by traffic	Gerow et al., 2010 ; Santos et al., 2011 ; Ruiz-Capillas et al., 2015 ; Santos et al., 2016
M5	Road type * distance to arable	Interaction between road type and the distance (metres) to arable land	The distribution of traffic differs throughout the landscape and along the rural-urban gradient	Department for Transport, 2022b
M6	Road type + condition + body mass	Combined effects of road type and the condition of the carcass (whole, partially degraded, severely degraded), whether large or small in size	The condition of a carcass may be dependent on how easily it is degraded by traffic, which itself may be related to body mass	Henry et al., 2021
M7	Body mass * condition	Interaction between the average body mass of species and condition of the carcass	The mass of the carcass may influence how quickly it becomes degraded	Gerow et al., 2010 ; Ruiz-Capillas et al., 2015

M8	Distance to arable + body mass + condition	Combined effects of the level of urbanity and condition of carcass, whether large or small	The rate of scavenging, which differs throughout the landscape, may differ depending on how easily a carcass can be removed from the road	Dhiab et al., 2023
M9	Air temperature	Average temperature (degrees) over a 24-hour period	Air temperature has been shown to affect the toughness and preservation of carcasses on the roads	Santos et al., 2011 ; Santos et al., 2016 ; Henry et al., 2021
M10	Precipitation	Average precipitation (millimetres) over a 24-hour period		
M11	Air temperature + precipitation + condition	Combined effects of climatic conditions and the condition of the carcass	Rainfall may affect the softening of carcass tissue, in turn the degradation from traffic and scavenger activity	
M12	Air temperature + precipitation + distance to arable	Combined effects of climatic conditions and the level of urbanity	Climatic conditions may affect the scavenging community, which itself differs with the level of urbanity	Santos et al., 2011

To calculate road mortality rates, λ (carcasses per km per day), Equation 1 was developed and used.

$$[1]\ \lambda = \frac{ps}{(1-e^{-pt}).d}\ \mathrm{km}^{-1}\ \mathrm{day}^{-1}$$

where *p* (estimated as the reciprocal of the average carcass persistence time) is the probability that a carcass is removed in t, *s* is the number of carcasses per unit distance (averaged over all of the surveys), e is Euler's number (2.718, commonly used in models of populations and exponential decay), *t* is the interval between surveys, and *d* is the detection probability specific to species body mass based on literature recommendations (Santos et al., 2016; see Appendix III for a derivation of this equation). Road mortality rates were estimated for the whole survey period collectively, as well as estimated for when surveys were conducted under COVID-19 lockdown restrictions vs 'normal' conditions (i.e., no restrictions; Institute for Government, 2022). The corrected road mortality rates were also compared to uncorrected road mortality rates (Appendix V), which were estimated by dividing the raw number of carcasses recorded by the total distance of road surveyed across the 269 road surveys.

To estimate the annual road mortality rate for each species, daily road mortality rates (λ) were multiplied by the length of the species annual activity period. This was taken as 365 days for all species that are active year-round. To account for a largely inactive hibernation period of west European hedgehogs and bats (Pipistrelle spp.), daily mortality rates were multiplied by 214 (representing 214 days, equivalent to an estimated average active period of seven months from April to October, inclusive; Medinas, Marques, and Mira, 2013; Bearman-Brown et al., 2020). However, it is important to note that west European hedgehogs and bats vary in the onset, duration, and end of their hibernation period, and hence when they could potentially be killed on roads at this time (Medinas, Marques, and Mira, 2013; Bearman-Brown et al., 2020). Therefore, annual estimates are probably conservative for these species.

To estimate the total number of individuals per species killed on roads annually in Nottinghamshire and to scale up to England and Great Britain (England, Scotland, Wales), a correction was applied for the slightly different road compositions in the survey route compared to the wider road networks. For this, carcass persistence per species per road type was estimated and were used to estimate species-specific road mortality rates for each road type. These rates were multiplied by the road proportions within the Nottinghamshire road network (688 km of main roads - A-roads only, 272 km of intermediate roads, 3,319 km of minor roads), the English road network (17,900 km of main roads – A-roads only, 12,400 km of intermediate roads, 155,200 km of minor roads), and the British road network (47,475 km of main roads - A-roads only, 30,416 km of intermediate roads, and 317,201 km of minor roads). It is recognised that there are a variety of potential inaccuracies associated with these extrapolations, and these are discussed in Section 3.5.

3.2.2.2 Temporal patterns of road mortality

As there were no differences in the road mortality of any species between respective months sampled in both 2020 and 2021 (Appendix IV), all road mortality records across all surveys were analysed together. To explore temporal patterns by day of the week and month, the amount of road mortality per survey was used as the dependent variable, rather than the raw counts. This standardised the variable number of surveys per day and month across the 1.5 years of road mortality surveys. Only species with more than ten records were analysed to increase the chances of producing robust estimates (Vittinghoff & McCulloch, 2007). Following Zuur et al. (2010), assumptions of a linear regression were examined, including the linearity of the relationship between predictor and outcome variables. Outliers and normality in the dependent variable of each species were examined visually and with a normal Q-Q plot, respectively. To deal with time-series independent data and non-linear dependent data, a separate Generalized Additive Model (GAM) was used to characterise the road mortality throughout the week and by month for the species with sufficient records. A Poisson family error distribution and log link function was used due to its appropriateness for non-negative counts and, for the most part, non-dispersed data. In cases of overdispersion that result in poor model fit, which was identified by an over-dispersion statistic of >2.0, a quasi-Poisson family was used. Day and month were modelled as a smoothing function using a cyclic cubic regression spline to account for continuity between days and months. Four knots were used for the day variable and six knots for the month variable, each because they are half of the length of the time-series (Wood, 2017). Analyses were implemented using the package '*mgcv*' (Wood, 2017) in R (version 3.6.1; R Core Development Team, 2022).

3.2.2.3 Spatial patterns of road mortality

The spatial distributions of road mortality were analysed for eight focal species with sufficient records for a logistic regression, based on the recommendation of having more than five records per variable included in the model (Vittinghoff & McCulloch, 2007). These species were common blackbird (*Turdus merula*), common pheasant (*Phasianus colchicus*), European or brown hare

(*Lepus europaeus*), European rabbit (*Oryctolagus cuniculus*), grey squirrel (*Sciurus carolinensis*), pigeon spp. (*Columbidae* spp.), sparrow spp. (*Passer* spp.), and hedgehog. A combination of road and habitat variables were chosen for analysis based on previous studies (Table 3.2). All spatial queries used to obtain road- or habitat-related variables were performed in ArcGIS 10.3.1 (ESRI, 2015). Using Ordnance Survey Mastermap Topography Layers and high resolution (<1 metre) Aerial Photography (Ordnance Survey, 2020), three habitat variables were extracted using the 'analysis' toolbox (Table 3.2). A sinuosity index was calculated by dividing 100 m segments of the road by the total distance between start and finish locations using the 'measure line' tool. Road slope was extracted from a digital elevation model created from a United States Geological Survey (USGS) raster. Daily (4am – 9pm) and nightly (9pm – 4am) traffic volume and speed were extracted from Nottinghamshire County Council's database.

Following Zuur et al. (2010), assumptions of a logistic regression were examined, including linearity of independent variables and log-odds based on visualisations from scatterplots. Initial assessments of multicollinearity between the explanatory variables were made using the correlation coefficients from Spearman's rank tests. Vehicle speed and road slope were collinear with traffic volume and the distance to garden, respectively, and so were not included in the analysis. Subsequent multicollinearity assessments were made using Variance Inflation Factors (VIF). The VIFs of the included variables did not exceed 1.42 in the final models and were deemed acceptable (a VIF under three is deemed appropriate; Zuur et al., 2010). Outliers and influential values were tested using standardised residuals and Cook's distance (Jones, 2019). Spatial patterns were modelled for each focal species separately by fitting a Generalised Linear Model (GLM) that compared actual road mortality locations to 100 times as many randomly generated points along the same roads. The random points were generated using the 'data management' tools in ArcGIS 10.3.1 (ESRI, 2015). As each road mortality record was independent and the data considers mutually exclusive outcomes (road mortality was either present or absent), a binomial family distribution with logit link function was used. Models were run in R (version 3.6.1; R Core Development Team, 2022) and fitted using the package '*lme4'* (version 1.21; Bates et al., 2015). The best-fitting model was identified using Akaike's Information Criterion (AICc; corrected for small sample sizes; Burnham & Anderson, 2004). Deviance and the distribution of residuals were checked to identify how well the model fit.

Table 3.2: *A priori* models for predictors of road mortality of key species

	Model	Description	Justification	Reference
M0	Null	No variables	-	-
M1	Daily or nightly traffic volume	Average number of vehicles of any type per day or night, taken from the closest year to the survey period. Day = 4am – 9pm, night = 9pm – 4am. Nightly traffic volume was used for hedgehogs only	Traffic speed has been shown to be a key factor in road mortality risk and hotspots of many species	Clevenger, Chruszcz and Gunson, 2002 ; D'Amico et al., 2015
M2	Distance to garden	Distance (metres) to land used for residential and private gardens. No difference was made between front and back gardens	Index for urbanity; species behaviour, movements, and abundance vary across the rural-urban gradient	Seo et al., 2013 ; Morelli, Benedetti and Delgado, 2020 ; Mayer et al., 2021 ; Valerio, Basile and Balestrieri, 2021
M3	Distance to woodland	Distance (metres) to land covered with trees or forest shrubs. No distinction was made for deciduous and broadleaved woodland	Woodlands affords many British species significant cover and foraging opportunities	Mayer et al., 2021 ; Valerio et al., 2021
M4	Presence of road verge	Distance (metres) to strips of natural land along the side of a road, often covered in grass and/or plants	Road verges have been shown to influence animal movement and foraging strategies near roads	Ruiz-Capillas et al., 2015 ; van der Horst et al., 2019
M5	Distance to garden + presence of a road verge + traffic volume	Combined effects of the level of urbanity, presence of a road verge, and traffic volume	Animal activity varies with the level of urbanity and, at smaller scales, may be influenced by road verges and traffic volumes	D'Amico et al., 2015 ; Ruiz-Capillas et al.. 2015 ; Morelli et al., 2020 ; Mayer et al., 2021
M6	Distance to garden * presence of a road verge	Interaction between the level of urbanity and the presence of a road verge	Different habitat types have varying extents of road verges, which can alter an animal's attraction to the roadside	Chambers et al., 2010 ; Mayer et al., 2021; Valerio et al., 2021

M7	Traffic volume * presence of a road verge	Interaction between traffic volume and the presence of a road verge	Different road types have varying extents of road verges, which can alter an animal's attraction to the roadside	Chambers et al., 2010 ; Seo et al., 2013
M8	Traffic volume * distance to garden	Interaction between traffic volume and the level of urbanity	The distribution of traffic differs throughout the landscape and along the rural-urban gradient	Mayer et al., 2021 ; Seo et al., 2013
M9	Sinuosity + topography + distance to garden	Combined effects of road characteristics and the level of urbanity	Road characteristics vary throughout the rural-urban gradient	de Carvalho, Bordignon, & Shapiro., 2014; Kang et al., 2016 Girardet et al., 2015; Grilo et al., 2012
M10	Sinuosity + topography	Slope: the change in elevation of road segment (degrees) Sinuosity: The curvature of 100 m road segments, as a sinuosity index Topography: the road is categorised as either depressed (lower than the banks), flat (road is level with the bank), raised (the road is higher than the banks and/or ditches are present), or with a combination (the bank of either side of the road differs)	Slope and the curvature of the road can affect the line of sight of both animal and driver, as well as driver speed. The banks and layout of a road may present physical impediments or barriers to animals needing to maneuver over the terrain.	
M11	Sinuosity + topography + traffic volume	Combined effects of road characteristics and traffic volume	Roads with different traffic volumes differ in their physical characteristics.	

3.3 Results

3.3.1 Carcass persistence and road mortality rates

Between May 2020 and November 2021, inclusive, 269 road surveys were conducted across a total of 18,749 km in an effort to document vertebrate road mortality. Overall, 2,072 road-killed vertebrates were found during the surveys, including 49 wild (non-domestic) species and one domestic species (four records of domestic cat *Felis catus*). Of the wild species, 54% (n = 27) of the recorded species or species groups (e.g. sparrows, where species separation was often difficult due to carcass damage and as such potentially two species were aggregated) were birds, 36% (n = 18) of species were mammals, and 8% (n = 4) of species were amphibians (Table 3.3). There were 53 carcasses (2.6%) that could not be identified to genus level. The sex of carcasses could be reliably recorded for three species: common blackbird, common pheasant, and west European hedgehog. Of these, males were more likely to be killed on roads than females (common blackbird: ♂150 ♀68, $X^{2:}$ 30.84, p-value: <0.001; common pheasant: ♂131 ♀63, X^2: 23.84, p-value: <0.001; west European hedgehog: ♂40 ♀18, X^2: 9,71, p-value: 0.002). Additionally, for the west European hedgehog, adults were more commonly killed on roads than juveniles (62 adults, 11 juveniles, X^2: 19.61, p-value: <0.001).

For all species combined, the number of carcasses per survey during COVID-19 lockdown restrictions was 5.16 compared to 8.82 when under ‘normal’ conditions (i.e., no restrictions, although some people remained to work from home). For the species-specific mortality rate estimations, 33 species were observed to have lower road mortality rates during the lockdown restrictions compared to ‘normal conditions’ (average 71% decrease ±29% SD). In contrast, ten species were observed to show an increase in road mortality rate during the same period (average 50% increase ±49% SD; Appendix V).

Table 3.3: Road-killed species observed during road surveys between May 2020 and November 2021, inclusive, their average carcass persistence, road mortality rate by day and year, and annual road mortality rates for Nottinghamshire, England, and Great Britain. Species are ordered from the highest annual road mortality rate to the lowest. SE = standard error. Ranges were calculated from SE.

Common name	**Scientific name**	**Raw roadkill records**	**% of roadkill records**	**Average carcass persistence time in days (SE)**	**λ, road mortality rate, km per day**	**Annual road mortality rate, km per year**	**Annual road mortality estimates for Nottinghamshire**	**Annual road mortality estimates for England**	**Annual road mortality estimates for Great Britain**
European rabbit	*Oryctolagus cuniculus*	362	17.47	3.73 (0.02)	0.0156 (0.0156–0.0156)	5.6904 (5.6845-5.6964)	24,218 (24,214-24,302)	885,491 (881,900-889,220)	2,032,679 (2,024,766-2,040,898)
Pigeon spp.	*Columba* spp.	342	16.51	4.41 (0.02)	0.0142 (0.0142-0.0142)	5.1759 (5.1715-5.1803)	22,719 (22,662-22,778)	990,172 (987,632-992,783)	2,103,517 (2,098,086-2,109,104)
Common blackbird	*Turdus merula*	236	11.39	3.18 (0.02)	0.0141 (0.0141-0.0142)	5.1580 (5.1471-5.1691) ♂ 3.5625, ♀ 1.5955 †	22,269 (22,154-22,393)	968,460 (963,460-973,815)	2,059,315 (2,048,317-2,071,146)
Grey squirrel	*Sciurus carolinensis*	223	10.76	4.63 (0.03)	0.0092 (0.091-0.092)	3.3414 (3.3371-3.3458)	14,484 (14,433-14,537)	629,977 (627,743-632,317)	1,339,617 (1,334,794-1,344,678)
Common pheasant	*Phasianus colchicus*	210	10.14	4.26 (0.03)	0.0088 (0.0088-0.0088)	3.2017 (3.1970-3.2064) ♂ 2.1497, ♀ 1.0520 †	13,667 (13,604-13,733)	594,452 (591,653-597,387)	1,264,806 (1,258,888-1,271,011)
Sparrow spp	*Passer* spp.	81	3.91	2.08 (0.05)	0.0084 (0.0083-0.0085)	3.0683 (3.0381-3.1003)	13,417 (13,107-13,831)	588,775 (575,681-606,177)	1,247,864 (1,218,713-1,287,421)
House mouse	*Mus musculus*	33	1.59	0.85 (0.11)	0.0057 (0.0052-0.0064)	2.0899 (1.9123-2.3288)	5,941 (5,326-6,952)	277,276 (248,604-324,445)	574,831 (515,110-673,607)
European hare	*Lepus europaeus*	88	4.25	4.96 (0.08)	0.0036 (0.0036-0.0036)	1.3011 (1.2972-1.3050)	5,555 (5,510-5,604)	241,152 (239,196-243,348)	513,428 (509,206-518,187)
Common frog	*Rana temporaria*	18	0.87	1.15 (0.2)	0.0025 (0.0023-0.0029)	0.9241 (0.8398-1.0501)	3,162 (2,957-3,765)	154,372 (128,836-145,581)	300,209 (271,447-332,986)
Smooth newt	*Lissotriton vulgaris*	7	0.34	1.01 (0.51)	0.0021 (0.0017-0.0038)	0.7827 (0.6126-1.3882)	2,348 (1,929-3,555)	109,773 (90,192-166,234)	224,357 (184,337-339,754)

Brown rat	*Rattus norvegicus*	37	1.79	3.67 (0.16)	0.0021 (0.0021-0.0022)	0.7786 (0.7706-0.7874)	3,272 (3,220-3,353)	146,289 (139,969-146,289)	302,968 (294,163-310,623)
West European hedgehog	*Erinaceus europaeus*	86	4.15	4.68 (0.08)	0.0035 (0.0035-0.0035)	0.7539 (0.7515-0.7564) ♂ 0.4997, ♀ 0.2542, Adult: 0.6307, Juvenile: 0.1159 †	3,227 (3,205-3,253)	140,347 (139,428-141,373)	298,418 (296,371-300,721)
Pipistrelle spp.	*Pipistrellus* spp.	12	0.58	1.09 (0.30)	0.0035 (0.0030-0.0044)	0.7476 (0.1290-0.1390)	2,835 (2,302-4,117)	132,557 (107,625-192,523)	270,923 (219,967-393,482)
Wood mouse	*Apodemus sylvaticus*	17	0.82	1.58 (0.23)	0.0020 (0.0019-0.0022)	0.7293 (0.6835-0.7932)	2,375 (2,220-2,369)	110,842 (103,626-110,794)	229,796 (214,405-226,443)
Thrush spp., except blackbirds	*Turdus* sp.	20	0.97	2.3 (0.24)	0.0020 (0.0019-0.0021)	0.7286 (0.7032-0.7606)	2,632 (2,505-2,934)	122,848 (116,939-136,795)	254,613 (242,074-286,245)
Dunnock	*Prunella modularis*	15	0.72	1.72 (0.27)	0.0017 (0.0016-0.0018)	0.6175 (0.5787-0.6729)	1,914 (1,787-2,143)	87,719 (81,759-98,428)	181,594 (169,413-203,481)
Carrion crow	*Corvus corone*	29	1.40	4.9 (0.24)	0.0012 (0.0012-0.0012)	0.4297 (0.4259-0.4340)	1,932 (1,868-2,025)	84,452 (81,599-88,550)	179,114 (173,135-187,733)
Eurasian wren	*Troglodytes troglodytes*	8	0.39	1.35 (0.46)	0.0010 (0.0009-0.0013)	0.3733 (0.3216-0.4892)	1,270 (1,108-1,656)	57,670 (50,076-75,715)	119,191 (103,672-156,074)
Stoat	*Mustela erminea*	17	0.82	3.42 (0.33)	0.0010 (0.0010-0.0010)	0.3642 (0.3558-0.3746)	1,665 (1,472-2,832)	72,902 (64,050-127,205)	154,628 (136,278-266,063)
Eurasian magpie	*Pica pica*	16	0.77	4.00 (0.39)	0.0009 (0.0009-0.0009)	0.3298 (0.3232-0.3381)	1,498 (1,363-1,993)	65,480 (59,306-88,401)	138,896 (126,040-186,910)
Collared dove	*Streptopelia decaocto*	14	0.68	2.75 (0.40)	0.0009 (0.0008-0.0009)	0.3196 (0.3068-0.3378)	1,304 (1,213-1,534)	56,304 (52,569-65,138)	120,020 (111,894-139,952)
Tawny owl	*Strix aluco*	18	0.87	5.8 (0.49)	0.0007 (0.0007-0.0007)	0.2589 (0.2557-0.2628)	1,112 (1,060-1,245)	48,393 (46,057-54,454)	102,899 (98,023-115,462)
Great crested newt	*Triturus cristatus*	3	0.14	1.6 (1.30)	0.0007 (0.0006-0.0027)	0.2558 (0.2021-0.9746)	834 (667-2,703)	38,988 (31,172-126,380)	79,685 (63,709-258,298)
Common buzzard	*Buteo buteo*	15	0.72	5.4 (0.58)	0.0006 (0.0006-0.0006)	0.2146 (0.2115-0.2185)	885 (848-959)	38,213 (36,577-41,612)	81,609 (78,058-88,210)

European mole	*Talpa europaea*	8	0.39	2.3 (0.97)	0.0005 (0.0005-0.0007)	0.1943 (0.1735-0.2509)	755 (678-735)	32,511 (29,404-34,359)	68,592 (61,838-70,225)
European polecat	*Mustela putorius*	4	0.19	4.00 (2.10)	0.0002 (0.0002-0.0002)	0.0618 (0.0571-0.0787)	43 (39-54)	1,107 (1,022-1,409)	2,936 (2,710-3,736)
Eurasian badger	*Meles meles*	15	0.72	6.00 (0.61)	0.0005 (0.0005-0.0005)	0.1747 (0.1718-0.1784)	718 (698-775)	31,091 (30,212-33,611)	66,327 (64,392-72,152)
Reeves' muntjac deer	*Muntiacus reevesi*	10	0.48	5.47 (0.96)	0.0004 (0.0004-0.0005)	0.1612 (0.1479-0.1836)	529 (423-655)	22,793 (11,992-28,202)	48,696 (31,349-60,192)
Common toad	*Bufo bufo*	2	0.10	0.69 (2.10)	0.0004 (0.0001-0.0002)	0.1493 (0.0682-0.0221)	175 (175-175)	8,166 (8,166-8,166)	16,690 (16,690-16-690)
Grey partridge	*Perdix perdix*	6	0.29	2.57 (0.88)	0.0004 (0.0004-0.0005)	0.1401 (0.1283-0.1660)	492 (455-589)	22,934 (21,223-27,500)	47,860 (44,363-57,190)
Common weasel	*Mustela nivalis*	4	0.19	2.89 (1.50)	0.0002 (0.0002-0.0003)	0.0899 (0.0808-0.1224)	343 (304-392)	14,818 (12,424-16,985)	32,152 (27,713-36,681)
Red-legged partridge	*Muntiacus reevesi*	9	0.43	4.98 (0.96)	0.0004 (0.0004-0.0004)	0.1330 (0.1290-0.1390)	548 (516-573)	23,841 (22,473-25,559)	50,757 (47,777-53,626)
Common shrew	*Sorex araneus*	3	0.14	1.61 (1.30)	0.0004 (0.0003-0.0013)	0.1279 (0.1010-0.4873)	417 (333-1351)	19,494 (15,586-63,190)	39,843 (31,855-129,149)
European robin	*Erithacus rubecula*	3	0.14	1.60 (1.30)	0.0003 (0.0003-0.0013)	0.1275 (0.1009-0.4717)	224 (224-224)	8,675 (8,675-8,675)	20,043 (20,043-20,043)
Barn owl	*Tyto alba*	8	0.39	4.55 (0.98)	0.0003 (0.0003-0.0003)	0.1203 (0.1160-0.1271)	444 (87-496)	19,173 (2,259-21,542)	40,412 (5,990-45,306)
Red fox	*Vulpes vulpes*	10	0.48	1.80 (0.41)	0.0003 (0.0003-0.0003)	0.1162 (0.1133-0.1205)	511 (490-566)	22,140 (21,243-24,595)	47,525 (45,639-52,638)
Eurasian Jay	*Garrulus glandarius*	4	0.19	2.89 (1.50)	0.0002 (0.0002-0.0003)	0.0899 (0.0808-0.1224)	194 (188-197)	9,201 (8,791-9,041)	18,837 (18,222-19,230)
European goldfinch	*Carduelis carduelis*	4	0.19	1.34 (0.91)	0.0002 (0.0004-0.0013)	0.0899 (0.1469-0.4571)	277 (277-277)	11,089 (11,089-11,089)	25,964 (25,964-25,964)
Common starling	*Sturnus vulgaris*	2	0.10	2.10 (2.30)	0.0002 (1.13 × 10^{-6}-0.0002)	0.0755 (0.0004-0.0603)	199 (0-245)	9,306 (1-11,460)	19,020 (3-23,422)
Common kestrel	*Falco tinnunculus*	3	0.14	3.79 (2.60)	0.0002 (0.0002-0.0003)	0.0626 (0.0560-0.1000)	218 (26-248)	9,456 (677-10,703)	19,904 (1,795-22,558)

Field vole	*Microtus agrestis*	4	0.19	2.89 (1.50)	0.0002 (0.0003-0.0005)	0.0618 (0.1212-0.1836)	535 (137-627)	23,204 (4,594-27,512)	49,737 (11,703-58,542)
Eurasian sparrow-hawk	*Accipiter nisus*	3	0.14	4.10 (2.90)	0.0002 (0.0003-0.0005)	0.0615 (0.0560-0.1000)	211 (131-244)	9,099 (6,118-10,529)	19,188 (12,506-22,181)
Western jackdaw	*Corvus monedula*	3	0.14	4.10 (2.90)	0.0002 (0.0002-0.0003)	0.0615 (0.0560-1.0000)	42 (38-69)	1,101 (1,002-1,790)	2,920 (2,656-4,748)
Roe deer	*Capreolus capreolus*	2	0.10	2.22 (2.40)	0.0001 (1.852×10^{-14} – 0.0001)	0.0295 (6.76×10^{-12} - 0.0241)	93 (91-94)	4,346 (4,270-4,394)	8,989 (8,805-9,107)
Common moorhen	*Gallinula chloropus*	1	0.05	n/a*	n/a*	n/a*	n/a*	n/a*	n/a*
Common quail	*Coturnix coturnix*	1	0.05	n/a*	n/a*	n/a*	n/a*	n/a*	n/a*
Mallard	*Anas platyrhynchos*	1	0.05	n/a*	n/a*	n/a*	n/a*	n/a*	n/a*
Pied wagtail	*Motacilla alba*	1	0.05	n/a*	n/a*	n/a*	n/a*	n/a*	n/a*
Yellow hammer	*Emberiza citrinella*	1	0.05	n/a*	n/a*	n/a*	n/a*	n/a*	n/a*
							Total: 162,612 (157,389-170,608)	Total: 6,965,582 (6,739,836-,349,714)	Total: 14,902,084 (14,420,533-15,683,501)

*Insufficient records for carcass persistence detection and therefore accurate road mortality rate estimation.

†Note that this includes individuals of unknown sex/age to the same sex/age ratio of known individuals.

Note that the annual road mortality estimates for Nottinghamshire, England, and Great Britain are potentially subject to extrapolation errors and should be interpreted with caution.

Of the wild animal carcases recorded (i.e., excluding domestic cats), 31.9% (660 carcasses) persisted for less than two days. Average carcass persistence ranged between 0.69 and 6.00 days (average 3.10 days ±4.61 SD). Carcass persistence was greatest for birds (3.40 days ±1.43 SD), followed by mammals (3.23 days ±1.51 SD), and amphibians (1.11 days ±0.31 SD). For the only species for which age of the carcass could be determined, hedgehogs, there was no difference between the carcass persistence of adults and juveniles (adults: 5.05 days ±0.11 SD, juveniles: 4.32 days ±0.52 SD; T-stat: -0.6565, p-value: 0.5135). The top four models explaining carcass persistence included road type (Table 3.4). The best fitting and most parsimonious model included an interaction between road type and body mass (Table 3.5), which explained 89% of the variation in the model. As per Figure 3.2 and Table 3.5, this top model indicated that carcass persistence increased significantly as body mass increased, although the effect of body mass lessened on busier roads.

Table 3.4: Ranked Generalised Linear Models predicting carcass persistence. AICc = Akaike's Information Criterion, Δi = delta AICc, ω = AICc weighting.

Co-variate	AICc	*Δi*	ω
Road type * body mass	9211.53	0.00	0.89
Road type + condition + body mass	9215.86	4.33	0.10
Road type * distance to arable	9220.83	9.30	0.01
Road type	9223.56	12.04	0.00
Distance to arable + body mass + condition	9227.10	15.57	0.00
Body mass	9228.11	16.58	0.00
Body mass * condition	9229.82	18.29	0.00
Air temperature + precipitation + condition	9231.58	20.05	0.00
Distance to arable	9236.36	24.83	0.00
Air temperature	9238.26	26.73	0.00
Null	9238.33	26.8	0.00
Air temperature + precipitation + distance to arable	9238.58	27.05	0.00
Precipitation	9240.33	28.81	0.00

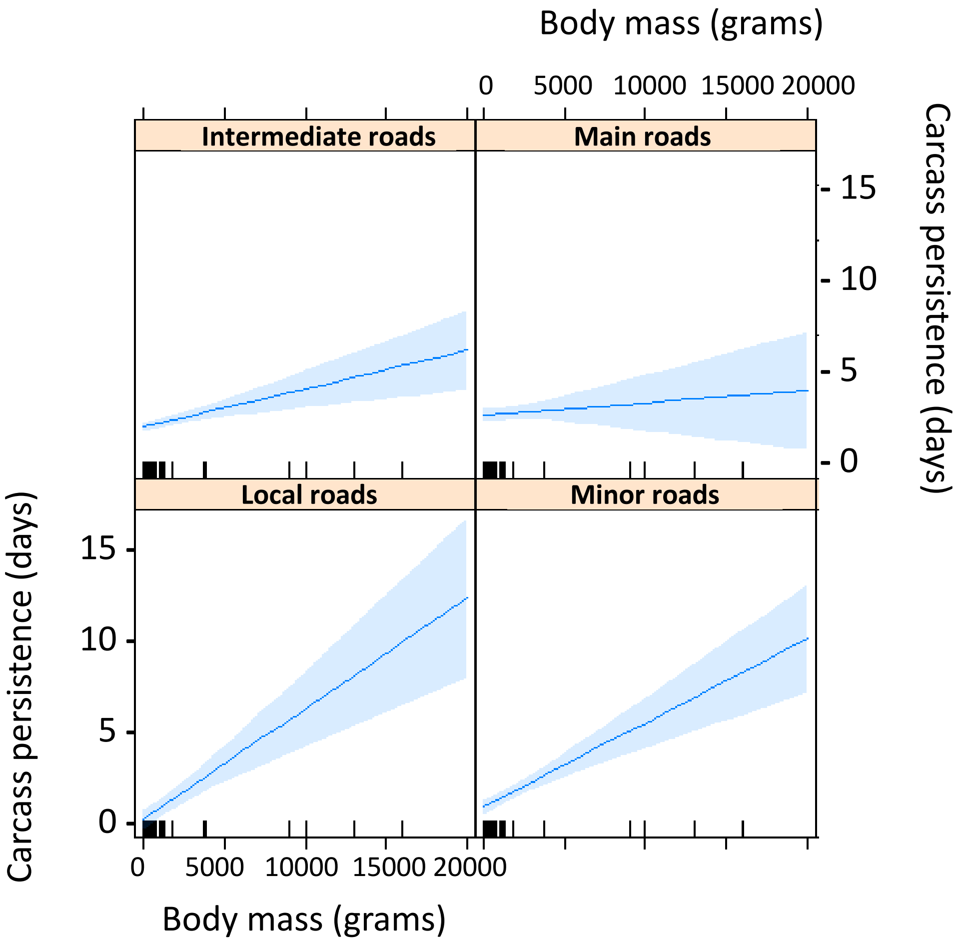


Figure 3.2: Plot of the interaction between road type and body mass explaining carcass persistence from the best-fitting Poisson Generalised Linear Model.

Table 3.5: Best-fitting Poisson Generalised Linear Model of carcass persistence. ** p≤ 0.01, *** p≤ 0.001.

Co-variate	Estimate	Standard Error	Z-value	p-value	
Intercept	0.574	0.057	11.013	<0.001	***
Body mass * Road Type	< - 0.001	<0.001	-3.124	0.002	**

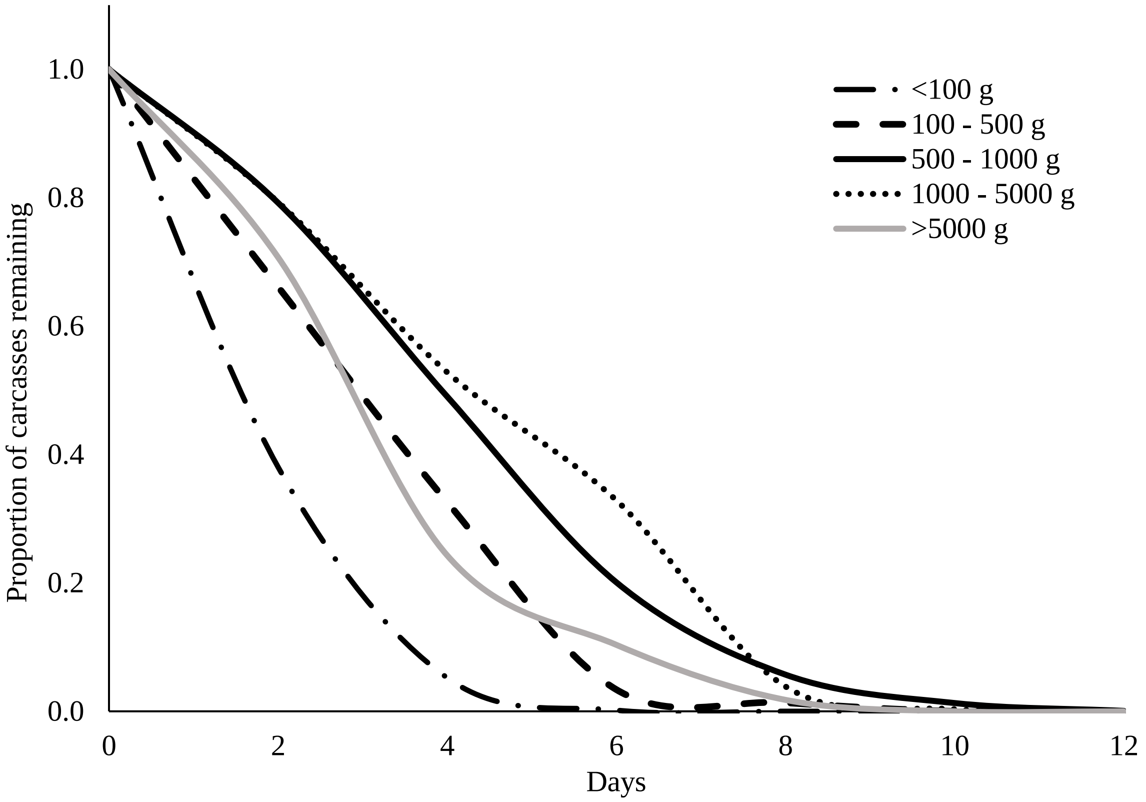


Figure 3.3: Carcass persistence of body mass categories of species recorded on road surveys between May 2020 and November 2021, inclusive.

When corrected for carcass persistence and detectability, road mortality rate estimates ranged from 0.03 to 5.69 carcasses/km/year across species, with the greatest rates estimated for birds (0.95 carcasses/km/year ±1.34 SD), followed by mammals (0.94 carcasses/km/year ±1.45 SD), and amphibians (0.53 carcasses/km/year ±0.35 SD). No reptiles were found over the course of the surveys. The corrected road mortality rate estimates were 1.2 to 11.5 times greater than uncorrected road mortality rates (average 3.3 times, ±2.5 SD; Appendix V).

3.3.2 Temporal patterns

When all species were combined, the number of carcasses per survey varied by month (e.d.f 3.748, F = 9.864, p-value = 0.005), with the smoothing function indicating that road mortality was greatest between early spring and late summer. Out of the 23 species analysed, the GAMs indicated clear seasonal variations for 16 species, with this seasonality being more prominent in mammals than birds (10 out of 11 mammals vs 3 out of 11 birds; Appendix IV). By contrast, there were no significant differences in road mortality records by day of the week i.e., Monday - Sunday (Appendix IV).

3.3.2.1 Seasonal variation in road mortality of mammals

Seasonal variation was statistically significant for all mammal species analysed except the house mouse, showing two broad patterns: unimodal and bimodal peaks of road mortality (Figure 3.4). A unimodal peak was found between summer and autumn for wood mice, grey squirrel, European rabbit, and European hare, compared to a spring unimodal peak for Eurasian badger. The two hibernating species, west European hedgehog and pipistrelle spp., showed a prolonged summer peak of road mortality between June and September. Brown rat and, although with small sample sizes, red fox and Reeves' Muntjac deer showed bi-modal road mortality with one peak in early spring and the other in early autumn.

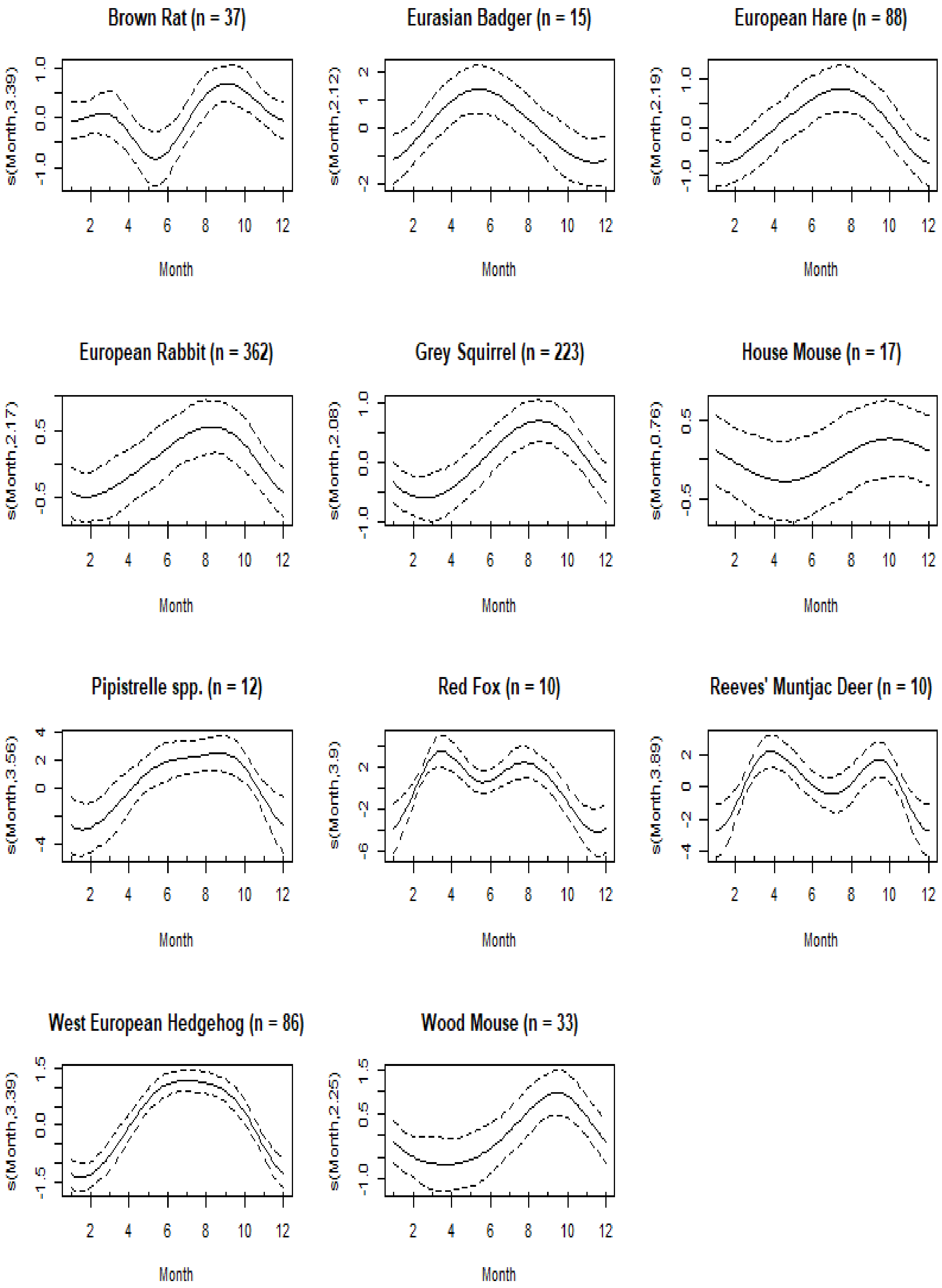


Figure 3.4: Seasonal variation in the road mortality of mammals i.e., the number of carcasses per survey by month, between May 2020 and November 2021, inclusive. Dashed lines show 95% confidence intervals.

There were clear sex differences in the seasonality in the road mortality of west European hedgehog with the highest frequencies of male road mortality in spring compared to that of females in autumn (Appendix VI). August and September were the only months where female fatalities were greater than male fatalities.

3.3.2.2 Seasonal variation in road mortality of birds and amphibians

Significant seasonality was found for common pheasant, Eurasian magpie, and pigeon spp. (Figure 5). By contrast, no significant seasonal variation was evident for all other passerine and predatory birds. Despite a lack of statistical significance, road mortality was highest between June and August for common blackbird, carrion crow, dunnock, sparrow spp., thrush species (Turdus spp.; excluding blackbirds), and pigeon spp. Eurasian magpie had a more prolonged peak of road mortality between April and August. Bi-modal road mortality was recorded for common buzzard, common pheasant, and tawny owl. Common frog had the greatest levels of road mortality in autumn (Figure 3.5).

Common blackbird showed little difference in the seasonality of road mortality between males and females. There were slight sex differences in the onset of heightened road mortality for common pheasant, with males showing an earlier road mortality peak in spring and females showing an earlier road mortality peak in autumn (Appendix VI).

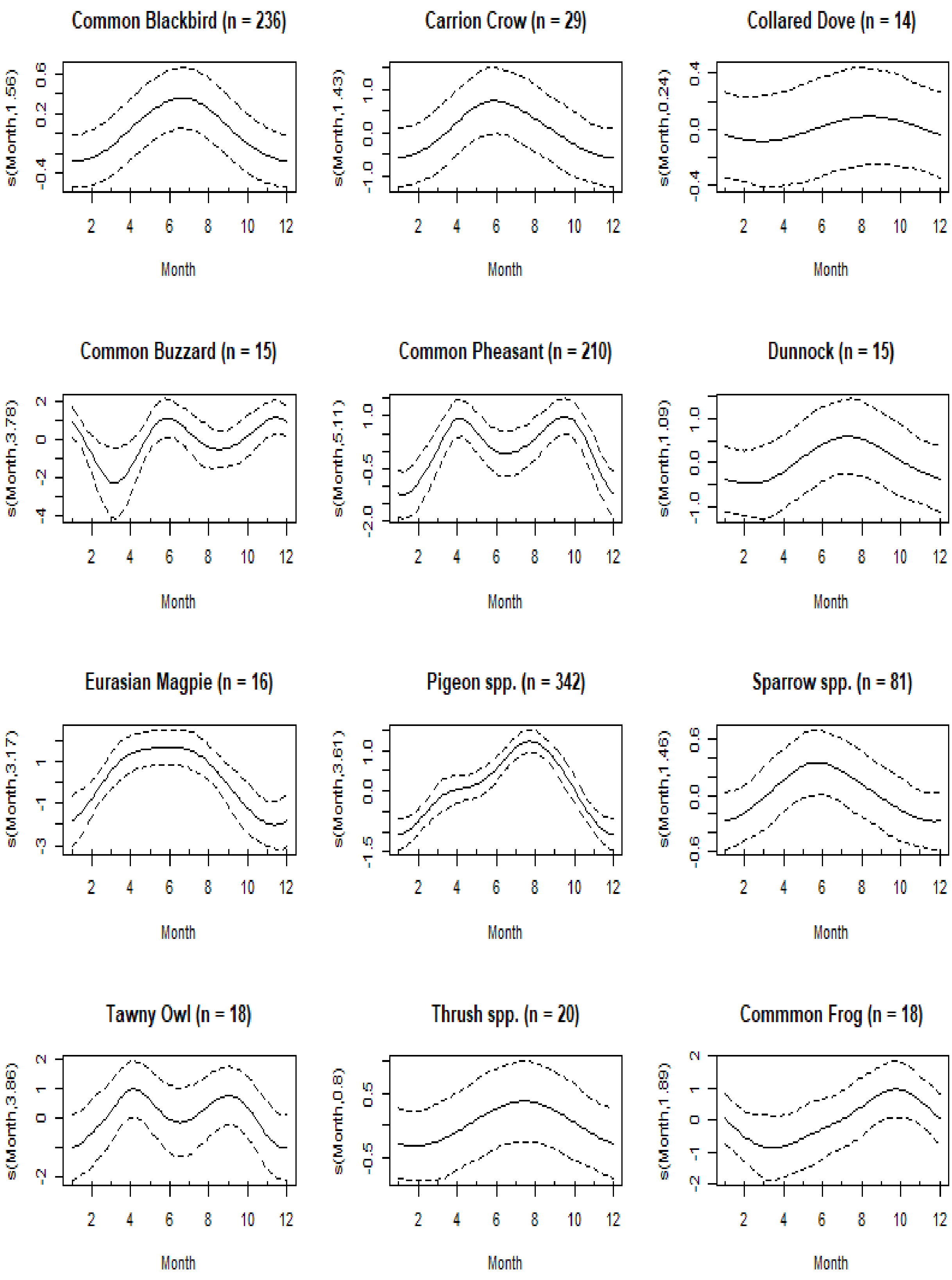


Figure 3.5: Seasonal variation in the road mortality of birds i.e., the number of carcasses per survey by month, between May 2020 and November 2021, inclusive. Dashed lines show 95% confidence intervals.

3.3.3 Spatial patterns

Across the eight focal species analysed, three best fitting and most parsimonious models were identified (Table 3.6). Although the interaction between traffic volume and the distance to garden was the top model for common blackbird, European hare, European rabbit, grey squirrel and pigeon spp., the direction of this relationship differed between species (Table 3.7). Roadkill of common blackbird and pigeon spp. was greater near gardens, whilst the opposite was found for European hare, European rabbit and grey squirrel (i.e., their roadkill hotspots were associated with rural landscapes). For all of these species, the relationship between roadkill location and gardens weakened with increasing traffic volume. Road verges were included in the top model for both sparrow spp. and west European hedgehog. Increasing proximity to road verges led to an increased likelihood of sparrow spp. roadkill, a relationship that was accentuated on busy roads. The interaction between the presence of a road verge and distance to gardens was the best fitting and most parsimonious model for west European hedgehog, indicating that road verges became particularly common roadkill hotspots close to gardens. Finally, common pheasant roadkill was predicted to increase on straighter and raised roads that were located away from gardens.

Table 3.6: Ranked Generalised Linear Models predicting the likelihood of road mortality in Nottinghamshire. AICc = Akaike's Information Criterion, Δi = delta AICc, ω = AICc weighting.

Species	**Co-variate**	**AICc**	***Δi***	**ω**
Common blackbird	Daily traffic volume*Distance to garden	-42616.36	0.00	0.73
	Distance to garden*Distance to road verge	-42613.92	2.45	0.21
	Sinuosity + Topography + Distance to garden	-42610.82	5.54	0.05
	Distance to garden	-42607.52	8.84	0.01
	Sinuosity + Topography + Daily traffic volume	-42598.60	17.76	0.00
	Sinuosity + Topography	-42598.20	18.16	0.00
	Daily traffic volume*Distance to road verge	-42598.16	18.20	0.00
	Distance to road verge	-42596.81	19.56	0.00
	Daily traffic volume	-42596.42	19.94	0.00
	Null	-42595.55	20.81	0.00
	Distance to woodland	-42593.67	22.69	0.00
Common pheasant	Sinuosity + Topography + Distance to garden	-37959.51	0.00	0.90
	Distance to garden*Distance to road verge	-37954.80	4.71	0.09
	Distance to garden	-37950.18	9.33	0.01
	Daily traffic volume*Distance to garden	-37949.58	9.93	0.01
	Sinuosity + Topography	-37922.01	37.5	0.00
	Sinuosity + Topography + Daily traffic volume	-37920.06	39.45	0.00
	Distance to road verge	-37917.67	41.84	0.00
	Daily traffic volume*Distance to road verge	-37914.49	45.02	0.00
	Daily traffic volume	-37903.28	56.23	0.00
	Null	-37902.38	57.13	0.00
	Distance to woodland	-37902.15	57.36	0.00
European hare	Daily traffic volume*Distance to garden	-15920.41	0.00	0.96
	Distance to garden*Distance to road verge	-15912.82	7.59	0.02
	Distance to garden	-15911.44	8.97	0.01
	Sinuosity + Topography + Distance to garden	-15908.99	11.42	0.00
	Daily traffic volume*Distance to road verge	-15893.59	26.82	0.00
	Daily traffic volume	-15891.31	29.09	0.00
	Sinuosity + Topography + Daily traffic volume	-15889.63	30.78	0.00
	Distance to road verge	-15886.31	34.1.0	0.00
	Sinuosity + Topography	-15881.66	38.75	0.00
	Null	-15880.58	39.83	0.00
	Distance to woodland	-15878.58	41.83	0.00
European rabbit	Daily traffic volume*Distance to garden	-65458.13	0.00	1.00
	Sinuosity + Topography + Distance to garden	-65443.33	14.8	0.00
	Sinuosity + Topography + Daily traffic volume	-65441.72	16.41	0.00
	Daily traffic volume*Distance to road verge	-65415.21	42.92	0.00

	Sinuosity + Topography	-65408.20	49.93	0.00
	Distance to garden*Distance to road verge	-65405.38	52.75	0.00
	Daily traffic volume	-65405.15	52.97	0.00
	Distance to garden	-65395.00	63.13	0.00
	Distance to road verge	-65365.98	92.14	0.00
	Null	-65339.38	118.75	0.00
	Distance to woodland	-65338.95	119.18	0.00
Grey Squirrel	Daily traffic volume*Distance to garden	-40270.86	0.00	0.98
	Distance to woodland	-40261.96	8.91	0.01
	Daily traffic volume*Distance to road verge	-40259.61	11.25	0.00
	Distance to garden*Distance to road verge	-40258.51	12.35	0.00
	Distance to road verge	-40256.53	14.33	0.00
	Daily traffic volume	-40255.87	14.99	0.00
	Sinuosity + Topography + Daily traffic volume	-40255.73	15.13	0.00
	Sinuosity + Topography + Distance to garden	-40253.27	17.6	0.00
	Sinuosity + Topography	-40251.59	19.27	0.00
	Distance to garden	-40249.4	21.47	0.00
	Null	-40248.97	21.90	0.00
Pigeon spp.	Daily traffic volume*Distance to garden	-61749.5	0.00	0.73
	Sinuosity + Topography + Daily traffic volume	-61746.95	2.56	0.20
	Daily traffic volume*Distance to road verge	-61743.42	6.09	0.03
	Daily traffic volume	-61742.74	6.77	0.02
	Distance to garden*Distance to road verge	-61736.62	12.88	0.00
	Sinuosity + Topography + Distance to garden	-61735.45	14.05	0.00
	Sinuosity + Topography	-61733.37	16.14	0.00
	Distance to road verge	-61732.56	16.95	0.00
	Distance to garden	-61731.39	18.11	0.00
	Distance to woodland	-61730.15	19.35	0.00
	Null	-61729.25	20.25	0.00
Sparrow spp.	Daily traffic volume*Distance to road verge	-14626.07	0.00	0.43
	Daily traffic volume	-14625.04	1.03	0.26
	Daily traffic volume*Distance to garden	-14624.30	1.77	0.18
	Sinuosity + Topography + Daily traffic volume	-14621.80	4.27	0.05
	Distance to garden*Distance to road verge	-14621.73	4.33	0.05
	Distance to garden	-14620.07	6.00	0.02
	Distance to road verge	-14617.16	8.91	0.00
	Null	-14617.03	9.04	0.00
	Sinuosity + Topography + Distance to garden	-14616.53	9.54	0.00
	Distance to woodland	-14615.91	10.16	0.00
	Sinuosity + Topography	-14613.92	12.15	0.00

West European hedgehog	Distance to garden*Distance to road verge	-15529.17	0.00	0.41
	Sinuosity + Topography + Distance to garden	-15528.57	0.60	0.31
	Distance to garden	-15526.62	2.55	0.12
	Sinuosity + Topography	-15526.21	2.96	0.09
	Sinuosity + Topography + Nightly traffic volume	-15524.28	4.89	0.04
	Distance to garden	-15523.76	5.41	0.03
	Null	-15519.56	9.61	0.00
	Distance to road verge	-15518.60	10.57	0.00
	Distance to woodland	-15517.86	11.31	0.00
	Nightly traffic volume	-15517.58	11.59	0.00
	Nightly traffic volume*Distance to road verge	-15515.31	13.86	0.00

Table 3.7: Best-fitting binomial Generalised Linear Model of the likelihood of road mortality in Nottinghamshire. * p≤ 0.05, ** p≤ 0.01, *** p≤ 0.001

Species	Co-variate	Estimate	Standard Error	Z-value	p-value	
Common blackbird	(Intercept)	-4.736	0.1261	-37.565	<0.001	***
	Daily traffic volume	<0.001	<0.001	3.583	<0.001	***
	Distance to garden	-0.0002	<0.001	-0.642	0.521	
	Daily traffic volume * Distance to garden	< -0.0001	<0.001	-2.197	0.028	*
Common pheasant	(Intercept)	-4.940	1.059	-4.666	<0.001	***
	Sinuosity	-1.045	0.915	-1.141	0.254	
	Topography	0.439	0.124	3.539	<0.001	***
	Distance to garden	0.001	<0.001	6.118	<0.001	***
European hare	(Intercept)	-5.965	0.300	-19.913	<0.001	***
	Daily traffic volume	<0.001	<0.001	4.043	<0.001	***
	Distance to garden	0.003	<0.001	5.708	<0.001	***
	Daily traffic volume * Distance to garden	< -0.001	<0.001	-3.728	<0.001	***
European rabbit	(Intercept)	-5.796	0.141	-41.150	<0.001	***
	Traffic volume	<0.001	<0.001	8.825	<0.001	***
	Distance to garden	0.002	0.002	8.557	<0.001	***
	Traffic volume * distance to garden	< -0.001	<0.001	-6.528	<0.001	***
Grey squirrel	(Intercept)	-5.032	0.142	-35.391	<0.001	***
	Traffic volume	<0.001	<0.001	4.918	<0.001	***
	Distance to garden	0.001	<0.001	1.746	0.081	*
	Traffic volume * Distance to garden	< -0.001	<0.001	-3.432	0.001	***
Pigeon spp.	(Intercept)	-4.792	0.109	-44.146	<0.001	***
	Daily traffic volume	<0.001	<0.001	3.834	<0.001	***
	Distance to garden	-0.001	0.003	-1.546	0.122	
	Daily traffic volume * Distance to garden	< -0.001	<0.001	-0.077	0.939	
Sparrow spp.	(Intercept)	-3.981	0.1793	-22.203	<0.001	***
	Daily traffic volume	<- 0.001	<0.001	-3.316	0.001	***
	Distance to road verge	-0.026	0.015	-1.731	0.084	

	Daily traffic volume * Distance to road verge	<0.001	<0.001	0.934	0.350	
West European hedgehog	(Intercept)	-4.248	0.143	-29.655	< 0.001	***
	Distance to garden	-0.002	0.001	-3.501	0.001	***
	Distance to road verge	-0.014	0.008	-1.761	0.078	
	Distance to garden * Distance to road verge	<0.001	<0.001	3.147	0.002	**

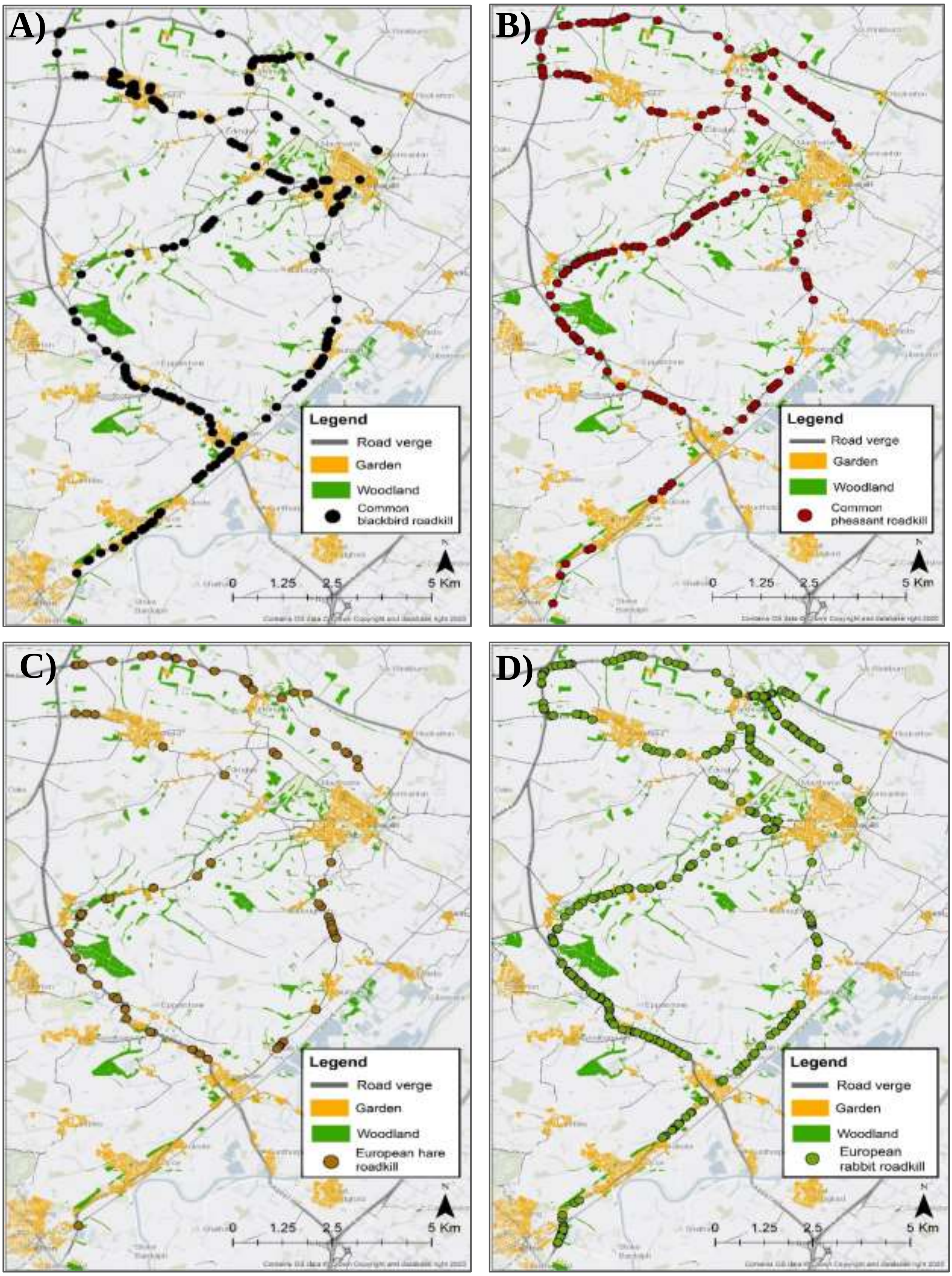
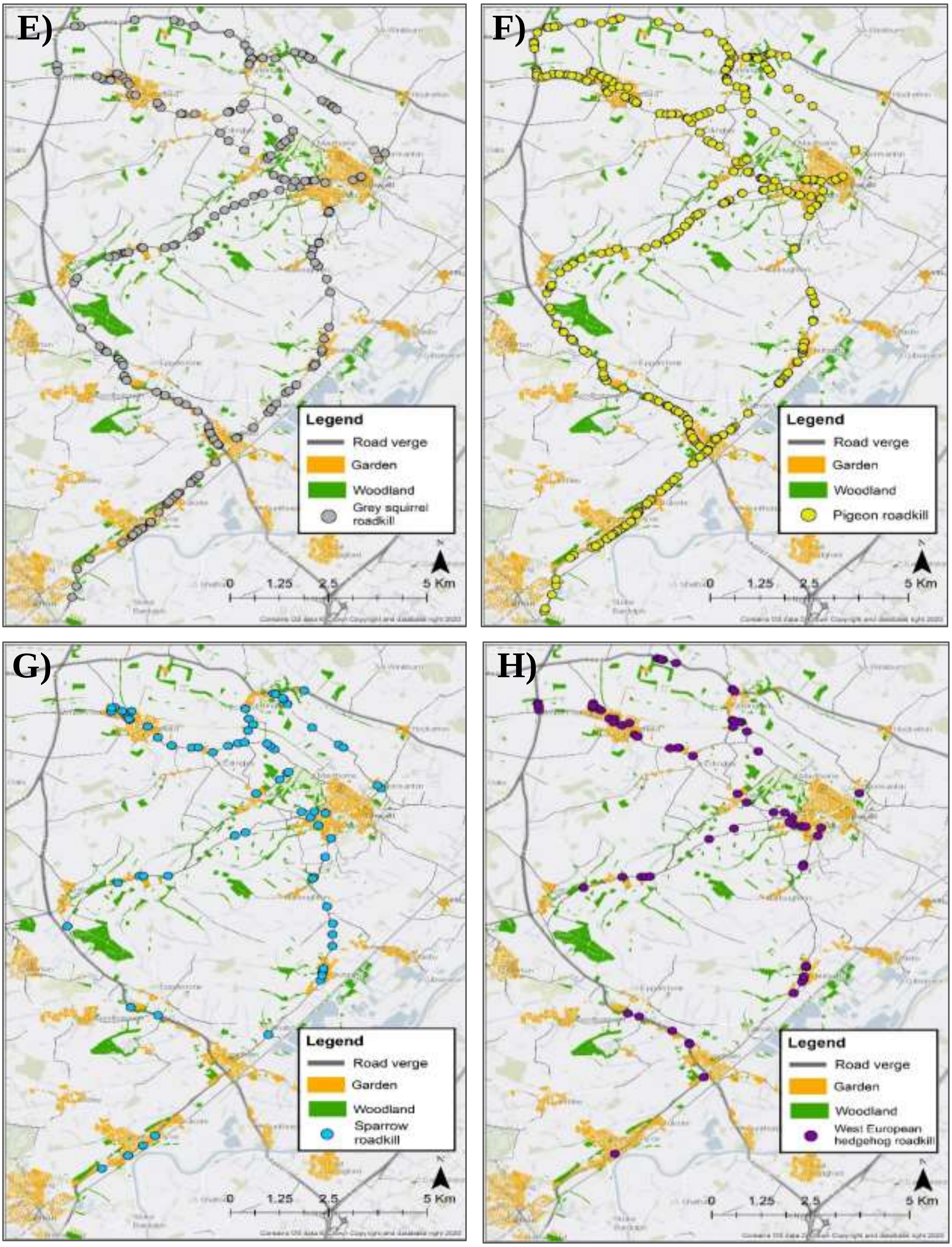


Figure 3.6: Locations of road mortality for eight top species observed during roadkill surveys in Nottinghamshire between May 2020 and November 2021, inclusive. A) Common blackbird, B) Common pheasant, C) European hare, D) European rabbit, E) Grey squirrel, F) Pigeon spp., G) Sparrow spp., H) West European hedgehog



Fiugre 3.6: Locations of road mortality for eight top species observed during roadkill surveys in Nottinghamshire between May 2020 and November 2021, inclusive. A) Common blackbird, B) Common pheasant, C) European hare, D) European rabbit, E) Grey squirrel, F) Pigeon spp., G) Sparrow spp., H) West European hedgehog

For common pheasant and common blackbird, the road mortality of both males and females was evenly spread across road types (common pheasant: $X^2 = 0.20$, p-value = 0.91; common blackbird: $X^2 = 1.55$, p-value = 0.46). By contrast, more male west European hedgehog were killed on main roads compared to their female conspecifics, but with little difference in the mortality of sexes on intermediate and minor roads ($X^2 = 7.57$, p-value = 0.02).

3.4 Discussion

As a first for Great Britain, analyses into the relative magnitude, composition, and spatio-temporal distribution of the road mortality of multiple species were conducted using accurate data from high-frequency surveys. The estimated road mortality rates of 0.03 to 5.69 carcasses/km/year for individual species are comparable to relatively recent year-round estimates from standardised studies, including from mainland Spain (0.02 – 1.42 individual/km/year; Puig & Sanz 2012), South Korea (1.47/km/year; Seo et al. 2013), and worldwide (0.005 - 10 individual/km/year; Grilo et al. 2021). By correcting for factors such as carcass persistence and detectability, confidence can be held in that the road mortality rates were underpinned by species ecology and not artefacts of bias. As such, these give insight into both relative road mortality between species and absolute road mortality, indicating that not all species are equally affected by roads. Importantly, using the corrections and calculations for road mortality rates as shown here, before-after studies could explore whether roadkill rates have been influenced by mitigation actions without concern over the effect of bias on differences in rates over time.

The highest road mortality rates were observed in species with high local abundance, which is often associated with fast life-histories (e.g., shorter life expectancies), fast reproduction (i.e., early maturity age, more litters/clutches per annum), and broader ecological niches (González-Suárez et al. 2018; Medrano-Vizcaíno et al., 2022). This includes European rabbit, pigeon spp., common blackbird, and grey squirrel. For such species, even the high road mortality rates recorded here may have little impact on the demography of populations. Although many of the species recorded during the surveys are common in Great Britain, some species are of conservation concern such as yellowhammer, grey partridge, and great crested newt (Department for Environment, Food and Rural Affairs [DEFRA], 2022), although they were recorded in small numbers. These species are understudied in relation to the threats from roads, yet a loss of a few individuals can have a disproportionate effect on already declining populations. Roadkill of these species should be considered for future research. No reptiles were found on the surveys, despite the presence of common lizard (*Zootoca vivipara*), slow worm (*Anguis fragilis*), grass snake (*Natrix helvetica*) and adder (*Vipera berus*) being present in the survey area (NBN Atlas, 2021). The lack of reptile records may be a function of both low local abundances and potential road avoidance behaviours, as reported for several snake species in the United States of America (USA; Shepard et al., 2008; Robson & Blouin-Demers, 2013).

The national estimates for Great Britain for many species were considerably higher than previous estimates, such as for Eurasian badgers, European polecats and barn owls (Neal and Cheeseman, 1996; Underhill, 2002; Ramsden, 2004). Particularly for smaller-bodied species, this may reflect the influence of correcting for carcass persistence and detectability when estimating road mortality rates (Gerow et al., 2010). Alternatively, it is possible that the estimates for Great Britain are over-estimates as species distribution and abundances are not uniform across the country (e.g., grey squirrels or great crested newts are far rarer in Scotland; NBN Atlas, 2021). As such, the national estimates for England, with its relatively more uniform habitat matrices, are likely to be more robust. These national estimates can be used for updating the conservation status of species (e.g., for hedgehogs; Wembridge et al., 2022) and monitoring species numbers over time, based on the positive relationship between population size and road mortality (George et al., 2011), as well as identifying species that require concerted, nationwide conservation efforts near roads.

Species for which accurate sex differentiation of road mortality was possible (common blackbird, common pheasant, and west European hedgehog), the records were male-dominated, substantiating patterns recorded for an array of terrestrial species (e.g., Klöcker et al. 2006; de Freitas et al. 2014). Driven by varying energetic input for breeding and rearing young, male individuals often have greater daily movements and home ranges than their female counterparts, at least for part of the year. This, in turn, can bring males into greater contact with roads. It is important to note, however, that this does not necessarily reflect a male-bias in the road mortality records due to a lack of context from the surrounding population structure (see Chapter 2 and Chapter 4).

3.4.1 Carcass persistence

The average carcass persistence of 3.10 days (±4.61 SD) identified here is similar or slightly longer than most previous estimates, including one day (Santos et al., 2011), 2.2 days (Lima Santos et al., 2017), 2.7 days (Henry et al., 2021), and 3.2 days (Gerow et al., 2010). The disparity in carcass persistence rates may be attributed to differences in road mortality record composition. Up to 75%

of the road mortality samples of Santos et al. (2011) and Lima Santos et al. (2017) comprised of small-bodied animals that have lower carcass persistence rates. Moreover, these studies were conducted in the tropics where faster degradation compared to temperate and/or dry regions can be attributed to warmer temperatures and a greater diversity of scavengers. By contrast, this study observed a more even spread of records across functional groups, of which small-bodied animals comprised 22.9%, and was conducted in temperate/dry conditions alike Gerow et al. (2010) and Henry et al. (2021). It is likely that the results presented here reflect a norm for temperature regions, which adds to the growing body of literature revealing that carcass persistence rates are context-specific.

The contribution of scavengers to decreasing carcass persistence rates has been well documented (Erritzoe, Mazgajski and Rejt, 2003; Antworth, Pike and Stevens, 2005; Santos et al., 2016; Henry et al., 2021). Scavenger influence is also suggested in this present study. Building on previous literature and as partially hypothesised, this influence is mediated through three key elements: road type, body mass, and condition of the carcass. Carcass persistence was lower on quieter roads, although this relationship weakened with increasing body mass. Quieter roads likely facilitate scavenger access to a carcass (Santos et al., 2016). Moreover, the abundance and diversity of birds of prey are often highest along intermediate roads compared to main roads (Planillo, Kramer-Schadt and Malo, 2015), increasing the intensity of scavenging activity on quieter roads. In addition, carcass persistence decreased with body size (Figure 3.2), which may be a function of small carcasses being subject to combined effects of degradation by vehicles, removal by decomposers, and high scavenger activity (Collinson et al., 2014). This may further explain why the relationship between carcass persistence and body mass lessened on busier roads. That is, even on minor roads where scavenging activity is high, scavengers cannot remove large and heavy carcasses effectively and efficiently, which remain identifiable and *in situ* for longer (Santos et al., 2011).

Corroborating Santos et al. (2016), carcass persistence was longer in areas of human habituation, a relationship that was accentuated on main roads. After motorways, urban main roads have the greatest average daily traffic volume of any road type and compared to their rural counterparts (Department for Transport, 2019). It may be that urban main roads pose too great a risk for scavengers and inhibit their access to carrion. Moreover, many scavengers in this study area are either more abundant in agricultural landscapes, namely kites (*Milvus milvus*) and buzzards, or are habitat generalists, namely carrion crows, Eurasian magpies, and red foxes. In this study, the geographic distribution of scavengers and traffic may have concentrated scavenging activity in rural areas.

This study provides evidence that sampling designs of future road surveys require concerted attention, ensuring that protocol is designed according to the study objectives. The effect of body mass on carcass persistence shown in this study reveals appropriate survey frequencies tailored to the target taxa (Table 3.8). These survey frequencies can be adopted by future research in temperate conditions to produce more accurate road mortality rates. Likewise, this study highlights that a consideration of the surrounding habitat (and by association, scavenging community) is essential for the proper interpretation of road mortality. Where possible, carcass persistence times, survey effort, and carcass detectability should be calculated and used in corrections (using the equation developed here, for example) to further increase the accuracy of road mortality estimations.

Table 3.8: Recommended survey frequency for body mass of focal species based on average carcass persistence times

Body mass of focal species	Suggested survey frequency to encounter 50% of carcasses	Suggested survey frequency to encounter 80% of carcasses
< 100 g	Daily	Daily
100 – 500 g	Alternate days	Daily
500 – 1000 g	Every four days	Alternate days
1000 – 5000 g	Every four days	Alternate days
> 5000 g	Alternate days	Daily

3.4.2 Temporal patterns

No significant differences were found in the frequency of road mortality by the day of the week. The lack of daily pattern contrasts those found for multiple species on Philip Island, Australia, and for deer in Austria where later in the week (Friday or the weekend) experienced greater road mortality frequencies than standard weekdays (Rendall et al., 2021; Steiner et al., 2021). The lack of short-term temporal patterns in this present study may reflect lower variation in the underlying causes – traffic volume and human activity – compared with the tourist or hunting hotspots studied by Rendall et al. (2021) and Steiner et al. (2021). This may be exaggerated in this present study whereby COVID-19 lockdowns led to more people working from home, leading to less pronounced differences between weekday and weekend traffic.

3.4.2.1 Unimodal seasonality

Many species appear more vulnerable to collisions during specific life-history periods although, as hypothesised, the timing of increased casualty rates was species-specific. Albeit with a small sample size (n = 15), the heightened Eurasian badger road mortality in spring observed in this study corresponds to the end of their main mating season. During this time, population-wide mobility is greater as both males and females make extra-territorial excursions (Kelly et al., 2020), bringing animals into more frequent contact with roads. Foraging may explain the disproportionately high occurrence of grey squirrel road mortality later in the year as suggested by research on a closely related species, the red squirrel (*Sciurus vulgaris*). Compared to arboreal activity, on-the-ground movements of red squirrels are highest in autumn as they food-cache for winter, requiring more frequent or longer foraging trips and increasing their exposure to traffic (Bosch & Lurz, 2012). Juvenile dispersal and the subsequent increase in animal abundance may be further underlying causes of the high road mortality frequencies of grey squirrel, house and wood mice, European hare, and European rabbit in autumn. These patterns are also reflected in analysis conducted on citizen science records (Raymond et al., 2020). Periods of dispersal often coincide with a net increase in movement as young individuals explore the landscape to establish their own territories, whilst young are also inexperienced around dangers such as vehicles (Grilo et al., 2009). Birds, for example, have been shown to adjust the timing of flight initiation depending on the speed from an oncoming vehicle. This is a behavioural adaptation that young individuals are less likely to have developed (Legagneux & Ducatez, 2013). Collectively, increased numbers and movements of (young) individuals increases the chance of road mortality in a population.

A single yet extended peak of activity, and therefore road mortality, for several species may be explained by the temporal convergence of activities. Hibernating species such as bats and west European hedgehog show condensed activity over a small number of months. During their active season, foraging, breeding, and raising young can overlap throughout a population (Medinas et al., 2013), although it is important to note the small sample size for bats (n = 12). The convergence of activities may also account for the unimodal peak for many passerine birds in this present study. Species such as common blackbird, Eurasian magpie and sparrow spp. are known to have more than one brood per year and, unlike mammals (Dawson et al., 2016), the time between breeding and dispersal is relatively short. The period of heightened activity and subsequent risk of collision is therefore extended over the year (Liordos et al., 2021).

3.4.2.2 Bimodal seasonality

The observed bimodal seasonality in the road mortality records reflect species-specific pulses of activity. The mating season may be the underlying cause of high incidences of road mortality for Reeves' muntjac deer in autumn and red fox in the spring due to associated increases in activity levels, albeit both had small sample sizes. In fact, male red fox have shown extraterritorial movements in late winter/spring for extrapair mating (Dorning & Harris, 2019) and moving through unfamiliar terrain is often associated with increased road mortality risk (Grueber et al., 2017). Juvenile dispersal likely explains a further peak in road mortality for Reeves' muntjac deer in spring, whilst a period of both juvenile dispersal and feeding young may explain red fox road mortality in autumn. Female red fox tend to increase movements to provision for their young by increasing the number of visits to the breeding site as cubs grow, reaching ten visits per night close to dispersal (Blanco, 1998). In support of this, feeding young was found to be the most vulnerable time for female red fox in Portugal (Grilo et al., 2009), reinforcing the role of biological periods in road mortality aggregations.

Life history traits may not solely account for road mortality patterns as human activity may also affect animal abundance or habitat availability, as also concluded by Raymond et al (2020). As brown rats include cereals as a substantial part of their diet, the autumn harvesting of arable farmland in Great Britain is a likely driver of their September roadkill peak. The loss of a food supply, as well as cover and protection, causes brown rats to disperse to more fruitful habitat such as urban areas, increasing their exposure to vehicles for a short period of time (Battisti et al., 2012). Consistent with this interpretation, brown rats do not have a restricted breeding period like other species, suggesting that fluctuations in vehicle collisions are associated with human behaviour (Orłowski & Nowak, 2006). The cessation of winter supplementary feeding and associated increase in foraging activity may be the underlying cause of increased frequencies of common pheasant road mortality in spring. Additionally, the high levels of common pheasant road mortality in autumn coincide with the large-scale release of individuals. The large numbers and naivety of released individuals increases their chances of collisions. These patterns are reflected in the slight sex differences in common pheasant road mortality. Intense foraging after winter occurs earlier in males to build fat reserves for territorial activities, generating an earlier road mortality peak in spring compared to females. Conversely, female common pheasant disperse earlier and further from their release pens in autumn, representing an earlier autumn peak compared to males (Madden & Perkins, 2017).

3.4.2.3 Spatial patterns

The spatial analyses for the eight focal species revealed that a combination of traffic, road design, and habitat characteristics best predicted road mortality locations. For common blackbird and pigeon spp., road mortality was positively associated with gardens, whilst the roadkill of common pheasant, European rabbit, European hare, grey squirrel was associated with more rural landscapes. Population sizes and/or activity levels of these species may be greater in the corresponding landscapes, corroborating previous research that road mortality is associated with species-specific high-quality habitat (D’Amico et al., 2015; Gunson et al., 2011). However, it remains possible that unknown factors within these landscapes increase individual risk to road mortality, rather than hotspots being a function of greater abundances and/or activity levels, which warrants further investigation.

The interactions between urbanity with traffic volume suggest that nuances in the spatial distribution of road mortality are at play. The relationships between road mortality and gardens, whether positive or negative, became less meaningful as traffic volume increased for grey squirrel, sparrow spp., common blackbird, pigeon spp., European hare and European rabbit. This was also true for the interaction between road verges and traffic volume that predicted sparrow spp. road mortality, indicating the over-arching role of traffic volume in the roadkill hotspots of these species. On main roads, animals have less time to successfully cross the road and drivers have less opportunity to safely avoid animals as the gaps between vehicles decrease (Jacobson et al., 2016). In Britain, 75% of main roads and 80% of intermediate roads intersect rural landscapes, compared to 57% of minor roads (Department for Transport, 2022a). In this way, a large amount of the road network becomes risky for rural species such as European rabbit and European hare, underlining a complex relationship between the placement of roads and surrounding habitat types that shapes road mortality hotspots.

Road verges were included in the top model of west European hedgehogs and sparrow spp. These relationships indicated that road mortality was often in close proximity to road verges, particularly so on roads with low traffic and close to built areas (Table 3.7). For both west European hedgehog and sparrow spp., this finding may reflect their attraction to residential areas. In addition, road verges often provide high primary production and, with a global coverage of 270,000 km^2 (Phillips et al., 2019), road verges provide key habitat patches, foraging opportunities and shelter within hostile immediate surroundings. This, in turn, may increase activity and animal abundances on the roadside and predispose them to a greater likelihood of a collision. West European hedgehogs have been shown to use road verges for nesting (Bearman-Brown et al., 2020) and movement corridors (Doncaster, Rondinini and Johnson., 2001), although evidence of attraction to road verges is mixed and dependent on landscape (Schaus-Calderón, 2021). Sparrow spp. in the USA, such as song sparrows (*Melospiza melodia*), were found to use road verges for travelling or for nesting-related activities (e.g., singing to defend their territories; Bélanger et al., 2021). It is possible therefore that the lower survival around roads can instigate source-sink dynamics, particularly if road verges fail to provide a corridor to favourable habitat. This conclusion was also surmised by Mumme et al. (2000), Grilo et al. (2012), and van der Horst et al. (2019), highlighting a major influence of roads on long-term (meta-)population dynamics and populations far from roads.

The best fitting model for common pheasant road mortality was the only top model to include road design characteristics. The increased likelihood of collision on straighter roads may be a function of increased driving speeds, which give drivers less time to respond to an animal in the road. As also surmised by Delgado et al. (2019), structurally complex roads with embankments or raised sections may hinder a driver's view of animals in the road, again reducing the driver's ability to respond efficiently and avoid a wildlife-vehicle collision.

One of the most common objectives of road mitigation is a reduction in total road mortality, rather than a reduction in mortality of specifics cohorts for example. In these circumstances, the aim is to benefit background mortality of a population or the safety of humans (i.e., from fatal collisions with large ungulates; Lin, 2016). The empirical mapping of road mortality hotspots in this study affords decision-makers with evidence-based prioritisation of the road segments with the greatest amount of roadkill. As such, the findings are applicable to enhancing targeted mitigation measures to produce maximum reductions of road mortality of focal taxa, simultaneously benefitting the cost-effectiveness of actions (see Chapter 7 for further study applications).

3.5 Limitations of the study

Several species had a low number of road mortality records, such as Eurasian wren and European robin, despite relatively high population abundances of these species in the surrounding area (Crowe et al., 2010). The sample sizes of certain species may therefore have led to large confidence intervals and false-negative seasonality in the estimation of rates and roadkill patterns. In fact, many of the passerines, with the exception of Eurasian magpie, that did not show seasonality had some of the lowest sample sizes of the species recorded. Whilst the regional and nationwide estimates of road mortality were corrected for road type proportions in the Nottinghamshire, English, and British road networks, there are other factors that can influence the accuracy of these rates, such as driver behaviour, habitat preferences, distribution, local abundances, species traits (Medrano-Vizcaíno et al., 2022). However, the necessary ecological information was not widely available across all target species analysed here. Thus, the estimates should be interpreted with caution.

3.6 Future research directions

Collecting data on population abundances and activity levels around roads (such as road crossing frequencies obtained from GPS tracking) is a key development in road mortality research. Doing so would provide a clearer understanding of the underlying causes of road mortality hotspots. That is, whether hotspots near to species-specific high habitat quality relate to higher abundances, indicating that animals are killed in proportion to the population, or whether factors in certain habitats increase individual vulnerability to collisions, for example in urban areas where traffic is greater.

Delineating the relationship between population abundance and road mortality rates could be a critical tool for tracking both long- and short-term population trends. Whilst some work has taken place on the subject (e.g., Gehrt 2002; George et al. 2011), there is a high degree of variability in the relationships. Further research into the validity and precision of monitoring populations in this way, especially the effects of confounding factors such as road density, is required.

3.7 Conclusion

By conducting one of the most intensive road mortality surveys to date, and for the first time in Great Britain, this study demonstrates that the short carcass persistence times have the potential to underestimate road mortality by up to 11.5 times. This raises concerns over the accuracy of previous survey estimates, revealing a need to adjust such estimates (using the equations and carcass persistence rates calculated here) and the subsequent conclusions on the urgency and scale of mitigation required. To ensure robust and unbiased assessments of road mortality in the future, this study offers guidelines for standardised methodology in the future. Specifically, road mortality surveys should be tailored to the body mass of focal species and to road types. Doing so would also substantially reduce logistical costs of data collection and provide maximal return for research investment. The role of biological traits and habitat associations in the spatial and temporal aggregations of road mortality suggest that the vulnerability to road mortality may persist over generations. As road development is associated with changes in habitat structure, the magnitude and patterns of road mortality should be monitored closely. Doing so will enable comparisons between different studies, sites, and over time to provide a comprehensive understanding of the relative changes to wildlife in dynamic road environments.

3.8 References

Ascensão, F., Kindel, A., Teixeira, F. Z., Barrientos, R., D'Amico, M., Borda-de-Água, L., & Pereira, H. M. (2019). Beware that the lack of wildlife mortality records can mask a serious impact of linear infrastructures. *Global Ecology and Conservation*, *19*, e00661. https://doi.org/10.1016/j.gecco.2019.e00661

Akrim, F., Mahmood, T., Andleeb, S., Hussain, R., & Collinson, W. J. (2019). Spatiotemporal patterns of wildlife road mortality in the Pothwar Plateau, Pakistan. *Mammalia*, *83*(5), 487–495. https://doi.org/10.1515/mammalia-2017-0101

Antworth, R. L., Pike, D. A., & Stevens, E. E. (2005). Hit and run: Effects of scavenging on estimates of roadkilled vertebrates. Southeastern Naturalist, *4*(4), 647-656. https://www.jstor.org/stable/3878229

Balčiauskas, L., Stratford, J., Balčiauskienė, L., & Kučas, A. (2020). Importance of professional roadkill data in assessing diversity of mammal roadkills. *Transportation Research Part D: Transport and Environment*, *87*. https://doi.org/10.1016/j.trd.2020.102493

Barg, A., MacPherson, J., & Caravaggi, A. (2022). Spatial and temporal trends in western polecat road mortality in Wales. *PeerJ*, *10*, e14291. https://doi.org/10.7717/PEERJ.14291/SUPP-2

Barrientos, R., Martins, R. C., Ascensão, F., D'Amico, M., Moreira, F., & Borda-de-Água, L. (2018). A review of searcher efficiency and carcass persistence in infrastructure-driven mortality assessment studies. *Biological Conservation, 222,* 146-153. https://doi.org/10.1016/j.biocon.2018.04.014

Barthelmess, E. L., & Brooks, M. S. (2010). The influence of body-size and diet on road-kill trends in mammals. *Biodiversity and Conservation*, *19*(6), 1611–1629. https://doi.org/10.1007/s10531-010-9791-3

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software, 67*(1), 1-48. https://doi.org/10.48550/arxiv.1406.5823

Battisti, C., Amori, G., De Felici, S., Luiselli, L., & Zapparoli, M. (2012). Mammal road-killing from a Mediterranean area in central Italy: Evidence from an atlas dataset. *Rendiconti Lincei*, *23*(2), 217–223. https://doi.org/10.1007/s12210-012-0163-7

Baxter-Gilbert, J. H., Riley, J. L., Neufeld, C. J. H., Litzgus, J. D., & Lesbarrères, D. (2015). Road mortality potentially responsible for billions of pollinating insect deaths annually. *Journal of Insect Conservation*, *19*(5), 1029–1035. https://doi.org/10.1007/S10841-015-9808-Z/TABLES/2

Bearman-Brown, L. E., Baker, P. J., Scott, D., Uzal, A., Evans, L., & Yarnell, R. W. (2020). Over-winter survival and nest site selection of the West-European hedgehog (*Erinaceus europaeus*) in arable dominated landscapes. *Animals*, *10*(9). https://doi.org/10.3390/ani10091449

Bélanger, L., Jobin, B., Lacroix, G., & Bédard, Y. (2021). Which bird species groups use highway roadside verges and why? *Northeastern Naturalist, 28*(4), 515-526. https://doi.org/10.1656/045.028.0409

Blanco, J. C. (1998). *Mamíferos de España*. Spain : Planeta.

Bosch, S., & Lurz, P. W. W. (2012). *The Eurasian red squirrel* Sciurus vulgaris. Germany : Westarp

Brockie, R. (2007). Notes on New Zealand mammals 4. Animal road-kill “blackspots”. *New Zealand Journal of Zoology*, *34*(4), 311–316. https://doi.org/10.1080/03014220709510090

Burgstahler, K., Isidro, J., van Vuren, D. H., Collins, A. C., Aliperti, J. R., & Wells, C. P. (2023). Daily roadkill monitoring and long-term population census reveal female-biased mortality for a small mammal along a wildland-urban interface. *Biological Conservation, 277.* https://doi.org/10.1016/j.biocon.2022.109863

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference understanding AIC and BIC in model selection. *Sociological Methods and Research*, *33*(2), 261–304. https://doi.org/10.1177/0049124104268644

Canal, D., Camacho, C., Martín, B., de Lucas, M., & Ferrer, M. (2018). Magnitude, composition and spatiotemporal patterns of vertebrate roadkill at regional scales: A study in southern Spain. *Animal Biodiversity and Conservation*, *41*(2), 281-300. https://doi.org/10.32800/abc.2018.41.0281

Chambers, B. K., Dawson, R., Wann, J., & Bencini, R. (2010). *Speed limit, verge width and day length are the major factors correlated with the number of road-kills of tammars (*Macropus eugenii*) on Garden Island, Western Australia.* In G. Coulson and M Eldridge (Eds)

Macropods: the biology of kangaroos, wallabies and rat-kangaroos. Australia : CSIRO Publishing

Clevenger, A. P., Chruszcz, B., & Gunson, K. E. (2002). Spatial patterns and factors influencing small vertebrate fauna road-kill aggregations. *Biological Conservation*, *109*(1), 15–26. https://doi.org/10.1016/S0006-3207(02)00127-1

Coelho, A., Coelho, I., Teixeira, F., & Kindel, A. (2017). *Siriema: road mortality software. User's Manual V. 2.0.* Universidade Federal do Rio Grande do Sul. https://doi.org/10.13140/RG.2.2.19953.38242

Collinson, W. J., Parker, D. M., Bernard, R. T. F., Reilly, B. K., & Davies-Mostert, H. T. (2014). Wildlife road traffic accidents: A standardized protocol for counting flattened fauna. *Ecology and Evolution, 4*(15), 3060–3071. https://doi.org/10.1002/ece3.1097

Crowe, O., Coombes, R. H., Lysaght, L., O'Brien, C., Choudhury, K. R., Walsh, A. J., … O'Halloran, J. (2010). Population trends of widespread breeding birds in the Republic of Ireland 1998–2008. *Bird Study*, *57*(3), 267–280. https://doi.org/10.1080/00063651003615147

D'Amico, M., Román, J., de los Reyes, L., & Revilla, E. (2015). Vertebrate road-kill patterns in Mediterranean habitats: Who, when and where. *Biological Conservation*, *191*, 234–242. https://doi.org/10.1016/j.biocon.2015.06.010

Dawson, A., King, V. M., Bentley, G. E., & Ball, G. F. (2016). Photoperiodic control of seasonality in birds. *Journal of Biological Rhythms, 16*(4), 365–380. https://doi.org/10.1177/074873001129002079

de Carvalho, N. C., Bordignon, M. O., & Shapiro, J. T. (2014). Fast and furious: A look at the death of animals on the highway MS-080, Southwestern Brazil. *Iheringia - Serie Zoologia*, *104*(1), 43–49. https://doi.org/10.1590/1678-4766201410414349

de Freitas, C. H., Justino, C. S., & Setz, E. Z. F. (2014). Road-kills of the giant anteater in south-eastern Brazil: 10 years monitoring spatial and temporal determinants. *Wildlife Research*, *41*(8), 673–680. https://doi.org/10.1071/WR14220

Delgado, J. D., Durán Humia, J., Rodríguez Pereiras, A., Rosal, A., del Valle Palenzuela, M., Morelli, F., ... Rodríguez Sánchez, J. (2019). The spatial distribution of animal casualties within a road corridor: Implications for roadkill monitoring in the southern Iberian rangelands. *Transportation Research Part D: Transport and Environment, 67*, 119-130. https://doi.org/10.1016/j.trd.2018.11.017

Department for Environment, Food and Rural Affairs, DEFRA. (2022). *Protected sites and species: detailed information.* Retrieved from https://www.gov.uk/topic/planning-development/protected-sites-species

Department for Transport. (2019). *Road traffic estimates in Great Britain: 2019*. Government of the United Kingdom. Retrieved from https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/916749/road-traffic-estimates-in-great-britain-2019.pdf.

Department for Transport. (2022a). *Road lengths in Great Britain (2021)*. Government of the United Kingdom. Retrieved from https://www.gov.uk/government/statistics/road-lengths-in-great-britain-2021/road-lengths-in-great-britain-2021

Department for Transport. (2022b). *Road traffic estimates in Great Britain: 2021*. Government of the United Kingdom. Retrieved from https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/1107056/road-traffic-estimates-in-great-britain-2021.pdf.

Dhiab, O., D'Amico, M., & Selmi, S. (2023). Experimental evidence of increased carcass removal along roads by facultative scavengers. *Environmental Monitoring and Assessment, 195*(1). https://doi.org/10.1007/S10661-022-10829-8

Dorning, J., & Harris, S. (2019). Quantifying group size in the red fox: impacts of definition, season and intrusion by non-residents. *Journal of Zoology, 308*(1), 37-46. . https://doi.org/10.1111/jzo.12650

Doncaster, C. P., Rondinini, C., & Johnson, P. C. D. D. (2001). Field test for environmental correlates of dispersal in hedgehogs *Erinaceus europaeus*. *Journal of Animal Ecology*, *70*(1), 33–46. https://doi.org/10.1111/J.1365-2656.2001.00471.X

Dulac, J. (2013). *Global land transport infrastructure requirements. Estimating road and railway infrastructure capacity and costs to 2050.* International Energy Agency. Retrieved from https://www.iea.org/reports/global-land-transport-infrastructure-requirements

Erritzoe, J., Mazgajski, T. D., & Rejt, Ł. (2003). Bird casualties on European roads — A review. *Acta Ornithologica, 38*(2), 77–93. https://doi.org/10.3161/068.038.0204

ESRI. (2015). *ArcGIS Desktop: 10.3.1.* Environmental Systems Research Institute. USA : California

Gehrt, S. (2002). Evaluation of spotlight and road-kill surveys as indicators of local raccoon abundance. *Wildlife Society Bulletin, 30*(2), 449-456. https://www.jstor.org/stable/3784503

George, L., Macpherson, J. L., Balmforth, Z., & Bright, P. W. (2011). Using the dead to monitor the living: Can road kill counts detect trends in mammal abundance? *Applied Ecology and Environmental Research*, *9*(1), 27–41. https://doi.org/10.15666/aeer/0901_027041

Gerow, K., Kline, N. C., Swann, D., & Pokorny, M. (2010). Estimating annual vertebrate mortality on roads at saguaro national park, Arizona. *Human-Wildlife Interactions, 4*(2), 283-292. https://doi.org/10.26077/DHG5-WG98

González-Suárez, M., Zanchetta Ferreira, F., & Grilo, C. (2018). Spatial and species-level predictions of road mortality risk using trait data. *Global Ecology And Biogeography*, *27*(9), 1093–1105. https://doi.org/10.1111/geb.12769

Grilo, C., Bissonette, J. A., & Santos-Reis, M. (2009). Spatial-temporal patterns in Mediterranean carnivore road casualties: Consequences for mitigation. *Biological Conservation*, *142*(2), 301–313. https://doi.org/10.1016/j.biocon.2008.10.026

Grilo, C., Borda-de-Água, L., Beja, P., Goolsby, E., Soanes, K., le Roux, A., ... González-Suárez, M. (2021). Conservation threats from roadkill in the global road network. *Global Ecology and Biogeography, 30*(11), 2200–2210. https://doi.org/10.1111/GEB.13375

Grilo, C., Sousa, J., Ascensão, F., Matos, H., Leitão, I., Pinheiro, P., ... Revilla, E. (2012). Individual spatial responses towards roads: implications for mortality risk. *PLOS ONE*, *7*(9), 1–11. https://doi.org/10.1371/journal.pone.0043811

Grueber, C. E., Reid-Wainscoat, E. E., Fox, S., Belov, K., Shier, D. M., Hogg, C. J., & Pemberton, D. (2017). Increasing generations in captivity is associated with increased vulnerability of Tasmanian devils to vehicle strike following release to the wild. *Scientific Reports*, *7*(1), 2161. https://doi.org/10.1038/s41598-017-02273-3

Guinard, É., Julliard, R., & Barbraud, C. (2012). Motorways and bird traffic casualties: Carcasses surveys and scavenging bias. *Biological Conservation*, *147*(1), 40–51. https://doi.org/10.1016/j.biocon.2012.01.019

Gunson, K. E., Mountrakis, G., & Quackenbush, L. J. (2011). Spatial wildlife-vehicle collision models: A review of current work and its application to transportation mitigation projects. *Journal of Environmental Management*, *92*(4), 1074–1082. https://doi.org/10.1016/j.jenvman.2010.11.027

Haigh, A., Kelly, M., Butler, F., & O’Riordan, R. M. (2014a). Non-invasive methods of separating hedgehog (*Erinaceus europaeus*) age classes and an investigation into the age structure of road kill. *Acta Theriologica*, *59*(1), 165–171. https://doi.org/10.1007/s13364-013-0142-0

Haigh, A., O’Riordan, R. M., & Butler, F. (2014b). Hedgehog *Erinaceus europaeus* mortality on Irish roads. *Wildlife Biology*, *20*(3), 155–160. https://doi.org/10.2981/wlb.12126

Henry, D. A. W., Collinson-Jonker, W. J., Davies-Mostert, H. T., Nicholson, S. K., Roxburgh, L., & Parker, D. M. (2021). Optimising the cost of roadkill surveys based on an analysis of carcass persistence. *Journal of Environmental Management*, *291*. https://doi.org/10.1016/j.jenvman.2021.112664

Huijser, M. P., Duffield, J. W., Clevenger, A. P., Ament, R. J., & McGowen, P. T. (2009). Cost-benefit analyses of mitigation measures aimed at reducing collisions with large ungulates in the United States and Canada: a decision support tool. *Ecology and Society*, *14*(2). https://doi.org/10.5751/ES-03000-140215

Institute for Government. (2022). Timeline of UK government coronavirus lockdowns and restrictions. Retrieved from https://www.instituteforgovernment.org.uk/data-visualisation/timeline-coronavirus-lockdowns

Jaarsma, C. F., van Langevelde, F., & Botma, H. (2006). Flattened fauna and mitigation: Traffic victims related to road, traffic, vehicle, and species characteristics. *Transportation Research Part D: Transport and Environment*, *11*(4), 264–276. https://doi.org/10.1016/j.trd.2006.05.001

Jacobson, S. L., Bliss-Ketchum, L. L., Rivera, C. E., & Smith, W. P. (2016). A behavior-based framework for assessing barrier effects to wildlife from vehicle traffic volume. Ecosphere, 7(4), e01345. https://doi.org/10.1002/ecs2.1345

Jones, P. R. (2019). A note on detecting statistical outliers in psychophysical data. *Perception, & Psychophysics*, *81*, 1189–1196. https://doi.org/10.3758/s13414-019-01726-3

Kang, W., Minor, E. S., Woo, D., Lee, D., & Park, C. R. (2016). Forest mammal roadkills as related to habitat connectivity in protected areas. *Biodiversity and Conservation*, *25*(13), 2673–2686. https://doi.org/10.1007/s10531-016-1194-7

Kelly, D. J., Gaughran, A., Mullen, E., MacWhite, T., Maher, P., Good, M., & Marples, N. M. (2020). Extra Territorial Excursions by Eurasian badgers are not limited by age, sex or season. *Scientific Reports*, *10*(1). https://doi.org/10.1038/s41598-020-66809-w

Klöcker, U., Croft, D. B., & Ramp, D. (2006). Frequency and causes of kangaroo-vehicle collisions on an Australian outback highway. *Wildlife Research*, *33*(1), 5–15. https://doi.org/10.1071/WR04066

Legagneux, P., & Ducatez, S. (2013). European birds adjust their flight initiation distance to road speed limits. *Biology Letters*, *9*(5). https://doi.org/10.1098/rsbl.2013.0417

Lima Santos, R. A., Santos, S. M., Santos-Reis, M., Picanço de Figueiredo, A., Bager, A., Aguiar, L. M. S., & Ascensão, F. (2016). Carcass persistence and detectability: Reducing the uncertainty surrounding wildlife-vehicle collision surveys. *PLOS ONE*, *11*(11), e0165608. https://doi.org/10.1371/journal.pone.0165608

Lima Santos, R. A., Ascensão, F., Ribeiro, M. L., Bager, A., Santos-Reis, M., & Aguiar, L. M. S. (2017). Assessing the consistency of hotspot and hot-moment patterns of wildlife road mortality over time. *Perspectives in Ecology and Conservation*, *15*(1), 56–60. https://doi.org/10.1016/J.PECON.2017.03.003

Lin, S. C. (2016). Landscape and traffic factors affecting animal road mortality. *Journal of Environmental Engineering and Landscape Management*, *24*(1), 10–20. https://doi.org/10.3846/16486897.2015.1098652

Liordos, V., Jokimäki, J., Kaisanlahti-Jokimäki, M. L., Valsamidis, E., & Kontsiotis, V. J. (2021). Niche analysis and conservation of bird species using urban core areas. *Sustainability (Switzerland)*, *13*(11), 1–15. https://doi.org/10.3390/su13116327

Madden, J. R., & Perkins, S. E. (2017). Why did the pheasant cross the road? Long-term road mortality patterns in relation to management changes. *Royal Society Open Science*, *4*(10). https://doi.org/10.1098/rsos.170617

Mayer, M., Coleman Nielsen, J., Elmeros, M., & Sunde, P. (2021). Understanding spatio-temporal patterns of deer-vehicle collisions to improve roadkill mitigation. *Journal of Environmental Management*, *295*. https://doi.org/10.1016/j.jenvman.2021.113148

Medinas, D., Marques, J. T., & Mira, A. (2013). Assessing road effects on bats: The role of landscape, road features, and bat activity on road-kills. *Ecological Research*, *28*(2), 227–237. https://doi.org/10.1007/s11284-012-1009-6

Medrano-Vizcaíno,P., Grilo, C., Silva Pinto, F. A., Carvalho, W. D., Melinski, R. D., Schultz, E. D. (2022). Roadkill patterns in Latin American birds and mammals. Global Ecology and Biogeography, 31(9), 1756-1783. https://doi.org/10.1111/geb.13557

Meijer, J. R., Huijbregts, M. A. J., Schotten, K. C. G. J., & Schipper, A. M. (2018). Global patterns of current and future road infrastructure. *Environmental Research Letters*, *13*(6). https://doi.org/10.1088/1748-9326/aabd42

Morelli, F., Benedetti, Y., & Delgado, J. D. (2020). A forecasting map of avian roadkill-risk in Europe: A tool to identify potential hotspots. *Biological Conservation*, *249*. https://doi.org/10.1016/j.biocon.2020.108729

Mumme, R. L., Schoech, S. J., Woolfenden, G. E., & Fitzpatrick, J. W. (2000). Life and death in the fast lane: demographic consequences of road mortality in the Florida Scrub-Jay. *Conservation Biology*, *14*(2), 501–512. https://doi.org/10.1046/j.1523-1739.2000.98370

NBN Atlas. (2021). Species Lists. Retrieved from https://lists.nbnatlas.org/public/speciesLists

Neal, E., & Cheeseman, C. (1996). *Badgers*. UK : T & A D Poyser.

Ordnance Survey. (2020). *EDINA Digimap*. University of Edinburgh. Retrieved from https://digimap.edina.ac.uk/os

Orłowski, G., & Nowak, L. (2006). Factors influencing mammal roadkills in the agricultural landscape of South-Western Poland. *Polish Journal of Ecology*, *54*(2), 283–294.

Phillips, B. B., Bullock, J. M., Osborne, J. L., & Gaston, K. J. (2019). Ecosystem service provision by road verges. *Journal of Applied Ecology*, *57*(3), 488-501. https://doi.org/10.1111/1365-2664.13556

Planillo, A., Kramer-Schadt, S., & Malo, J. E. (2015). Transport infrastructure shapes foraging habitat in a raptor community. *PLOS ONE*, *10*(3), e0118604. https://doi.org/10.1371/JOURNAL.PONE.0118604

Puig, J., & Sanz, L. (2012). Wildlife roadkills and underpass use in Northern Spain. *Environ. Eng. and Manag J*, *11*(6), 1141-1147. https://doi.org/10.30638/eemj.2012.138

R Core Development Team. (2022). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing. https://www.r-project.org/

Ramsden, D. J. (2004). *Barn owls and major roads. Results and recommendations from a 15 year research project*. Barn Owl Trust. Retrieved from https://www.barnowltrust.org.uk/product/barn-owls-and-major-roads-results-and-recommendations-from-a-15-year-research-project/

Ratton, P., Secco, H., & da Rosa, C. A. (2014). Carcass permanency time and its implications to the roadkill data. *European Journal of Wildlife Research*, *60*(3), 543–546. https://doi.org/10.1007/S10344-014-0798-Z/FIGURES/2

Raymond, S., Schwartz, A. L. W., Thomas, R. J., Chadwick, E., & Perkins, S. E. (2021). Temporal patterns of wildlife roadkill in the UK. *PLOS ONE*, *16*(10), e0258083. https://doi.org/10.1371/JOURNAL.PONE.0258083

Rendall, A. R., Webb, V., Sutherland, D. R., White, J. G., Renwick, L., & Cooke, R. (2021). Where wildlife and traffic collide: Roadkill rates change through time in a wildlife-tourism hotspot. *Global Ecology and Conservation*, *27*, e01530. https://doi.org/10.1016/J.GECCO.2021.E01530

Robson, L., & Blouin-Demers, G. (2013). Eastern hognose snakes (*Heterodon platirhinos*) avoid crossing paved roads, but not unpaved roads. *Copeia*, *2013*(3), 507-511. https://doi.org/10.1643/CE-12-033

Ruiz-Capillas, P., Mata, C., & Malo, J. E. (2015). How many rodents die on the road? Biological and methodological implications from a small mammals' roadkill assessment on a Spanish motorway. *Ecological Research*, *30*(3), 417–427. https://doi.org/10.1007/s11284-014-1235-1

Rydell, J., Eklöf, J., Sánchez-Navarro, S. (2017). Age of enlightenment: Long-term effects of outdoor aesthetic lights on bats in churches. *Royal Society Open Science*, *4*(12). https://doi.org/10.1098/rsos.171630

Santos, S. M., Carvalho, F., & Mira, A. (2011). How long do the dead survive on the road? Carcass persistence probability and implications for road-kill monitoring surveys. PLOS ONE, 6(9), e25383. https://doi.org/10.1371/journal.pone.0025383

Santos, S. M., Marques, J. T., Lourenço, A., Medinas, D., Barbosa, A. M., Beja, P., & Mira, A. (2016). Sampling effects on the identification of roadkill hotspots: Implications for survey design. *Journal of Environmental Management*, *162*, 87–95. https://doi.org/10.1016/J.JENVMAN.2015.07.037

Schaus-Calderón, J. S. (2021). *Responses of the West European hedgehog to urbanisation: impact on population dynamics, animal movement and habitat selection.* [PhD Thesis, Nottingham Trent University].

Schwartz, A. L. W., Williams, H. F., Chadwick, E., Thomas, R. J., & Perkins, S. E. (2018). Roadkill scavenging behaviour in an urban environment. *Journal of Urban Ecology*, *4*(1), 1–7. https://doi.org/10.1093/jue/juy006

Seiler, A., & Helldin, J. O. (2006). *Mortality in wildlife due to transportation.* In J. Davenport., & J. L. Davenport (Eds) The Ecology of Transportation: Managing Mobility for the Environment (pp. 165–189). Berlin : Springer

Seo, C., Thorne, J. H., Choi, T., Kwon, H., & Park, C. H. (2013). Disentangling roadkill: the influence of landscape and season on cumulative vertebrate mortality in South Korea. *Landscape and Ecological Engineering*, *11*(1), 87–99. https://doi.org/10.1007/s11355-013-0239-2

Shepard, D. B., Kuhns, A. R., Dreslik, M. J., & Phillips, C. A. (2008). Roads as barriers to animal movement in fragmented landscapes. *Animal Conservation*, *11*(4), 288-296. https://doi.org/10.1111/j.1469-1795.2008.00183.x

Slater, F. M. (2002). An assessment of wildlife road casualties - the potential discrepancy between numbers counted and numbers killed. *Web Ecology*, *3*(1), 33–42. https://doi.org/10.5194/we-3-33-2002

Steiner, W., Scholl, E. M., Leisch, F., & Hacklander, K. (2021). Temporal patterns of roe deer traffic accidents: Effects of season, daytime and lunar phase. *PLOS ONE*, *16*(3), 16–19. https://doi.org/10.1371/journal.pone.0249082

Raymond, S., Schwartz, A. L. W., Thomas, R. J., Chadwick, E., & Perkins, S. E. (2021). Temporal patterns of wildlife roadkill in the UK. *PLOS ONE*, *16*(10), e0258083. https://doi.org/10.1371/JOURNAL.PONE.0258083

Teixeira, F. Z., Coelho, A. V. P., Esperandio, I. B., & Kindel, A. (2013). Vertebrate road mortality estimates: Effects of sampling methods and carcass removal. *Biological Conservation*, *157*, 317–323. https://doi.org/10.1016/J.BIOCON.2012.09.006

Tejera, G., Rodríguez, B., Armas, C., & Rodríguez, A. (2018). Wildlife-vehicle collisions in Lanzarote Biosphere Reserve, Canary Islands. *PLOS ONE*, *13*(3). https://doi.org/10.1371/journal.pone.0192731

Underhill, J. E. (2002). Roads and wildlife: a study of the effects of roads on mammals in roadside habitats. [PhD Thesis, University of Birmingham].

Valerio, F., Basile, M., & Balestrieri, R. (2021). The identification of wildlife-vehicle collision hotspots: Citizen science reveals spatial and temporal patterns. *Ecological Processes*, *10*(1). https://doi.org/10.1186/s13717-020-00271-4

van der Horst, S., Goytre, F., Marques, A., Santos, S., Mira, A., & Lourenço, R. (2019). Road effects on species abundance and population trend: a case study on tawny owl. *European Journal of Wildlife Research*, *65*(6), 1–11. https://doi.org/10.1007/S10344-019-1325-Z/FIGURES/7

Vittinghoff, E., & McCulloch, C. E. (2007). Relaxing the rule of ten events per variable in logistic and cox regression. *American Journal of Epidemiology*, *165*(6), 710–718. https://doi.org/10.1093/AJE/KWK052

Wembridge, D., Johnson, G., Al-Fulaij, N., & Langton, S. (2022). *The State of Britain's Hedgehogs 2022*. People's Trust for Endangered Species and the British Hedgehog Preservation Society. Retrieved from https://www.hedgehogstreet.org/wp-content/uploads/2022/02/SoBH-2022-Final.pdf

Wood, S. N. (2017). Generalized additive models: An introduction with R (2nd Ed.). New York : Chapman and Hall.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14. https://doi.org/10.1111/J.2041-210X.2009.00001.X

Appendices III – VI

Appendix III: A mathematical derivation of a general model for estimating road mortality rates (individuals/km/year) from counts of casualties from systematic, repeated road surveys

Casualties occur at a constant rate, λ, and are removed at a rate, μ, proportional to the density of casualties, s (= n/l), where n is the total number of casualties recorded, l is the total distance surveyed, and d is the detection probability specific to body size. At time $t = 0$, $s = 0$ and $ds/dt = \lambda$. As t increases, s approaches a maximum value, s' at which $ds/dt = 0$ and $\mu = \lambda$.

For repeat surveys (i.e., of the same road section), t is the time between surveys when casualties are removed after each survey.

Let p be the probability that a carcass is removed in time t.

$ds/dt = \lambda - \mu$

$\quad = \lambda - ps$

Integrating to find s as a function of t,

$dt/ds = 1/(\lambda - ps)$

$\int dt = \int 1/(\lambda - ps)ds$

$t = -1/p.\ln(\lambda - ps) + (\ln c)/p$ where $(\ln c)/p$ is a constant.

When $t = 0$, $s = 0$, and $c = \lambda$

substituting for c and rearranging,

$\lambda = ps/(1 - e^{-pt}).d$

where p is the reciprocal of mean persistence time of a carcass, t_r (analogous to the radioactive decay constant).

As $t \rightarrow$ infinity, $s \rightarrow s'$ and

$\lambda = ps'$

$\quad = n/l.t_r$

Appendix IV: Results of General Additive Model and chi-squared (X^2) test comparing road mortality by day, month and year for species recorded during road surveys in Nottinghamshire. $* p \leq 0.05$, $** p \leq 0.01$, $*** p \leq 0.001$. **Species are ordered alphabetically.**

Species	Day of the week			Month				Year	
	e.d.f.	F-value	p-value	e.d.f.	F-value	p-value		X^2 statistic	p-value
Brown rat	1.133	1.208	0.214	3.388	4.004	0.030	*	0.004	0.952
Carrion crow	<0.001	0.000	0.458	1.434	0.961	0.107		0.002	0.966
Collared dove	<0.001	0.000	0.565	0.243	0.076	0.324		0.004	0.950
Common blackbird	<0.001	0.000	0.600	1.564	0.591	0.051		0.083	0.771
Common buzzard	<0.001	0.000	0.489	3.780	2.235	0.151		0.010	0.920
Common frog	1.028	0.932	0.256	1.887	1.291	0.106		0.011	0.915
Common pheasant	1.086	1.191	0.207	5.112	2.595	0.020	*	0.015	0.903
Dunnock	<0.001	0.000	0.594	1.092	0.514	0.196		0.002	0.964
Eurasian badger	0.615	0.514	0.278	2.120	2.820	0.022	*	0.01	0.920
Eurasian magpie	1.75	4.176	0.087	3.166	4.534	0.018	*	0.003	0.954
European hare	0.524	0.357	0.336	2.192	3.351	0.015	*	0.021	0.880
European rabbit	0.742	0.568	0.302	2.175	2.387	0.036	*	0.093	0.760
Grey squirrel	<0.001	0.000	0.541	2.820	4.154	0.007	**	0.009	0.926
House mouse	<0.001	0.000	0.647	0.759	0.328	0.222		0.001	0.978
House sparrow sp.	1.045	0.991	0.243	1.457	1.090	0.864		0.029	0.860
Pigeon sp.	1.26	1.585	0.175	3.606	20.660	<0.001	***	0.240	0.625
Pipistrelle sp.	1.669	4.449	0.074	3.564	4.197	0.037	*	0.005	0.943
Red fox	0.445	0.390	0.251	3.897	6.325	0.017	*	0.012	0.911
Reeves' Muntjac Deer	<0.001	0.000	0.576	3.887	5.106	0.028	*	0.012	0.911
Tawny owl	1.351	2.295	0.117	3.856	0.681	0.244		0.017	0.900
Thrush spp. (excluding blackbirds)	0.533	0.431	0.287	0.799	0.379	0.195		0.002	0.960
West European hedgehog	<0.001	0.000	0.582	3.393	22.35	<0.001	***	0.029	0.865
Wood mouse	<0.001	0.000	0.939	2.254	3.663	0.012	*	0.003	0.954

Appendix V: Differences between corrected and uncorrected road mortality rates, and between road mortality rates that were estimated from surveys under COVID-19 lockdown restrictions vs under 'normal' conditions (i.e., no restrictions).

The corrected rates were estimates using Equation 1 (i.e., correcting for survey frequency, carcass persistence, and detection probability). The uncorrected rates were estimated by dividing the raw number of carcasses recorded by the total distance of road surveyed across the 269 road surveys. Species are ordered from the highest annual road mortality rate to the lowest.

Species	***n***	**Uncorrected road mortality rate (km per day)**	**Percentage difference to corrected road mortality rate**	**Difference in value to corrected road mortality rate†**	**Road mortality rate under COVID-19 lockdown restrictions (km per day)**	**Road mortality rate under 'normal' conditions (km per day)**	**Percentage difference between road mortality rates with and without restrictions**	**Difference in value between road mortality rates with and without restrictions**
European rabbit	362	0.00965	-38%	1.6	0.00898	0.01793	50%	2.0
Pigeon spp.	342	0.00912	-36%	1.6	0.00533	0.01726	69%	3.2
Common blackbird	236	0.00629	-55%	2.2	0.00930	0.01594	42%	1.7
Grey squirrel	223	0.00595	-35%	1.5	0.00674	0.01028	34%	1.5
Common pheasant	210	0.00560	-36%	1.6	0.00556	0.00996	44%	1.8
European hare	81	0.00235	-34%	1.5	0.00162	0.00438	63%	2.7
West European hedgehog	33	0.00229	-35%	1.5	0.00218	0.00399	45%	1.8
Sparrow spp.	88	0.00216	-74%	3.9	0.00460	0.00971	53%	2.1

Brown rat	18	0.00099	-54%	2.2	0.00205	0.00220	7%	1.1
Wood mouse	7	0.00088	-85%	6.5	0.00616	0.00571	-8%	0.9
Carrion crow	37	0.00077	-34%	1.5	0.00036	0.00144	75%	4.0
Thrush spp.	86	0.00053	-73%	3.7	0.00089	0.00237	63%	2.7
Common frog	12	0.00048	-81%	5.3	0.00437	0.00204	-114%	0.5
Tawny owl	17	0.00048	-32%	1.5	0.00105	0.00062	-68%	0.6
Stoat	20	0.00045	-55%	2.2	0.00078	0.00093	16%	1.2
House mouse	15	0.00045	-77%	4.4	0.00313	0.00170	-84%	0.5
Eurasian magpie	29	0.00043	-53%	2.1	0.00050	0.00104	52%	2.1
Eurasian badger	8	0.00040	-16%	1.2	0.00000	0.00063	100%	n/a
Common buzzard	17	0.00040	-32%	1.5	0.00070	0.00057	-22%	0.8
Dunnock	16	0.00040	-76%	4.2	0.00050	0.00208	76%	4.2
Collared dove	14	0.00037	-57%	2.3	0.00028	0.00107	74%	3.9
Pipistrelle spp.	18	0.00032	-91%	10.9	0.00387	0.00345	-12%	0.9
Red fox	3	0.00027	-16%	1.2	0.00014	0.00038	63%	2.7
Reeves' muntjac deer	15	0.00027	-40%	1.7	0.00039	0.00047	16%	1.2
Red-legged partridge	8	0.00024	-34%	1.5	0.00000	0.00048	100%	n/a
Barn owl	4	0.00021	-35%	1.5	0.00018	0.00038	52%	2.1
Eurasian wren	15	0.00021	-79%	4.8	0.00113	0.00101	-12%	0.9
European mole	10	0.00021	-60%	2.5	0.00030	0.00070	58%	2.4

Smooth newt	2	0.00019	-91%	11.5	0.00408	0.00161	-153%	0.4
Grey partridge	6	0.00016	-58%	2.4	0.00000	0.00051	100%	n/a
Field vole	4	0.00011	-71%	3.5	0.00000	0.00049	100%	n/a
Common weasel	9	0.00011	-57%	2.3	0.00027	0.00024	-12%	0.9
Eurasian jay	3	0.00011	-57%	2.3	0.00000	0.00032	100%	n/a
European goldfinch	3	0.00011	-79%	4.8	0.00000	0.00068	100%	n/a
European polecat	8	0.00011	-37%	1.6	0.00019	0.00017	-12%	0.9
Common kestrel	10	0.00008	-53%	2.1	0.00000	0.00023	100%	n/a
Common shrew	4	0.00008	-77%	4.4	0.00000	0.00046	100%	n/a
Eurasian sparrowhawk	4	0.00008	-53%	2.1	0.00000	0.00022	100%	n/a
European robin	2	0.00008	-77%	4.4	0.00155	0.00000	100%	n/a
Great crested newt	3	0.00008	-89%	8.8	0.00000	0.00092	100%	n/a
Western jackdaw	4	0.00008	-53%	2.1	0.00000	0.00022	100%	n/a
Common starling	3	0.00005	-74%	3.9	0.00000	0.00027	100%	n/a
Common toad	3	0.00005	-87%	7.7	0.00000	0.00054	100%	n/a
Roe deer	2	0.00005	-34%	1.5	0.00000	0.00021	100%	n/a

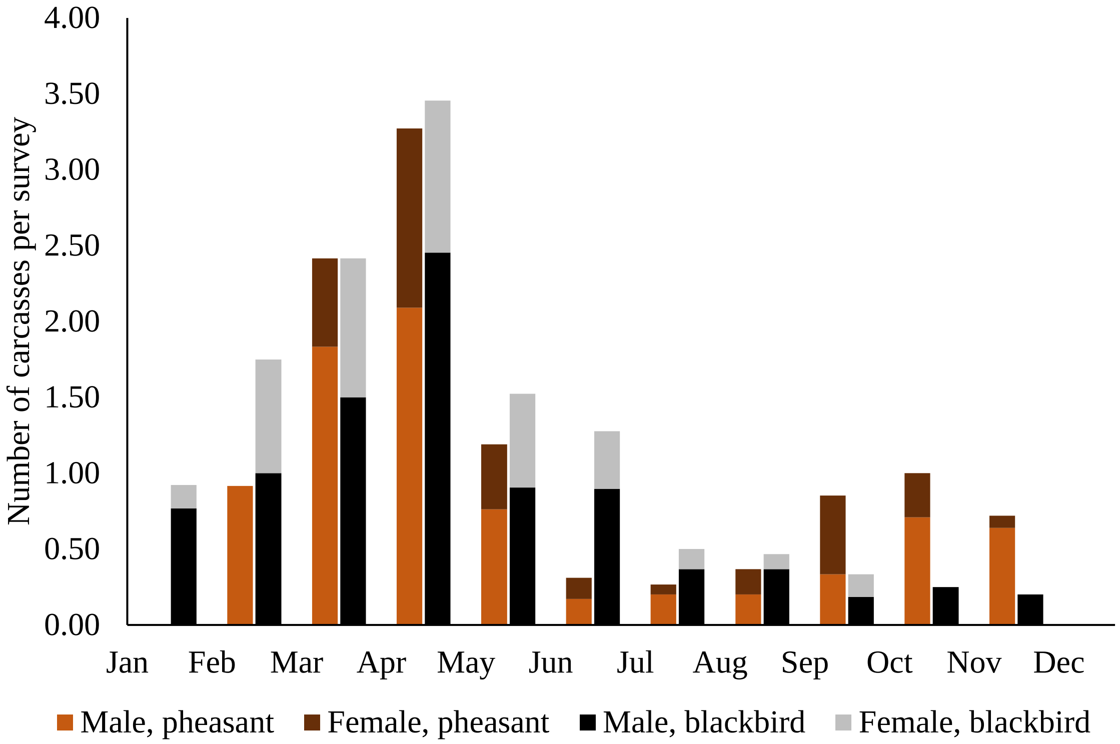
Common moorhen	1	0.00003	n/a*	n/a*	n/a*	n/a*	n/a*	n/a
Common quail	1	0.00003	n/a*	n/a*	n/a*	n/a*	n/a*	n/a
Mallard	1	0.00003	n/a*	n/a*	n/a*	n/a*	n/a*	n/a
Pied wagtail	1	0.00003	n/a*	n/a*	n/a*	n/a*	n/a*	n/a
Yellow hammer	1	0.00003	n/a*	n/a*	n/a*	n/a*	n/a*	n/a

*Insufficient records for carcass persistence detection and therefore accurate (i.e., corrected) road mortality rate estimation.

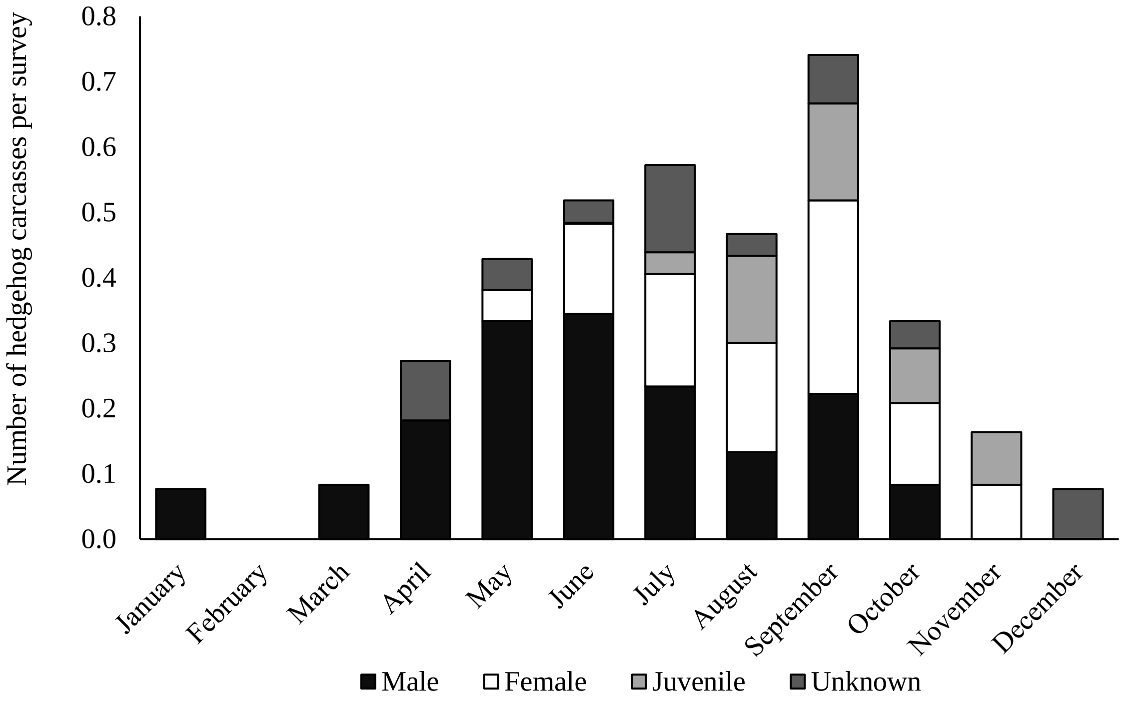
†For example, the corrected road mortality rate for pigeon spp. is 1.6 times larger than the uncorrected rate for the species.

Appendix VI: Seasonal differences in the road mortality A) between sexes of common pheasant and common blackbird and B) between sexes and age groups of west European hedgehog from May 2020 and November 2021.

A)



B)



CHAPTER 4: Impacts and Potential Mitigation of Road Mortality for Hedgehogs in Europe

Based on the review article in the peer-reviewed journal *Animals:*

Moore, L. J., Petrovan, S. O., Baker, P. J., Bates, A. J., Hicks, H. L., Perkins, S. E., & Yarnell, R. W. (2020). Impacts and potential mitigation of road mortality for hedgehogs in Europe. *Animals*, *10*(9), 1523. https://doi.org/10.3390/ani10091523

4.1 General 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 (Ibisch et al., 2016; Meijer et al., 2018). Interest in the ecological impacts of roads has grown since the mid-20th century, with formal recognition of a new field, road ecology, by Forman and Alexander in 1998. This branch of ecological research has revealed the extensive role that roads play in direct and indirect habitat loss and alteration. Traffic noise, light pollution, and chemical pollution (salt, heavy metals, herbicides) are all identified as important correlates of habitat modification, fragmentation and changes in animal movement in road-dominated environments (Coffin, 2007).

Perhaps the most conspicuous impact of roads are wildlife–vehicle collisions (WVCs) that result in the death of millions of animals worldwide every year (Seiler and Helldin, 2006). Biological characteristics of the animals themselves (e.g., age, sex and movement), biotic factors (e.g., time of day, season), traffic and road characteristics (e.g., traffic volume, road width, sinuosity) and environmental characteristics (e.g., topography, neighbouring habitat structure) all interact to form a species-specific spatiotemporal distribution of WVCs (Morelle et al., 2013). The consequences of road mortality are typically two-fold: (1) direct depletion of individuals from a population and/or (2) fragmentation of populations and reduced gene flow (Huijser and Bergers, 2000; Fahrig and Rytwinski, 2009; Meek, 2009). Importantly, these consequences can alter meta-population structure and population fitness, in turn increasing the risk of local extinction (Dexter et al., 2018). Roads are therefore considered responsible for the nationwide decline of certain species and a limiting factor in the recovery of others (Trombulak & Frissell, 2000; Carvalho & Mira, 2011). 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 (Morelle et al., 2013). In comparison, fewer studies have examined smaller mammal species, such as hedgehogs (*Erinaceidae* spp).

There are five species of hedgehog with all or part of their range in Europe, although hedgehog taxonomy has been debated due to contradictions between molecular and morphological phylogenies (Bannikova et al., 2014). The west European hedgehog (*Erinaceus europaeus*) is distributed over Ireland, Great Britain, and western mainland Europe. The Algerian hedgehog (*Atelerix algirus*) is present in North Africa and was introduced to Spain and several Mediterranean islands (García-Rodríguez and Puig-Montserrat, 2014). The northern white-breasted hedgehog (*Erinaceus roumanicus*) is distributed throughout Central and Eastern Europe, whilst the southern white-breasted hedgehog (*Erinaceus concolor*) is present in Eastern Europe and Southwestern Asia (Bolfíková & Hulva, 2012). The long-eared hedgehog (*Helmiechinus auritus*) maintains part of its predominately Middle Eastern range in Cyprus and Ukraine (Bannikova et al., 2014).

Although hedgehog density has been reported to be up to 35% lower near roads (Huijser, Bergers and De Vries, 1998), road-killed hedgehogs are a very familiar sight across Europe and are frequently the main mammal roadkill recorded in citizen science projects and expert multispecies roadkill surveys (Gruychev, 2018; Tejera et al., 2018). For example, an estimated 113,000–340,000 *E. europaeus* individuals are killed on roads every year in Great Britain (Wembridge et al., 2016) and the Netherlands (Huijser, 1997), and 230,000–350,000 individuals every year in Belgium (Holsbeek et al., 1999). Comparisons between short-term studies are difficult as roadkill rates can fluctuate with changes in hedgehog density, road conditions, and traffic volume (Brockie et al., 2009). Alternatively, long-term roadkill data are valuable to observe changes in temporal behaviour or monitor population trends (Schwartz et al., 2020). For example, Reichholf (2015) and Müller (2018) found hedgehog road mortality to have steadily decreased since the 1970s in Germany, and Wilson and Wembridge (2018) found similar patterns in Britain since 2001. It is claimed that these changes reflect the marked declines over the past two decades of *E. europaeus* in several countries across Europe (Hof & Bright, 2016; Müller, 2018). *A. algirus* has also shown reduced abundance and local extinctions in its introduced range in Europe (García-Rodríguez and Puig-Montserrat, 2014). However, sufficient population data to identify nationwide declines of any hedgehog species are currently limited to the UK (Roos, Johnston and Noble, 2012; Pettett et al., 2018), the Netherlands (Poel et al., 2015) and, to a lesser extent, Denmark (Krange, 2015) and Germany (Müller, 2018). Traffic-related mortality has been implicated as a significant component of hedgehog population declines and also constitutes a welfare concern (Huijser & Bergers, 2000;

Reichholf, 2015; Wembridge et al., 2016; Wright et al., 2020). In recent times, the field has used nationwide monitoring schemes such as “The Road Lab” (formally named “Project Splatter”), a citizen science study in the UK that collates such data (Bíl et al., 2020). 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 (Brockie et al., 2009; Wright et al., 2020). Records of hedgehog road mortality have also been used to estimate annual road mortality (Huijser, 1997; Holsbeek et al., 1999; Wembridge et al., 2016), track epizootics (Brockie et al., 2009) and have the potential to estimate population abundance (George et al., 2011). 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 (van der Ree et al., 2009).

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 (Selva et al., 2011; Meijer et al., 2018) and road networks continue to expand rapidly. In Europe, an average of 70,000 km of new roads are built every year (Eurostat, 2013) and many existing roads are modernised or widened (Dom & Ridder, 2002). Road development, however, is not consistent across European countries (Selva et al., 2011). Coupled with the assertion that road mortality is the leading cause of human-induced vertebrate mortality on land (Forman & Alexander, 1998; Hill et al., 2019), road ecology is a critical frontier of applied scientific research. As several European hedgehog species are declining and disproportionately represented in roadkill records (Holsbeek et al., 1999), understanding how important road mortality is for population trends is a necessary step for hedgehog conservation. This review aims to consolidate the current knowledge on the consequences of road mortality for the viability of hedgehog populations in Europe. Online databases were used to search for and appraise published, peer-reviewed articles on hedgehog road ecology, complemented by government reports on road statistics. This review synthesises information on the possible direct role that road mortality plays in population declines. It then discusses the individual-level risk of road mortality and the contribution of hedgehog–vehicle collisions to much-discussed fragmentation effects and associated genetic heterozygosity. Finally, this review identifies opportunities for road mitigation for hedgehogs, current knowledge gaps and priorities for future research.

4.2 Does road mortality really reflect population persistence?

It is difficult to confirm or refute the impact of road mortality on population trends because population persistence depends on a complex set of inter-related factors (Moore et al., 2023). Several criteria exist to evaluate the ecological effects of road mortality. For example, the total number of road-killed animals must be considered in the context of population size (Wembridge et al., 2016), reproductive output, immigration and emigration rates (Row, Blouin-Demers and Weatherhead, 2007) and whether WVCs are compensatory or additive to other forms of mortality (Seiler and Helldin, 2006). To date, research has only partially met these criteria. Recent year-round studies have evidenced an average 0.001–3.65 hedgehog casualties/km/year for all European species across several European countries (Table 4.1).

Table 4.1: Estimates of the mean number of hedgehogs killed on roads per kilometre per year in different European countries. Data are derived from systematic, year-round studies.

Species	Country	Year(s) of study	Mean number of road casualties/km/year	Surveyed road types	Habitats along survey route	Reference
E. europaeus	Ireland	2008–2010	0.001	National and regional roads	Residential, rural, woodland, and built-up areas	Haigh, O'Riordan and Butler, 2014b
	Finland	2004–2005	0.007	National, regional, and local roads	Residential, forests and built-up areas	Rautio et al., 2016
	Spain	2001–2003	0.76–1.42	National roads	Forests	Puig & Sanz, 2012
	Slovakia	2000–2002	1.6	National, regional, and local roads	Agricultural land, forests, and nature preserves	Hell et al., 2005
E. europaeus and *E. concolor*	Poland	2001–2003	0.07	National, regional, and local roads	Arable land and built-up areas	Orłowski & Nowak, 2004
A. algirus	Lanzarote	2010–2011	0.65	National, regional, and local roads	Urban areas and Badlands	Tejera et al., 2018
E. roumanicus	Bulgaria	2017	0.06–0.08	National and regional roads	Rural areas	Mikov & Georgiev, 2018
	Bulgaria	2015–2017	0.23	National roads	Arable land, riparian vegetation, and forests	Gruychev, 2018
	Ukraine	2000–2009	0.73	National, regional, and local roads	Urban areas and forests	Пархоменко, 2017
	Slovakia	2008–2012	1.52–2.68	National roads	Agricultural land, grasslands, forest, riparian and built-up areas	Bitušík et al., 2017
	Ukraine	2002–2005	3.65	National roads	Marshes, forests and urban areas	Загороднюк, 2006

Counts of the hedgehogs killed on roads indicate the extent of (lethal) collisions with vehicles and can be used to quantify differences between species, countries, and road types if the survey methodology is clearly described. However, they do not indicate the relative importance of traffic-related deaths in the context of populations as a whole (Seiler and Helldin, 2006), and there are issues of standardisation between studies due to differences in study design, effort, frequency, and duration. Notably, these issues include accurately accounting for variable carcass persistence (Santos, Carvalho and Mira, 2011; Santos et al., 2016). Examining the proportion of a population killed on roads every year is more informative. Previous studies of *E. europaeus* have calculated that traffic casualties amount to 9–26% of the total (nationwide) population size in the Netherlands (Huijser, 2000) and 10–30% in Great Britain (Wembridge et al., 2016), assuming the population estimates are accurate (Pettett et al., 2018). 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 (Kristiansson, 1990) and 24% in Poland (Orłowski & Nowak, 2004). Examining the proportional loss at the local scale is instrumental for targeted conservation action. This is because the impact of roads may be different between local populations due to regional variation in habitat type, quality, population densities and road networks (Seiler, 2003).

Another promising indication of the population-level effects of road mortality is to compare it with mortality from other sources and identify its contribution to cumulative annual mortality. This can be used to assess the impact of traffic collisions on the mortality:recruitment ratio (Seiler and Helldin, 2006). *E. europaeus* is the most studied hedgehog species worldwide and mortality of the species has been investigated using radio-tracking methods (Rautio et al., 2016), capture–mark–recapture methods (Kristiansson, 1990) and data from rescue centres (Reeve & Huijser, 1999; Table 4.2). It should be noted that the small sample sizes in the reported studies in Table 4.2 and their study design can skew the relative importance of a cause of death, and that there will naturally be local variation in the occurrence of each mortality factor. Although the studies are an important first step in refining an understanding on mortality, the results should be interpreted with caution. The 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 (Péron, 2013). Determining how plausible compensation is for hedgehogs is hampered by a lack of data on female hedgehog fecundity, such as the proportion of females that breed successfully, the mean number of litters per female annually and mean litter size, as well as juvenile survival rates. However, the evidence for ongoing hedgehog declines suggests that compensation might not be occurring (Hof & Bright, 2016). It is likely that the declines of hedgehog populations across Europe are a result of a combination of factors. For example, intensified agricultural practices, molluscicide and rodenticide poisoning, badger predation and loss of habitat have also been raised as important correlates of reduced population density and local extinction risk (Dowding et al., 2010; Hubert et al., 2011; Reichholf, 2015; Pettett et al., 2018; Rasmussen et al., 2019). Disentangling the relative impact of factors to population demography, which is likely to be area-specific, remains a principal goal to improve hedgehog conservation.

Table 4.2. Percentage of deaths by different sources for studied *E. europaeus* individuals in Europe.

Location	Year of Study	Number of Individuals	Roads	Natural Predation (Badger and Fox)	Unnatural Predation (Dog and Cat)	Illness [a]	Poison	Other [b]	Unknown	Reference
UK and the Netherlands	1999	~83580	8.8	Not included	2.3	58.5	4.3	26.0	Not included	Reeve & Huijser, 1999
UK	1988	109	78.0	Not included	Not included	Not included	2.8	1.8	17.4	Dickman, 1988
UK	1981	22	18.2	31.8	13.6	Not included	4.5	31.8	Not included	Reeve, 1981
UK	1992	8	25.0	75.0	Not included	Not included	Not included	Not included	Not included	Doncaster, 1992
UK	2019	7	43.0	43.0	Not included	14.0	Not included	Not included	Not included	Yarnell et al., 2019
UK	1998	7	57.0	14.0	Not included	14.0	Not included	14.0	Not included	Reeve, 1998
Finland	2016	106	72.6	Not included	0.9	20.7	Not included	1.8	4.0	Rautio et al., 2016
Denmark	2019	9	Not included	Not included	22.0	22.0	11.0 [c]	44.0	Not included	Rasmussen et al., 2019

[a] includes parasitological, pathological (e.g., starvation and gangrenous limb) and bacteriological findings (e.g., *Salmonella*); [b] includes drowning, injury from agricultural or garden tools and fire; [c] speculated but not confirmed.

4.3 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 (Aresco, 2005). Differential risk is a function of risk per crossing, which largely depends on animal crossing speed, traffic volume and road width, multiplied by the frequency of crossing. This is associated with individual responses to roads and biological characteristics, such as reproductive strategy and pre-hibernation foraging (Hels & Buchwald, 2001). Individual-based movement patterns cause different exposure to traffic in the environment (Row et al., 2007), which has important repercussions for reproductive output (Dexter et al., 2018). For example, for species such as hedgehogs that have a promiscuous mating system and maternal natal care, adult females have a more important role in population growth than males (Rautio et al., 2014). Moreover, the frequency distribution of age-at-death in a population is central to life history evolution and population dynamics (Dexter et al., 2018; Rasmussen et al., 2023).

No studies have empirically examined the individual-based risk of road mortality over time for hedgehogs, nor the potential variation in carcass detectability or persistence between different age groups. Current knowledge relies on data on the sex ratio and age structure of casualties. During a study of *E. europaeus* over 259.5 km of road in Ireland, Haigh et al. (2014b) revealed that 65% (67 out of 103) of individuals killed on roads were male. Moreover, Haigh, Butler & O'Riordan (2014a) tested several techniques to age hedgehogs, such as dentary bone analysis, jaw and hind foot length. These produced accurate age assessments and identified that the mean age of road-killed hedgehogs was 1.94 years. These findings were similar to those of Rasmussen et al. (2023) where the mean age-at-death of road-killed individuals was 2.1 years. Similarly, Goransson et al. (1976) found that 80% of *E. europaeus* traffic casualties in Sweden were males who had survived one winter. To understand the significance of sex- and age-specific road mortality to population dynamics, these figures should be considered in the context of the number of individuals in that sex/age class in the wider population. Moreover, it is possible that, due to their small size, juvenile hedgehogs are readily scavenged or not detected during driving surveys.

The majority of hedgehogs are reproductively active in their second year (after one successful hibernation; Kristiansson, 1990; Haigh et al., 2014a). Although research into the road mortality of different sexes and age groups is sparse, the majority of studies indicate that reproductively active males are most commonly killed on roads (Rasmussen et al., 2023). Male hedgehogs have larger home ranges and nightly movements than females (Glasby and Yarnell, 2013; García-Rodríguez and Puig-Montserrat, 2014), particularly during the breeding season (Rautio et al., 2013). 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 (Haigh et al., 2014b). 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 (Marchand & Litvaitis, 2004). On the one hand, the disproportionate loss of adult males may not be as consequential for population growth as adult female deaths (Seiler and Helldin, 2006). On the other hand, males are more commonly killed before or during breeding season, unlike females (Haigh et al., 2014b). There is a possibility that fewer males successfully contribute to the gene pool and the relatedness in a population increases over time. If severe enough, this may cause a decrease in population fitness associated with inbreeding depression (Jaeger et al., 2005; see Section 4.4.1), although research on the topic remains limited.

4.4 The role of road mortality in fragmentation effects

Habitat fragmentation by transport infrastructure and the associated development has become one of the greatest threats to biodiversity (Dom & Ridder, 2002). The consequences of road-induced fragmentation for the integrity of natural environments are well-researched (Kormann et al., 2012; Cullen et al., 2016). Several different, yet not mutually exclusive, mechanisms restrict animal dispersal across roads—lethal road collisions, the avoidance of the road or roadside habitat and the inability to traverse the road or nearby area, such as due to a central median or parallel drainage ditch (Plante et al., 2019). 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 (Bontadina, 1991; L. Moore, unpublished data). For hedgehogs, road mortality is considered a more severe restriction to dispersal on smaller roads. For example, *E. roumanicus* in Bulgaria (Bíl et al., 2020) and *E. concolor* in Turkey (Özcan & Özkazanç, 2017) were shown to have greater casualty rates on quieter, regional roads than highways. This may result from quieter roads allowing more crossing attempts (Dowding et al., 2010), having fewer physical barriers than major roads and/or their placement in areas with higher hedgehog densities. In severe cases, increased road mortality could lead to death rates exceeding birth rates, which may change a local population to a sink (Grilo et al., 2012).

Road mortality has been shown to be the largest contributor to population fragmentation (Jackson & Fahrig, 2011; Grilo et al., 2012), albeit not always (Forman & Alexander, 1998). It is possible that physical barriers such as roadside fencing and road avoidance behaviour cause fragmentation via more stringent restrictions to movement. Both physical barriers and road avoidance behaviour are particularly common on roads with higher traffic volumes and speeds (Plante et al., 2019). Dowding et al. (2010) reported avoidance of foraging near roads, but not of crossing quieter roads, by *E. europaeus*. Moreover, Rondinini & Doncaster (2002) 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). In corroboration with Rondinini & Doncaster (2002), a traffic volume of 3000 vehicles/day (common for busy urban roads) in New Zealand led to the isolation of *E. europaeus* populations (Brockie et al., 2009).

This combined effect of road mortality and avoidance for fragmentation is readily explained by the traffic flow theory, which postulates a positive and asymptotic relationship between traffic volume and roadkill counts. Road mortality will increase with rising traffic volume until reaching an asymptote, when the busy roads (with greater noise levels) form complete barriers and are avoided, or the roads suppress population size and reduce the number of individuals crossing roads (van Langevelde & Jaarsma, 2005). It is likely that roads constitute semi-permeable barriers for hedgehogs and that the extent of fragmentation is context-specific.

4.4.1 Biomolecular insights into fragmentation

Recent advances in genetic approaches have bridged the gap between molecular and road ecology to address the chronic impacts of fragmentation (Balkenhol & Waits, 2009). Insights into the genetic effects of hedgehog population fragmentation have grown since the development of eleven nuclear microsatellite primers (genetic markers) for *E. europaeus* by Becher & Griffiths (1997) and Henderson et al. (2000). The markers have been used to genotype several closely related hedgehog species and can identify genetic similarities between individuals and, therefore, the level of inbreeding (Bolfíková & Hulva, 2012). The variability of genetic markers is particularly important for small mammals such as hedgehogs, where fragmentation is likely to act at microspatial scales (Becher & Griffiths, 1998). Braaker et al. (2017) reported that two main rivers and major transport infrastructure (a four-lane highway and railroads) separate three genetic clusters of the *E. europaeus* population in Zurich. Moreover, combined movement models and microsatellite data indicated that fragmentation and high resistance in the urban matrix of Zurich, predominately from highways, footpaths, buildings and water bodies, contribute to the genetic structure of the hedgehog population at the local level, i.e., within clusters (Braaker et al., 2017). The weak correlation between genetic structure and geographical distance in several additional hedgehog studies indicates that linear infrastructure restricts gene flow enough to affect genetic heterozygosity (Becher & Griffiths, 1998; Curto et al., 2019; Rasmussen et al., 2020). 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 (Moran et al., 2009). Inbreeding coefficients would be reduced as a litter can consist of several half-siblings. The reality of this, however, remains untested and Barthel (2019) reported potentially early signs of inbreeding in *E. europaeus* subpopulations in Berlin. A promising yet relatively unused strategy for examining population isolation is genetic pedigree analysis, which uses microsatellites to detect migration rates (e.g., across roads) and local geographies of closely related individuals. This forms a quantitative tool to identify the likelihood of inbreeding and whether the population is acting as a sink population (Kormann et al., 2012; Proctor et al., 2020).

4.5 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 (Trombulak & Frissell, 2000). A growing number of legal imperatives, such as Article 10 of the European Union's Habitat Directive (92/43/EEC) and the National Environmental Policy Act (1969), as well as international guidelines, such as the United Nations' Sustainable Development Goals, motivate transport planners to safeguard habitat connectivity and ecosystem functioning. This means that newer major roads, in particular those built in Central and Eastern Europe, often have integrated wildlife crossings, such as underpasses or overpasses (Dom & Ridder, 2002). Minor roads, however, receive less attention despite the majority of road networks consisting of these low-traffic roads (Jackson & Fahrig, 2011). 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 (Lin, 2016).

4.5.1 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 (Bergers & Nieuwenhuizen, 1999). Instead, combining fencing with road tunnels or green bridges such as overpasses is widely advocated for many species (van der Ree et al., 2009; Helldin & Petrovan, 2019). This method strives to reduce barrier effects by providing both a reduction in road mortality and conserving or increasing landscape permeability (Seiler and Helldin, 2006). Several studies have documented varied levels of crossing structure use by *E. concolor* in Greece (Tritsis, 2011), *E. europaeus in* Spain (Mata et al., 2008; Puig & Sanz, 2012), Portugal (Ascensão & Mira, 2007), the UK (Eldridge & Wynn, 2011; Jarvis et al., 2019), and Poland (Myslajek et al., 2016; Ważna et al., 2020), and *Erinaceinae* sp. in Spain (Yanes et al., 1995; see review by De Vries, 1999). This variation in tunnel use is likely due, in part, to differences in tunnel design, location, and surrounding habitat, suggesting that the uptake of mitigation depends on the optimality of species-specific features. For example, hedgehogs have been shown to frequent tunnels with a greater openness ratio (short in length, high and wide) nearer urban areas (Ascensão & Mira, 2007). Moreover, previous studies demonstrate that hedgehogs avoid areas with predator (Eurasian badger *Meles meles*) odour, although the avoidance did not always persist (Ward et al., 1997; Doncaster, 1999). Badgers are known to utilise road tunnels (Eldridge & Wynn, 2011), sometimes very regularly, and whether this negatively influences hedgehog use of road mitigation structures remains unknown.

4.5.2 Traffic calming measures

Crossing structures are often concentrated at clusters of roadkill (Clevenger & Waltho, 2005). However, this hotspot approach is contentious; several authors propose that a lack of road mortality may signal a previously declined population or a population that exhibits high road avoidance behaviour (Ascensão et al., 2019). If so, the necessity for mitigation to assist in population recovery or protection is overlooked. Similarly, the fencing associated with crossing structures could block locations of frequent successful crossings if inappropriately placed. Instead, smaller-scale traffic calming measures that increase driver awareness may be equally effective and substantially cheaper. These aim to enhance preferred crossing sites, which do not necessarily correspond with roadkill hotspots, in order to reduce the use of riskier crossing locations (Meek, 2009; Grilo et al., 2012). Traffic calming measures adopted in the past include speed bumps, speed restrictions and warning signs (Lin, 2016). These initiatives may be particularly effective for hedgehogs given that they frequently attempt to cross quieter roads (Dowding et al., 2010). Whilst a reduction in speed would be expected to result in a substantial reduction in roadkill (Hobday et al., 2008), the realised effect depends on several factors. This includes whether drivers adhere to the speed regulations, which can be difficult to govern (Dique et al., 2003), and whether, even at a slower speed, a driver can see and avoid a small animal at night.

4.5.3 Habitat management

Additional mitigation possibilities include managing roadside habitats by increasing habitat quality, local connectivity (Lin, 2016) and changing road verge management (Clevenger, Chruszcz and Gunson, 2003). 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 (Clevenger & Kociolek, 2013; but see Canal et al., 2019). The use of central medians by fauna has not been well-studied and, if they are in fact beneficial to animal movement across a road, their removal may exacerbate barrier effects (Plante et al., 2019). Modifying hedgerows, which act as conduits of hedgehog movements, near roads is also likely to be an important action. For example, Huijser (2000) 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.

4.5.4 Road configuration

In Western Europe, many major roads were built more than 40 years ago with little consideration for wildlife (Selva et al., 2011). Retrofitting crossing structures can be an expensive undertaking, and their construction is often logistically challenging (van Strien & Grêt-Regamey, 2016). 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 (van der Ree et al., 2011). Previous multi-species simulation studies have reported that road mortality rates and population persistence were improved when traffic volume was concentrated on fewer roads (Jaeger et al., 2006; Rhodes et al., 2014). Surprisingly, van Strien & Grêt-Regamey (2016) reported opposite results for hedgehogs. These studies reinforce the significance of whole landscape planning. In particular, 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* (Bitušík et al., 2017; Gruychev, 2018).

4.6 Current knowledge gaps and future directions

Major impediments to furthering knowledge on hedgehog road ecology are the high labour and monetary costs linked to collecting relevant data for at least one population—that is, road casualty rates, movement and population structure data (and optionally genetic information). Moreover, although GPS devices are increasingly utilised for movement studies (Dexter et al., 2018; Bencin et al., 2019), including for hedgehogs (Braaker et al., 2017; Barthel, 2019), the high initial costs often reduce sample sizes and lead to results with poor statistical inference (see Hebblewhite & Haydon, 2010 for a full review). Understanding the ramifications of hedgehog road mortality is further hindered by the lack of basic biological and ecological knowledge on some species such as *E. concolor,* as well as uncertain rigor of population and road casualty estimations for other species. Current population estimates are from citizen science surveys and extrapolations of presence-only density estimates in different habitat types (Harris et al., 1995; Mathews et al., 2018). The assumptions associated with these methods make estimates of population size equivocal (Wembridge et al., 2016). Improved population estimates are critical to validate existing findings and could be achieved by large-scale collaborations or more standardised citizen science, such as using camera traps and random encounter methods (Petrovan, Vale and Sillero, 2020; Schaus-Calderón et al., 2020). Moreover, roadkill estimates of many species are likely to be underestimated due to scavengers removing carcasses and varying carcass detectability due to factors such as carcass decay, the driver's speed and the animal's body size (Grilo et al., 2012; Schwartz et al., 2018). As a result, raw carcass data must be corrected for carcass persistence and detection probability to obtain accurate estimates of the number of animals killed on roads, as demonstrated by Péron et al. (2013) and Santos et al. (2016). Similarly, it is likely that a small proportion of hedgehog–vehicle collisions do not result in instantaneous death and that a hedgehog's delayed traffic-induced death off the road is not counted. The possible role of wildlife hospitals in affecting estimates of mortality rates and genetic fragmentation is also important to consider. Particularly common for *E. europaeus* in Western Europe, wildlife rehabilitators care for and release injured hedgehogs that would otherwise die (Yarnell et al., 2019). While this is undoubtedly valuable for the species' conservation, future road ecology analyses must consider confounding factors such as these.

Of particular significance is that studies seldom examine road mortality in the context of a population's intrinsic growth rate. Considering growth rates reveals less of a "snapshot" of mortality and determines whether populations can sustain current and future road casualty rates. Future research should explicitly model the sensitivity of population growth curves to sex- and age-specific road mortality, using methods such as population viability models and elasticity analysis (Row et al., 2007). Population modelling could be further used on existing data sets, such as from nationwide citizen science projects, to accurately estimate yearly road mortality or, for populations with both road mortality and density estimates, an estimate of local demographic compensation. Another informed approach could incorporate population density, the sex and age of casualties and other sources of mortality into the framework of compensation-additive mortality (Péron, 2013). This explores whether road mortality is compensatory and removes the already "doomed surplus" in a population or is additive by increasing total mortality (Seiler, 2003). For example, if road-killed individuals have a poor body condition (e.g., they are affected by parasites or other diseases), the severity of road mortality is reduced as their likelihood of long-term survival is low regardless of traffic (Rautio et al., 2016).

The efficacy of road mitigation measures for wildlife is rarely tested; this poses significant constraints on justifying mitigation efforts and adapting strategies for maximum benefit. Many studies are either too short or adopt study designs that cannot demonstrate causality to population viability, such as gene flow or lasting reductions in road mortality (van der Grift et al., 2013). In the future, studies should employ long-term monitoring of mitigation measures and before-after-control-impact (BACI) or control-impact experimental designs, where possible. These studies allow for changes in the investigated population parameters, such as density, sex ratio or genetic diversity, to be soundly attributed to the mitigation measures (Glista et al., 2009). Future research should also present more holistic mitigation recommendations by examining socioeconomic factors such as vehicle and pedestrian travel efficiency (van Strien & Grêt-Regamey, 2016) and the cost-effectiveness of strategies (Helldin & Petrovan, 2019; Table 4.3). The challenge of accommodating both hedgehog and anthropogenic demands on the landscape highlights the crucial role of interdisciplinary and collective thinking in road ecology (Trombulak & Frissell, 2000).

Table 4.3. Summary of published findings, as well as gaps in the literature and recommendations for future research as discussed in this review.

Published findings	Gaps in understanding as revealed by this review	Directions for future research as recommended by this review
Traffic collisions may cause an annual loss of 3–24% of a local hedgehog population, and 9–30% of a nationwide population (Kristiansson, 1990; Huijser, 2000; Orłowski & Nowak, 2004; Wembridge et al., 2016). Road mortality is consistently in the top three contributors to total mortality (Dickman, 1988; Hubert et al., 2011).	The accuracy of current local and total population estimates. Whether populations can compensate for road mortality with increased survival and/or fecundity.	Establishing standardised surveys for improved population estimates. Long-term population studies to evaluate road mortality in the context of population growth.
Hedgehog roadkill is disproportionately clustered in suburban areas and consists predominately of males and adults (Hels & Buchwald, 2001; Dom & Ridder, 2002; Poel et al., 2015; Pettett et al., 2018).	Whether carcass detectability and persistence vary between age groups. How road and habitat characteristics influence road mortality risks between demographic groups over time.	Studies into the road crossing behaviour of different demographic groups. Evaluating the consequences of sex- and age-specific road mortality on hedgehog population trends.
Hedgehog populations appear particularly vulnerable to fragmentation effects (Grilo et al., 2012; Poel et al., 2015). Hedgehog populations exhibit distinct genetic substructure, often in relation to linear infrastructure (Becher & Griffiths, 1997; Curto et al., 2019; Rasmussen et al., 2020).	Whether the hedgehog's promiscuity and heteropaternal superfecundity can lessen the impacts of isolation on genetic structure.	Establishing isolation effects from roads, such as using inbreeding coefficients or genetic pedigree analysis.
Exclusionary fences alone are not an appropriate mitigation measure for hedgehog road mortality (Bergers & Nieuwenhuizen, 1999). Hedgehogs infrequently use crossing structures (Bergers & Nieuwenhuizen, 1999; Ascensão & Mira, 2007; Helldin & Petrovan, 2019).	The population-level responses to mitigation measures. Whether the use of road crossing structures by badgers impacts their efficacy for hedgehogs. Whether traffic-calming methods are an effective and relatively cheap option for road mitigation.	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.

4.7 Conclusion

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. The literature presents several evaluative criteria for this purpose, including proportional loss, differential vulnerability between demographic groups and the fecundity of the remaining population. Previous studies are in general agreement that adult males are more prone to road mortality than females 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. These difficulties remain the primary challenges for hedgehog conservation throughout Europe. Future research should prioritise the inclusion of sex- and age-specific fecundity and survival rates in population models and analyses. This review highlights the importance of long-term monitoring and robust experimental design such as BACI for effective decision-making by conservation practitioners and policy makers. 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.

4.8 References

Aresco, M. J. (2005). The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. *Biological Conservation, 123*(1), 37–44. https://doi.org/10.1016/j.biocon.2004.10.006

Ascensão, F., Kindel, A., Teixeira, F. Z., Barrientos, R., D’Amico, M., Borda-de-Água, L., & Pereira, H. M. (2019). Beware that the lack of wildlife mortality records can mask a serious impact of linear infrastructures. *Global Ecology and Conservation, 19,* e00661 https://doi.org/10.1016/j.gecco.2019.e00661

Ascensão, F., & Mira, A. (2007). Factors affecting culvert use by vertebrates along two stretches of road in southern Portugal. *Ecological Research, 22*(1), 57–66. https://doi.org/10.1007/s11284-006-0004-1

Balkenhol, N., & Waits, L. P. (2009). Molecular road ecology: Exploring the potential of genetics for investigating transportation impacts on wildlife. *Molecular Ecology, 18*(20), 4151–4164. https://doi.org/10.1111/j.1365-294X.2009.04322.x

Bannikova, A., Lebedev, V., Abramov, A., & Rozhnov, V. (2014). Contrasting evolutionary history of hedgehogs and gymnures (Mammalia : Erinaceomorpha) as inferred from a multigene study. *Biological Journal of the Linnean Society, 112*(3), 499–519. https://doi.org/10.1111/bij.12299

Barthel, L. M. F. (2019). *Population structure and behaviour of the European hedgehog in an urbanized world*. [PhD Thesis, Freie Universität Berlin].

Becher, S. A., & Griffiths, R. (1997). Isolation and characterization of six polymorphic microsatellite loci in the European hedgehog *Erinaceus europaeus*. *Molecular Ecology, 6*(1), 89–90. https://doi.org/10.1046/j.1365-294X.1997.00159.x

Becher, S. A., & Griffiths, R. (1998). Genetic differentiation among local populations of the European hedgehog (Erinaceus europaeus) in mosaic habitats. *Molecular Ecology*, *7*(11), 1599–1604. https://doi.org/10.1046/j.1365-294x.1998.00457.x

Bencin, H. L., Prange, S., Rose, C., & Popescu, V. D. (2019). Roadkill and space use data predict vehicle-strike hotspots and mortality rates in a recovering bobcat (*Lynx rufus*) population. *Scientific Reports*, *9*(1), 15391. https://doi.org/10.1038/s41598-019-50931-5

Bergers, P. J. M., & Nieuwenhuizen, W. (1999). Viability of hedgehog populations in central Netherlands. *Lutra, 42*, 65–75. https://research.wur.nl/en/publications/viability-of-hedgehog-populations-in-central-netherlands

Bíl, M., Heigl, F., Janoška, Z., Vercayie, D., & Perkins, S. E. (2020). Benefits and challenges of collaborating with volunteers: Examples from National Wildlife Roadkill Reporting Systems in Europe. *Journal for Nature Conservation, 54*, 125798. https://doi.org/10.1016/j.jnc.2020.125798

Bitušík, P., Kocianová-adamcová, M., Brabec, J., Malina, R., Tesák, J., & Urban, P. (2017). The effects of landscape structure and road topography on mortality of mammals : A case study of two different road types in Central Slovakia. *Lynx*, *48*(1), 39–51. https://doi.org/10.2478/lynx-2017-0003

Bolfíková, B., & Hulva, P. (2012). Microevolution of sympatry: Landscape genetics of hedgehogs *Erinaceus europaeus* and *E. roumanicus* in Central Europe. *Heredity*, *108*(3), 248–255. https://doi.org/10.1038/hdy.2011.67

Bontadina, F. (1991). *Straßenüberquerungen von Igeln (*Erinaceus europaeus*).* [PhD Thesis, University of Zurich].

Braaker, S., Kormann, U., Bontadina, F., & Obrist, M. K. (2017). Prediction of genetic connectivity in urban ecosystems by combining detailed movement data, genetic data and multi-path modelling. *Landscape and Urban Planning*, *160*, 107–114. https://doi.org/10.1016/j.landurbplan.2016.12.011

Brockie, R. E., Sadleir, R. M. F. S., & Linklater, W. L. (2009). Long-term wildlife road-kill counts in New Zealand. *New Zealand Journal of Zoology*, *36*(2), 123–134. https://doi.org/10.1080/03014220909510147

Canal, D., Camacho, C., Martín, B., de Lucas, M., & Ferrer, M. (2019). Fine-scale determinants of vertebrate roadkills across a biodiversity hotspot in Southern Spain. *Biodiversity and Conservation*, *28,* 3239-3256. https://doi.org/10.1007/s10531-019-01817-5

Carvalho, F., & Mira, A. (2011). Comparing annual vertebrate road kills over two time periods, 9 years apart: a case study in Mediterranean farmland. *European Journal of Wildlife Research*, *57*, 157–174. https://doi.org/10.1007/s10344-010-0410-0

Clevenger, A. P., Chruszcz, B., & Gunson, K. E. (2003). Spatial patterns and factors influencing small vertebrate fauna road-kill aggregations. *Biological Conservation*, *109*(1), 15–26. https://doi.org/10.1016/S0006-3207(02)00127-1

Clevenger, A. P., & Kociolek, A. v. (2013). Potential impacts of highway median barriers on wildlife: state of the practice and gap analysis. *Environmental Management*, *52*(5), 1299–1312. https://doi.org/10.1007/s00267-013-0155-0

Clevenger, A., & Waltho, N. (2005). Performance indices to identify attributes of highway crossing structures facilitating movement of large mammals. *Biological Conservation*, *121*(3), 453–464. https://doi.org/doi:10.1016/j.biocon.2004.04.025

Coffin, A. W. (2007). From roadkill to road ecology: A review of the ecological effects of roads. *Journal of Transport Geography*, *15*(5), 396–406. https://doi.org/10.1016/j.jtrangeo.2006.11.006

Cullen, L., Stanton, J. C., Lima, F., Uezu, A., Perilli, M. L. L., & Resit Akcakaya, H. (2016). Implications of fine-grained habitat fragmentation and road mortality for jaguar conservation in the Atlantic forest, Brazil. *PLOS ONE*, *11*(12), e0167372. https://doi.org/10.1371/journal.pone.0167372

Curto, M., Winter, S., Seiter, A., Schmid, L., Scheicher, K., Barthel, L. M. F., Plass, J., & Meimberg, H. (2019). Application of an SSR-GBS marker system on investigation of European Hedgehog species and their hybrid zone dynamics. *Ecology and Evolution*, *9*(5), 2814–2832. https://doi.org/10.1002/ece3.4960

De Vries, J. G. (1999). Hedgehogs on the road: from research to practice. *Lutra*, *42*, 99–110.

Dexter, C. E., Appleby, R. G., Scott, J., Edgar, J. P., & Jones, D. N. (2018). Individuals matter: Predicting koala road crossing behaviour in south-east Queensland. *Australian Mammalogy*, *40*(1), 67–75. https://doi.org/10.1071/AM16043

Dickman, C. R. (1988). Age-related dietary change in the European hedgehog, Erinaceus europaeus. *Journal of Zoology*, *215*(1), 1–14. https://doi.org/10.1111/j.1469-7998.1988.tb04881.x

Dique, D. S., Thompson, J., Preece, H. J., Penfold, G. C., Villiers, D. L. de, & Leslie, R. S. (2003). Koala mortality on roads in south-east Queensland: the koala speed-zone trial. *Wildlife Research*, *30*(4), 419. https://doi.org/10.1071/WR02029

Dom, A., & Ridder, W. de. (2002). Paving the way for EU enlargement (Report no. 32). *European Environment Agency.* Retrieved from https://www.eea.europa.eu/publications/environmental_issue_report_2002_24/file

Doncaster, C. P. (1992). Testing the role of intraguild predation in regulating hedgehog populations. *Proceedings of the Royal Society B: Biological Sciences*, *249*(1), 113–117. https://doi.org/10.1098/rspb.1992.0092

Doncaster, C. P. (1999). Can badgers affect the use of tunnels by hedgehogs? A review of the literature. *Lutra*, *42*, 59–64.

Dowding, C. V., Harris, S., Poulton, S., & Baker, P. J. (2010). Nocturnal ranging behaviour of urban hedgehogs, *Erinaceus europaeus*, in relation to risk and reward. *Animal Behaviour*, *80*(1), 13–21. https://doi.org/10.1016/j.anbehav.2010.04.007

Eldridge, B., & Wynn, J. (2011). Use of badger tunnels by mammals on highways agency schemes in England. *Conservation Evidence*, *8*, 53–57. www.ConservationEvidence.com

Eurostat (2013). *Transport database: Road Transport Infrastructure.* European Commission. Retrieved from https://ec.europa.eu/eurostat/web/transport/data/database

Fahrig, L., & Rytwinski, T. (2009). Effects of roads on animal abundance: An empirical review and synthesis. *Ecology and Society*, *14*(1). https://doi.org/10.5751/ES-02815-140121

Forman, R. T. T., & Alexander, L. E. (1998). Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, *29*(1), 207–231. https://doi.org/10.1146/annurev.ecolsys.29.1.207

García-Rodríguez, S., & Puig-Montserrat, X. (2014). Algerian hedgehog (*Atelerix algirus* Lereboullet, 1842) habitat selection at the northern limit of its range. *Galemys, Spanish Journal of Mammalogy*, *26*, 49–56. https://doi.org/10.7325/galemys.2014.a5

George, L., Macpherson, J. L., Balmforth, Z., & Bright, P. W. (2011). Using the dead to monitor the living: Can road kill counts detect trends in mammal abundance? *Applied Ecology and Environmental Research*, *9*(1), 27–41. https://doi.org/10.15666/aeer/0901_027041

Glasby, L., & Yarnell, R. W. (2013). Evaluation of the performance and accuracy of Global Positioning System bug transmitters deployed on a small mammal. *European Journal of Wildlife Research*, *59*(6), 915–919. https://doi.org/10.1007/s10344-013-0770-3

Glista, D. J., DeVault, T. L., & DeWoody, J. A. (2009). A review of mitigation measures for reducing wildlife mortality on roadways. In *Landscape and Urban Planning*, *91*(1), 1–7. https://doi.org/10.1016/j.landurbplan.2008.11.001

Goransson G., Karlsson J., L. A. (1976). Road mortality of the hedgehog *Erinaceus europaeus* in southern Sweden. *Fauna Flora*, *71*(1), 1–6. https://agris.fao.org/agris-search/search.do?recordID=SE19760115214

Grilo, C., Sousa, J., Ascensão, F., Matos, H., Leitão, I., Pinheiro, P., Costa, M., Bernardo, J., Reto, D., Lourenço, R., Santos-Reis, M., & Revilla, E. (2012). Individual spatial responses towards roads: implications for mortality risk. *PLOS ONE*, *7*(9), 1–11. https://doi.org/10.1371/journal.pone.0043811

Gruychev, G. V. (2018). Animal road mortality (Aves & Mammalia) from the new section of the Maritsa Highway (South Bulgaria). *Ecologia Balkanica*, *10*(1), 11–18. https://ecologia-balkanica.com/?page_id=195

Haigh, A., Kelly, M., Butler, F., & O’Riordan, R. M. (2014a). Non-invasive methods of separating hedgehog (*Erinaceus europaeus*) age classes and an investigation into the age structure of road kill. *Acta Theriologica*, *59*(1), 165–171. https://doi.org/10.1007/s13364-013-0142-0

Haigh, A., O’Riordan, R. M., & Butler, F. (2014b). Hedgehog *Erinaceus europaeus* mortality on Irish roads. *Wildlife Biology*, *20*(3), 155–160. https://doi.org/10.2981/wlb.12126

Harris, S., Morris, P., Wray, S., & Yalden, D. (1995). *A Review of British Mammals : Population Estimates and Conservation Status of British Mammals Other Than Cetaceans.* The Joint Nature Conservation Committee. Retrieved from https://research-information.bris.ac.uk/en/publications/a-review-of-british-mammals-population-estimates-and-conservation-2

Hebblewhite, M., & Haydon, D. T. (2010). Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2303–2312. https://doi.org/10.1098/rstb.2010.0087

Hell, P., Plavý, R., Slamečka, J., & Gašparík, J. (2005). Losses of mammals (Mammalia) and birds (Aves) on roads in the Slovak part of the Danube Basin. *European Journal of Wildlife Research, 51*(1), 35–40. https://doi.org/10.1007/s10344-004-0068-6

Helldin, J. O., & Petrovan, S. O. (2019). Effectiveness of small road tunnels and fences in reducing amphibian roadkill and barrier effects at retrofitted roads in Sweden. *PeerJ, 7,* e7518. https://doi.org/10.7717/peerj.7518

Hels, T., & Buchwald, E. (2001). The effect of road kills on amphibian populations. *Biological Conservation*, *99*(3), 331–340. https://doi.org/10.1016/S0006-3207(00)00215-9

Henderson, M., Becher, S. A., Doncaster, C. P., & Maclean, N. (2000). Five new polymorphic microsatellite loci in the European hedgehog Erinaceus europaeus. *Molecular Ecology*, *9*(11), 1932–1934. https://doi.org/10.1046/j.1365-294X.2000.01080-9.x

Hill, J. E., DeVault, T. L., & Belant, J. L. (2019). Cause-specific mortality of the world's terrestrial vertebrates. *Global Ecology and Biogeography, 28*(5), 680–689. https://doi.org/10.1111/geb.12881

Hobday, A. J., Scientific, T. C., & Minstrell, M. L. (2008). Distribution and abundance of roadkill on Tasmanian highways : Human management options. *Wildlife Research, 35,* 712-726. https://doi.org/10.1071/WR08067

Hof, A. R., & Bright, P. W. (2016). Quantifying the long-term decline of the West European hedgehog in England by subsampling citizen-science datasets. *European Journal of Wildlife Research*, *62*(4), 407–413. https://doi.org/10.1007/s10344-016-1013-1

Holsbeek, L., Rodts, J., & Muyldermans, S. (1999). Hedgehog and other animal traffic victims in Belgium: results of a countryside survey. *Lutra, 42,* 111–119.

Hubert, P., Julliard, R., Biagianti, S., & Poulle, M. L. (2011). Ecological factors driving the higher hedgehog (*Erinaceus europaeus*) density in an urban area compared to the adjacent rural area. *Landscape and Urban Planning, 103*(1), 34–43. https://doi.org/10.1016/j.landurbplan.2011.05.010

Huijser, M. P. (1997). The mortality rate in a hedgehog (*Erinaceus europaeus*) population: the relative importance of road kills. In *Habitat Fragmentation & Infrastructu*re. Retrieved from https://research.wur.nl/en/publications/the-mortality-rate-in-a-hedgehog-erinaceus-europaeus-population-t

Huijser, M. P. (2000). *Life on the edge. Hedgehog traffic victims and mitigation strategies in an anthropogenic landscape.* [PhD Thesis, Wageningen University].

Huijser, M. P., & Bergers, P. J. M. (2000). The effect of roads and traffic on hedgehog (*Erinaceus europaeus*) populations. *Biological Conservation, 95*(1), 111–116. https://doi.org/10.1016/S0006-3207(00)00006-9

Huijser, M. P., Bergers, P. J. M., & De Vries, J. G. (1998). Hedgehog traffic victims: how to quantify effects on the population level and the prospects for mitigation. In *Proceedings of the International Conference on Wildlife Ecology and Transportation.* 10-12 February 1998, Florida Department of Transportation (pp. 171–180). USA: Florida.

Ibisch, P. L., Hoffmann, M. T., Kreft, S., Pe'Er, G., Kati, V., Biber-Freudenberger, L., DellaSala, D. A., Vale, M. M., Hobson, P. R., & Selva, N. (2016). A global map of roadless areas and their conservation status. *Science*, *354*(6318), 1423–1427. https://doi.org/10.1126/science.aaf7166

Jackson, N. D., & Fahrig, L. (2011). Relative effects of road mortality and decreased connectivity on population genetic diversity. *Biological Conservation, 144,* 3143–3148. https://doi.org/10.1016/j.biocon.2011.09.010

Jaeger, J. A. G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B., & Von Toschanowitz, K. T. (2005). Predicting when animal populations are at risk from roads: An interactive model of road avoidance behavior. *Ecological Modelling*, *185*(2–4), 329–348. https://doi.org/10.1016/j.ecolmodel.2004.12.015

Jaeger, J. A. G., Fahrig, L., & Ewald, K. C. (2006). Does the configuration of road networks influence the degree to which roads affect wildlife populations? In *Proceedings of the 2005 International Conference on Ecology and Transportation*, 29 August – 5 September 2005, North Carolina State University (pp 351–365). USA: California.

Jarvis, L. E., Hartup, M., & Petrovan, S. O. (2019). Road mitigation using tunnels and fences promotes site connectivity and population expansion for a protected amphibian. *European Journal of Wildlife Research*, *65*(2). https://doi.org/10.1007/s10344-019-1263-9

Kormann, U., Gugerli, F., Ray, N., Excoffier, L., & Bollmann, K. (2012). Parsimony-based pedigree analysis and individual-based landscape genetics suggest topography to restrict dispersal and connectivity in the endangered capercaillie. *Biological Conservation*, *152*, 241–252. https://doi.org/10.1016/j.biocon.2012.04.011

Krange, M. (2015). *Change in the occurrence of the West European Hedgehog (*Erinaceus europaeus*) in western Sweden during 1950-2010*. [PhD Thesis, Karlstad University].

Kristiansson, H. (1990). Population variables and causes of mortality in a hedgehog (*Erinaceous europaeus*) population in southern Sweden. *Journal of Zoology*, *220*(3), 391–404. https://doi.org/10.1111/j.1469-7998.1990.tb04314.x

Lin, S. C. (2016). Landscape and traffic factors affecting animal road mortality. *Journal of Environmental Engineering and Landscape Management*, *24*(1), 10–20. https://doi.org/10.3846/16486897.2015.1098652

Marchand, M. N., & Litvaitis, J. A. (2004). Effects of habitat features and landscape composition on the population structure of a common aquatic turtle in a legion undergoing rapid development. *Conservation Biology, 18*(3), 758–767. https://doi.org/10.1111/j.1523-1739.2004.00019.x

Mata, C., Hervás, I., Herranz, J., Suárez, F., & Malo, J. (2008). Are motorway wildlife passages worth building? Vertebrate use of road-crossing structures on a Spanish motorway. *Journal of Environmental Management, 88*(3), 407-415. https://doi.org/10.1016/j.jenvman.2007.03.014

Mathews, F., Kubasiewicz, L. M., Gurnell, J., Harrower, C. A., McDonald, R. A., & Shore, R. F. (2018). *A review of the population and conservation status of British mammals.* The Joint Nature Conservation Committee. Retrieved from http://publications.naturalengland.org.uk/publication/5636785878597632

Meek, R. (2009). Patterns of reptile road-kills in the Vendée region of western France. *Herpetological Journal, 19*(3), 135-142. https://www.thebhs.org/publications/the-herpetological-journal/volume-19-number-3-july-2009/553-04-patterns-of-reptile-road-kills-in-the-vendee-region-of-western-france.

Meijer, J. R., Huijbregts, M. A. J., Schotten, K. C. G. J., & Schipper, A. M. (2018). Global patterns of current and future road infrastructure. *Environmental Research Letters*, *13*(6), 064006. https://doi.org/10.1088/1748-9326/aabd42

Mikov, A. M., & Georgiev, D. G. (2018). On the road mortality of the Northern White-Breasted Hedgehog (*Erinaceus roumanicus* Barrett-Hamilton, 1900) in Bulgaria. *Ecologia Balkanica, 10*(1), 19–23. http://web.uni-plovdiv.bg/mollov/EB/2018_vol10_iss1/19-23_eb.18102.pdf

Moore, L. J., Petrovan, S. O., Bates, A. J., Hicks, H. L., Baker, P. J., Perkins, S. E., & Yarnell, R. W. (2023). Demographic effects of road mortality on mammalian populations: a systematic review. *Biological Reviews* [Online Early View]. https://doi.org/10.1111/brv.12942

Moran, S., Turner, P. D., & O'Reilly, C. (2009). Multiple paternity in the European hedgehog. *Journal of Zoology*, *278*(4), 349–353. https://doi.org/10.1111/j.1469-7998.2009.00583.x

Morelle, K., Lehaire, F., & Lejeune, P. (2013). Spatio-temporal patterns of wildlife-vehicle collisions in a region with a high-density road network. *Nature Conservation, 5,* 53–73. https://doi.org/10.3897/natureconservation.5.4634

Müller, F. (2018). Langzeit-Monitoring der Strassenverkehrsopfer beim Igel (*Erinaceus europaeus* L.) zur Indikation von Populationsdichteveränderungen entlang zweier Teststrecken im

Landkreis Fulda. *Beiträge Zur Naturkunde in Osthessen*, *54*, 21–26. https://www.vno-fulda.de/Publikationen.html

Myslajek, R. W., Nowak, S., Kurek, K., Tolkacz, K., & Gewartowska, O. (2016). Utilisation of a wide underpass by mammals on an expressway in the Western Carpathians, S Poland. *Folia Zoologica*, *65*(3), 225–232. https://doi.org/10.25225/fozo.v65.i3.a8.2016

Orłowski, G., & Nowak, L. (2004). Road mortality of hedgehogs *Erinaceus* spp. in farmland in Lower Silesia (south-western Poland). *Pol. J. Ecol, 52*(3), 377-382. https://miiz.waw.pl/pliki/article/ar52_3_14.pdf

Özcan, A. U., & Özkazanç, N. K. (2017). Identifying the hotspots of wildlife–vehicle collision on the Çankırı–kırıkkale highway during summer. *Turkish Journal of Zoology*, *41*(4), 722–730. https://doi.org/10.3906/zoo-1601-64

Péron, G. (2013). Compensation and additivity of anthropogenic mortality: Life-history effects and review of methods. *Journal of Animal Ecology*, *82*(2), 408–417. https://doi.org/10.1111/1365-2656.12014

Péron, G., Hines, J. E., Nichols, J. D., Kendall, W. L., Peters, K. A., & Mizrahi, D. S. (2013). Estimation of bird and bat mortality at wind-power farms with superpopulation models. *Journal of Applied Ecology*, *50*(4), 902–911. https://doi.org/10.1111/1365-2664.12100

Petrovan, S. O., Vale, C. G., & Sillero, N. (2020). Using citizen science in road surveys for large-scale amphibian monitoring: are biased data representative for species distribution? *Biodiversity and Conservation*, *29*(6), 1767–1781. https://doi.org/10.1007/s10531-020-01956-0

Pettett, C. E., Johnson, P. J., Moorhouse, T. P., & Macdonald, D. W. (2018). National predictors of hedgehog *Erinaceus europaeus* distribution and decline in Britain. *Mammal Review*, *48*(1), 1–6. https://doi.org/10.1111/mam.12107

Plante, J., Jaeger, J. A. G., & Desrochers, A. (2019). How do landscape context and fences influence roadkill locations of small and medium-sized mammals? *Journal of Environmental Management*, *235*, 511–520. https://doi.org/10.1016/j.jenvman.2018.10.093

Poel, J. L. van de, Dekker, J., & Langevelde, F. van. (2015). Dutch hedgehogs *Erinaceus europaeus* are nowadays mainly found in urban areas, possibly due to the negative effects of badgers *Meles meles*. *Wildlife Biology*, *21*(1), 51–55. https://doi.org/10.2981/wlb.00072

Proctor, M. F., Kasworm, W. F., Teisberg, J. E., Servheen, C., Radandt, T. G., Lamb, C. T., Kendall, K. C., Mace, R. D., Paetkau, D., & Boyce, M. S. (2020). American black bear population fragmentation detected with pedigrees in the transborder Canada–United States region. *Ursus*, *2020*(31e1), 1-15. https://doi.org/10.2192/URSUS-D-18-00003R2

Puig, J., & Sanz, L. (2012). Wildlife roadkills and underpass use in Northern Spain. *Environmental Engineering and Management Journal, 11*(6), 1141-1147. https://doi.org/10.30638/eemj.2012.138

Rasmussen, S. L., Berg, T. B., Martens, H. J., & Jones, O. R. (2023). Anyone can get old—all you have to do is live long enough: understanding mortality and life expectancy in European hedgehogs (*Erinaceus europaeus*). *Animals, 13*(4), 626. https://doi.org/10.3390/ANI13040626

Rasmussen, S. L., Jones, O. R., Berg, T. B., & Dabelsteen, T. (2019). The ecology of suburban juvenile European hedgehogs (*Erinaceus europaeus*) in Denmark. *Ecology and Evolution*, *9*(23), 13174-13187. https://doi.org/10.1002/ece3.5764

Rasmussen, S., Nielsen, J., Jones, O. R., Berg, T. B., & Pertoldi, C. (2020). Genetic structure of the European hedgehog (*Erinaceus europaeus*) in Denmark. *PLoS One,* 15(1), e0227205. https://doi.org/10.1371/journal.pone.0227205

Rautio, A., Isomursu, M., Valtonen, A., Hirvelä-Koski, V., & Kunnasranta, M. (2016). Mortality, diseases and diet of European hedgehogs (*Erinaceus europaeus*) in an urban environment in Finland. *Mammal Research*, *61*(2), 161–169. https://doi.org/10.1007/s13364-015-0256-7

Rautio, A., Valtonen, A., Auttila, M., & Kunnasranta, M. (2014). Nesting patterns of European hedgehogs (*Erinaceus europaeus*) under northern conditions. *Acta Theriologica*, *59*(1), 173–181. https://doi.org/10.1007/s13364-013-0150-0

Rautio, A., Valtonen, A., & Kunnasranta, M. (2013). The effects of sex and season on home range in European hedgehogs at the northern edge of the species range. *Annales Zooogici. Fennici*, *50*(1), 107–123. https://doi.org/10.5735/086.050.0110

Reeve, N. J. (1981). *A field study of the hedgehog (*Erinaceus europaeus*) with particular reference to movements and behaviour*. [PhD Thesis, University of London].

Reeve, N. J. (1998). The survival and welfare of hedgehogs (*Erinaceus europaeus*) after release back into the wildlife. *Animal Welfare*, *7*(2), 189–202. https://doi.org/10.1017/S0962728600020492

Reeve, N. J., & Huijser, M. P. (1999). Wildlife rescue centre records as a means of monitoring relative change in mortality factors affecting hedgehogs (*Erinaceus europaeus*). *Lutra*, *42*(1), 7–24.

Reichholf, J. H. (2015). Starker Rückgang der Häufigkeit überfahrener Igel *Erinaceus europaeus* in Südostbayern und seine Ursachen. *Mitteilungen Der Zoologischen Gesellschaft Braunau, 11*(3), 309–314. https://www.zobodat.at/pdf/Braunau_11_2015_0309-0314.pdf

Rhodes, J. R., Lunney, D., Callaghan, J., & McAlpine, C. A. (2014). A few large roads or many small ones? How to accommodate growth in vehicle numbers to minimise impacts on wildlife. *PLOS ONE*, *9*(3), e91093. https://doi.org/10.1371/journal.pone.0091093

Rondinini, C., & Doncaster, C. P. (2002). Roads as barriers to movement for hedgehogs. *Functional Ecology*, *16*(4), 504–509. https://doi.org/10.1046/j.1365-2435.2002.00651.x

Roos, S., Johnston, A., & Noble, D. (2012). *UK hedgehog datasets and their potential for long-term monitoring* (BTO Research Report No. 598). The British Trust for Ornithology, commissioned and funded by People's Trust for Endangered Species and the British Hedgehog Preservation Society. Retrieved from https://www.bto.org/our-science/projects/gbw/publications/papers/monitoring/btorr598

Row, J. R., Blouin-Demers, G., & Weatherhead, P. J. (2007). Demographic effects of road mortality in black ratsnakes (*Elaphe obsoleta*). *Biological Conservation*, *137*(1), 117–124. https://doi.org/10.1016/j.biocon.2007.01.020

Santos, R. A. L., Santos, S. M., Santos-Reis, M., Picanço de Figueiredo, A., Bager, A., Aguiar, L. M. S., & Ascensão, F. (2016). Carcass persistence and detectability: reducing the uncertainty surrounding wildlife-vehicle collision surveys. *PLOS ONE*, *11*(11), e0165608. https://doi.org/10.1371/journal.pone.0165608

Santos, S. M., Carvalho, F., & Mira, A. (2011). How long do the dead survive on the road? Carcass persistence probability and implications for road-kill monitoring surveys. *PLOS ONE*, *6*(9), e25383. https://doi.org/10.1371/journal.pone.0025383

Schaus-Calderón, J., Uzal, A., Gentle, L. K., Baker, P. J., Bearman-Brown, L., Bullion, S., Gazzard, A., Lockwood, H., North, A., Reader, T., Scott, D. M., Sutherland, C. S., & Yarnell, R. W. (2020). Application of the Random Encounter Model in citizen science projects to monitor animal densities. *Remote Sensing in Ecology and Conservation*, *6*(4), 514-528. https://doi.org/10.1002/rse2.153

Schwartz, A. L. W., Shilling, F. M., & Perkins, S. E. (2020). The value of monitoring wildlife roadkill. *European Journal of Wildlife Research*, *66*(1). https://doi.org/10.1007/s10344-019-1357-4

Schwartz, A. L. W., Williams, H. F., Chadwick, E., Thomas, R. J., & Perkins, S. E. (2018). Roadkill scavenging behaviour in an urban environment. *Journal of Urban Ecology*, *4*(1), 1–7. https://doi.org/10.1093/jue/juy006

Seiler, A. (2003). *The toll of the automobile: Wildlife and roads in Sweden*. [PhD Thesis, Swedish University of Agricultural Sciences].

Seiler, A., & Helldin, J. O. (2006). *Mortality in wildlife due to transportation.* In J. Davenport., & J. L. Davenport (Eds) The Ecology of Transportation: Managing Mobility for the Environment (pp. 165–189). Berlin : Springer

Selva, N., Kreft, S., Kati, V., Schluck, M., Jonsson, B. G., Mihok, B., Okarma, H., & Ibisch, P. L. (2011). Roadless and low-traffic areas as conservation targets in Europe. *Environmental Management*, *48*(5), 865–877. https://doi.org/10.1007/s00267-011-9751-z

Tejera, G., Rodríguez, B., Armas, C., & Rodríguez, A. (2018). Wildlife-vehicle collisions in lanzarote biosphere reserve, Canary Islands. *PLOS ONE*, *13*(3), e0192731. https://doi.org/10.1371/journal.pone.0192731

Tritsis, K. M. (2011). Assessment of the use of crossing structures by mammals along Egnatia Motorway in Northern Greece. [Master's Thesis, University of Kiel].

Trombulak, S. C., & Frissell, C. A. (2000). Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*, *14*(1), 18–30. https://doi.org/10.1046/j.1523-1739.2000.99084.x

van der Grift, E. A., van der Ree, R., Fahrig, L., Findlay, S., Houlahan, J., Jaeger, J. A. G., Klar, N., Madriñan, L. F., & Olson, L. (2013). Evaluating the effectiveness of road mitigation measures. *Biodiversity and Conservation*, *22*(2), 425–448. https://doi.org/10.1007/s10531-012-0421-0

van der Ree, R., Heinze, D., Mccarthy, M., & Mansergh, I. (2009). Wildlife tunnel enhances population viability. *Ecology and Society*, *14*(2). http://www.ecologyandsociety.org/vol14/iss2/art7/

van der Ree, R., Jaeger, J. A. G., van der Grift, and E. A., Clevenger, A. P. (2011). Effects of roads and traffic on wildlife populations and landscape function road ecology is moving toward larger scales. *Ecology and Society*, *16*(1). http://www.ecologyandsociety.org/vol16/iss1/art48/

van Langevelde, F., & Jaarsma, C. F. (2005). Using traffic flow theory to model traffic mortality in mammals. *Landscape Ecology*, *19*(8), 895–907. https://doi.org/10.1007/s10980-005-0464-7

van Strien, M. J., & Grêt-Regamey, A. (2016). How is habitat connectivity affected by settlement and road network configurations? Results from simulating coupled habitat and human networks. *Ecological Modelling*, *342*, 186–198. https://doi.org/10.1016/j.ecolmodel.2016.09.025

Ward, J. F., Macdonald, D. W., & Doncaster, C. P. (1997). Responses of foraging hedgehogs to badger odour. *Animal Behaviour*, *53*(4), 709–720. https://doi.org/10.1006/anbe.1996.0307

Ważna, A., Kaźmierczak, A., Cichocki, J., Bojarski, J., & Gabryś, G. (2020). Use of underpasses by animals on a fenced expressway in a suburban area in western Poland. *Nature Conservation*, *39*, 1–18. https://doi.org/10.3897/natureconservation.39.33967

Wembridge, D. E., Newman, M. R., Bright, P. W., & Morris, P. A. (2016). An estimate of the annual number of hedgehog (*Erinaceus europaeus*) road casualties in Great Britain. *Mammal Communications, 2*, 8–14. https://www.mammal.org.uk/wp-content/uploads/2016/04/MC1605_HedgehogsRoads_Wembridge.pdf

Wilson, E., & Wembridge, D. E. (2018). *The State of Britain's Hedgehogs 2018*. People's Trust for Endangered Species and the British Hedgehog Preservation Society. Retrieved from https://www.hedgehogstreet.org/wp-content/uploads/2018/02/SoBH-2018_final-1.pdf

Wright, P. G. R., Coomber, F. G., Bellamy, C. C., Perkins, S. E., & Mathews, F. (2020). Predicting hedgehog mortality risks on British roads using habitat suitability modelling. *PeerJ*, 7: e8154. https://doi.org/10.7717/peerj.8154

Yanes, M., Velasco, J. M., & Suárez, F. (1995). Permeability of roads and railways to vertebrates: The importance of culverts. *Biological Conservation, 71*(3), 217–222. https://doi.org/10.1016/0006-3207(94)00028-O

Yarnell, R. W., Surgey, J., Grogan, A., Thompson, R., Davies, K., Kimbrough, C., & Scott, D. M., (2019). Should rehabilitated hedgehogs be released in winter ? A comparison of survival , nest use and weight change in wild and rescued animals. *European Journal of Wildlife Research, 65*. https://doi.org/10.1007/s10344-018-1244-4

Загороднюк, І. (2006). Загибель тварин на дорогах : оцінка впливу автотранспорту на популяції диких і свійських тварин (In English: Mortality of animals on roads: assessment of vehicle traffic's influence at populations of wild and domestic animals.). *Proceedings of the Theriological School., 8*, 120–125. http://terioshkola.org.ua/library/pts8-synantr/pts8-33zag-roadkill.pdf

Пархоменко, В. (2017). Загибель ссавців на автошляхах північно - східної україни (In English: Death of mammals on the roads of northeastern Ukraine). *Proceedings of the Theriological School., 15*, 139–149. https://doi.org/10.15407/ptt2017.15.139

CHAPTER 5: Beyond the Individual; Multisite Population-Level Consequences of Road Mortality on a Declining Mammal

5.1 Introduction

The global road network is one of the largest human footprints on earth and is expected to more than double in extent over the next three decades (Dulac, 2013). Road networks have become the leading anthropogenic cause of mortality for many species (Hill et al., 2019) and as such, roadkill is often implicated in the decline, slowed recovery, and hindered range expansion of many threatened wildlife populations around the world (Rytwinski & Fahrig, 2012). Consequently, several policies and directives worldwide (e.g., Endangered Species Act, Bonn Convention, and EU Biodiversity Strategy) provide strong legislative encouragement for research into, and mitigation of, wildlife road mortality (van der Grift et al., 2016).

Appropriately targeted wildlife management and conservation near roads requires a focus on population viability (Moore et al., 2023). There have been numerous calls for impactful research that evaluates the effects of roads at the population level, rather than the more frequently estimated individual level such as via roadkill rates and locations (Roedenbeck et al., 2007; Rytwinski & Fahrig, 2012; Barrientos et al., 2021). However, the collection of the fine-scale data on population characteristics needed to accompany roadkill data, usually achieved by long-term, intensive demographic surveys, is constrained by high labour, logistical, and financial costs (Roedenbeck et al., 2007). Moreover, accessing survey sites across residential and privately owned land may be challenging where permission is required. It is therefore difficult to avoid erroneous ecological conclusions and extract meaningful insight from roadkill data. To date, very few studies have assessed the long-term consequences of road mortality on wildlife populations (Barrientos et al., 2021; Moore et al., 2023).

Whether road mortality significantly influences population viability will depend on the percentage of individuals killed on roads annually in different sites and on how road mortality interacts with life history elements that affect population growth, such as sex-specific survivorship and reproduction (Mumme et al., 2000; Moore et al., 2023). In particular, the interplay between various local threats can affect whether anthropogenic mortality is additive or compensatory to natural mortality, and therefore whether total mortality rates are affected (Péron et al., 2016). For gray wolves (*Canis lupus*) in the United States of America (USA), for example, additive effects of anthropogenic mortality such as hunting and vehicle collisions were more pronounced in areas of high anthropogenic pressure, such as from lethal removal following livestock predation, compared to areas of low anthropogenic pressure (Murray et al., 2010). The magnitude and direction of the interplay between mortality factors, and so the relative importance of road mortality, is likely to be context specific and influenced by population dynamics, road and habitat configuration. How intrinsic and extrinsic pressures in different habitats interact with road mortality to (de)stabilise populations remains an important ecological question.

Population stability around roads is further dependent on the mortality: recruitment ratio. Increased reproduction at low densities and low survival may facilitate compensation of road mortality (Prange, Gehrt, & Wiggers, 2003). For example, two black bear (*Ursus americanus*) populations under hunting management in the USA showed greater overall mortality than a non-harvested population but, supporting the compensatory hypothesis, the average litter sizes were 31–36% greater (Gantchoff et al., 2020). However, survival- and density-dependent reproduction is not thought to be consistent amongst species. Instead, reproduction may be influenced by factors such as predation and food abundance (Hubert et al., 2011). Whether reproductive rates of roadside populations are sufficient to compensate for road mortality has rarely been addressed.

Throughout Europe, there are considerable claims that road mortality is a significant driver of the ongoing and apparently substantial population declines of the west European hedgehog (hereafter ‘hedgehog’; Kristiansson, 1990; Wembridge et al., 2016). The estimated 66% decline in UK population size since 1950 (Roos, Johnston and Noble, 2012) has prompted urgent calls for targeted research and conservation management (Johnson, 2015). Despite a range of studies documenting hedgehog road mortality rates (see summary by Moore et al., 2020), how these relate to local demographics and mortality factors (e.g., illness, predation, poisoning, and injuries from garden machinery; Rautio et al., 2016; Rasmussen et al., 2019; Burroughes, Dowler and Burroughes, 2021) remains unknown. As such, the role of road mortality in limiting hedgehog populations has long been deemed to be one of the most significant unknowns in the population biology of this species (Parkes, 1975; Johnson, 2015). Given that conservation management takes place at the local scale, it is important to understand and consider local population viability for evidence-based and cost-effective action.

Using a comparative study design, the overall aim of this study was to assess the impacts of road mortality on the persistence and conservation status of local hedgehog populations. Specifically, the objectives of this study were to (1) estimate the percentage of hedgehogs killed on roads annually in four distinct local populations, and (2) estimate the structure, annual survival probability, cause-specific mortality, and reproductive rates of the four local populations to provide demographic context to the road mortality figures. Based on nationwide data (Wembridge et al., 2016), it is hypothesised that up to 30% of a hedgehog population in this study will be killed on roads annually. Likewise, due to the inherent differences in intrinsic and extrinsic factors affecting populations over space (Ramp and Ben-Ami, 2006), it is expected that populations inhabiting more residential areas, compared to rural landscapes, will be more resilient to road mortality. The integration of a population's demographic variables with local threats used in this study is applicable to any population intersected by roads and is critical for prescribing cost-effective management targets. Moreover, by analysing a potential driver of hedgehog decline, this study is a key step in determining how to best utilise limited resources for a species of conservation concern.

5.2 Methods and materials

5.2.1 Study sites

Four sites ranging from 0.7 – 1.0 km^2 in area were surveyed in Nottinghamshire, UK, between May 2020 and November 2021 (Figure 5.1). Located in the East Midlands of the UK, the landscape surrounding the study sites is lowland and comprised of large settlements and smaller villages, arable farmland, and pastures (Table 5.1; Figure 5.2). The climate is temperate with warm, dry summers and cool, wet winters (Met Office, 2022).

The four study sites were selected to (1) encompass a range of road types and densities, (2) have road types in relative similar proportion to the British road network, and (3) range in habitat types, human and housing densities (Table 5.1) to obtain a variety of hedgehog population sizes based on the positive relationship between built area and hedgehog densities (Hof and Bright, 2009; Schaus-Calderón et al., 2020; Turner, Freeman and Carbone, 2021). Habitat composition and road density of the study sites was mapped using OS Mastermap Topography Layers and high-resolution (<1 metre) Aerial Photography (Ordnance Survey, 2020). The study sites were between 1.7 km and 7.5 km apart and no hedgehogs were observed to have moved between the study locations during the surveys based on recaptures in this study and the GPS data obtained in Chapter 6. This implies that little migration occurred between the study sites during data collection and that for this study, each site was an independent local hedgehog population.

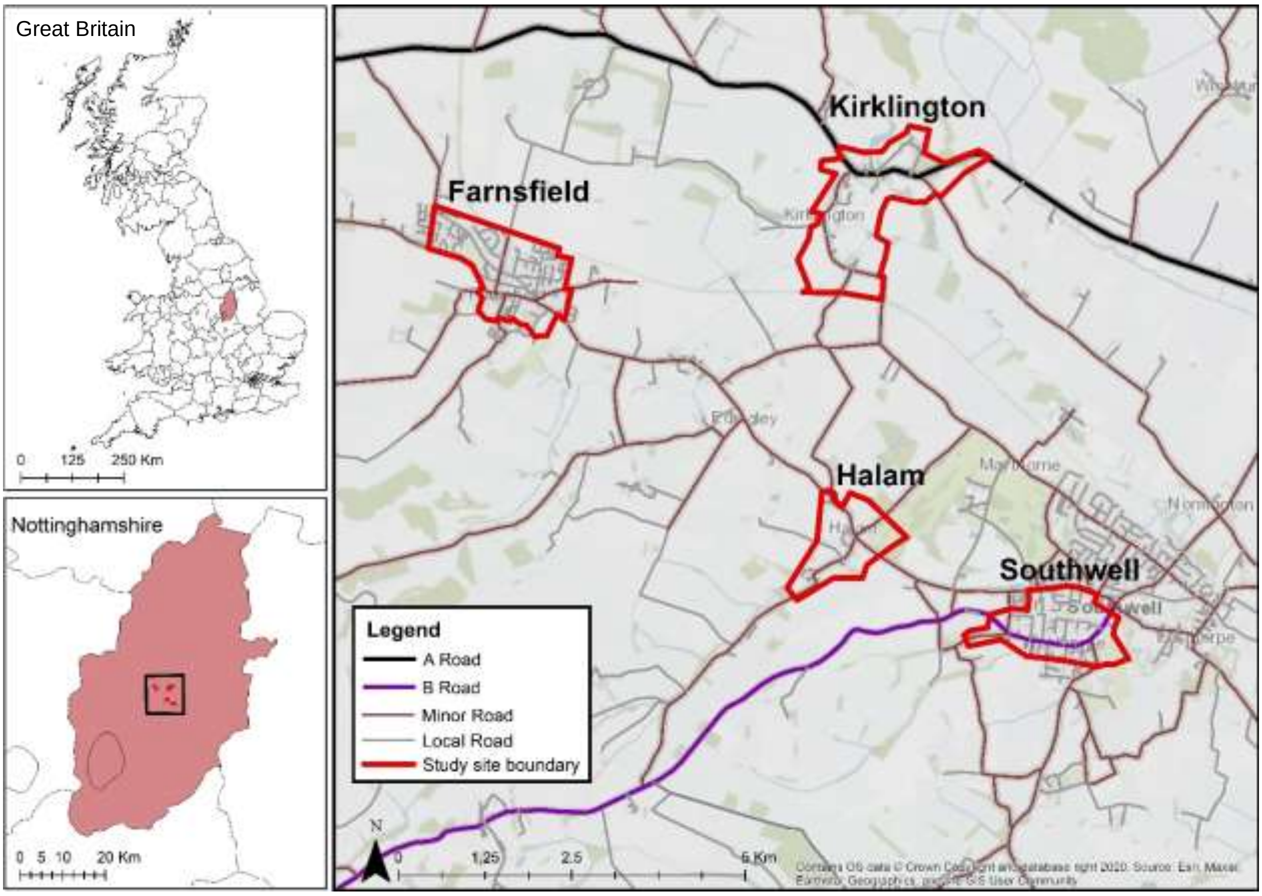


Figure 5.1: Four study sites (outlined in red) in Nottinghamshire that were surveyed between May 2020 and November 2021. Top left: location of Nottinghamshire in Great Britain. Bottom left: location of the study sites within Nottinghamshire.

a) Farnsfield

b) Southwell

d) Kirklington

c) Halam

Figure 5.2: Four study sites (outlined in red) surveyed between May 2020 and November 2021 in central Nottinghamshire, Great Britain. Note that the area surveyed in Farnsfield (1 km^2), Kirklington (0.9 km^2) and Halam (0.7 km^2) covers the entirety of the residential area, whilst only a portion of the larger town of Southwell was surveyed to maintain a feasible survey area (0.8 km^2). Source: Esri. “World Imagery” [basemap].

Table 5.1: Description of the size and both natural and developed characteristics of the four study sites surveyed between May 2020 and November 2021, inclusive.

		Farnsfield	**Southwell**	**Kirklington**	**Halam**
Centroid coordinates		53.104373 -1.034839	53.077462 -0.964150	53.108353 -0.989831	53.083347 -0.989660
Study site area (km^2)		1.0	0.8	0.9	0.7
Road types		Minor and local roads	Intermediate road, minor and local roads	Main road, minor and local roads	Minor and local roads
Road density (km / km^2)		15.1	12.2	5.8	9.8
Housing density (settlements / km^2)		2306	2009	301	436
Habitat composition (percentage)	**Amenity**	10.9	14.9	3.6	15.2
	Arable	0.0	0.0	29.0	10.6
	Garden	58.6	52.6	17.3	29.7
	Grassland†	1.1	1.8	3.8	3.4
	Pasture	0.1	0.0	27.6	18.2
	Built area*	27.1	28.0	9.9	13.3
	Water	0.1	<0.1	1.1	0.9
	Woodland	2.2	2.7	7.6	8.8

** Built area includes buildings, roads, and hardstanding. †Grassland includes improved, semi-improved and un-improved grasslands of acid, neutral or calcareous soil, excluding amenity grassland.*

5.2.2 Roadkill surveys

Driving searches for hedgehog road mortality were conducted within the four study sites on alternate days (3-4 times a week) between 14th of May 2020 and 30th November 2021, inclusive. The searches were part of the wider roadkill survey detailed in Chapter 3 and so were standardised to the same route for each survey. The searches for hedgehog carcasses also took place within a 100 m radius of the boundary of each site. This is because hedgehogs considered part of the population may have had home ranges on the edges of the surveyed area and been susceptible to vehicle collisions outside of the study site. A 100 m radius was considered sufficient to encompass home ranges in a similar habitat that are, on average, 0.22 km^2 ± 0.05 SE for male hedgehogs and

0.02 km^2 ± 0.01 SE for female hedgehogs (Pettett et al., 2017). The roadkill survey route covered as much of the tarmacked road network within each study site as possible in order to achieve accurate road mortality records. This equated to a coverage of 7.1 km in Farnsfield (73.0% of all roads at this site), 6.8 km in Southwell (75.5%), 4.8 km in Kirklington (91.8%), and 3.8 km in Halam (96.8%). Collectively, the roadkill surveys consisted of 8.1% main roads, 8.3% intermediate roads (i.e., B-roads), 47.9% minor roads (i.e., roads that link villages and towns), and 35.7% local roads (i.e., residential roads), which were similar in proportion to the wider British road network (Department for Transport, 2019).

Immediately following observation by car, road-killed animals were examined on foot and Global Positioning System (GPS) co-ordinates were recorded using a handheld GPS device (Garmin 60 GPS unit; mean accuracy 3 m). Individual sex (based on external genital morphology; Morris, 2018), age category (based on hind foot length; Haigh et al., 2014b) and individual identification (based on numbered, coloured heat-shrink tags; see Section 5.2.3) of the carcass were recorded where possible. Although the hind foot length protocol derived by Haigh et al. (2014b) was based on a relatively small sample size, this method remains the most applicable to age categorisation of hedgehogs in the field. Carcasses were not removed from the road in order to measure carcass persistence. Instead, extensive notes and photographs of the location, appearance, and any discernible features of the carcass were noted to avoid double-counting. It is important to note that the roadkill surveys started one month before the nocturnal spotlight surveys (see Section 5.2.3) due to the national COVID-19 lockdown restrictions. Overall, 24% of the roadkill surveys took place during a national lockdown where road traffic was up to 49% lower than the equivalent month the year before (Department for Transport, 2022b).

5.2.3 Population dynamics

The four sites were studied using nocturnal spotlight surveys between June 2020 and October 2021, inclusive, to estimate hedgehog population parameters such as population size, reproductive rates, and annual survival probability. Spotlight surveys were shown to balance the costs and practicality of surveys with hedgehog detections, particularly over short vegetation cover as in this present study (Bearman-Brown et al., 2020). Likewise, spotlight surveys have greater capture rates compared to alternatives such as live-trapping (L. Moore, unpublished data), and provide demographic data, such as individual sex and age, that other methods such as camera trapping and footprint tunnels do not (Schaus-Calderón et al., 2020; Willaims et al., 2018). Hedgehog densities were estimated by modelling individual encounter history data using multi-session spatial capture-recapture (SCR) methods (Efford, 2013; Sutherland, Royle and Linden, 2019). SCR is a key advancement upon traditional (i.e., non-spatial) capture-recapture methods because it incorporates (meta)data such as movement, the spatial deployment of detectors and space use (activity centres) of individuals to estimate population density from spatially referenced detections (Royle et al., 2017). Hedgehogs were surveyed at night due to their nocturnal behaviour, during their active period (April – October inclusive), and on foot along pre-defined transects. To maximise coverage within each study site, transects were placed across publicly accessible spaces, such as roads, public footpaths, cemeteries, and sports fields, as well as private land for which landowner permission was granted, such as gardens, private pasture, woodland, and orchards (Appendix VII). As such, the length of each transect was 7.68 km in Farnsfield, 8.38 km in Southwell, 5.74 km in Kirklington, and 6.14 km in Halam. Transects were designed to cover as much accessible area within each study site as possible and were walked once in each survey night with the direction reversed on alternate surveys. Ten spotlight surveys were conducted at each of the four sites in each of three time periods (i.e., 30 nights survey data for each site): one pre-reproduction survey (April - June 2021) and two post-reproduction surveys (July – October 2020 and July – October 2021). Surveying across three time periods was adopted in order to allow inferences about reproductive rates. Ten spotlight surveys per time period was also deemed appropriate to obtain recapture rates sufficient for accurate SCR analyses (Schaus-Calderón et al., 2020). The sessions were two-weeks long to likely maintain a closed population, as per SCR assumptions (Royle et al., 2017). All hedgehogs found were approached on foot and captured by hand, weighed (in grams) using an electronic balance (Salter 1035 platform scale. Salter Housewares: Manchester, UK) and sexed (Morris, 2018). Animals were categorised as adults if they were found during the pre-reproduction survey (i.e., they had survived one winter hibernation period), irrespective of weight. Hedgehog weights fluctuate throughout the year, with adults generally weighing >600 g later in the year. Therefore, all animals found in the post-reproduction surveys weighing <600 g were classified as juveniles (Young et al., 2006; Hubert et al., 2011).

Spines of healthy adult and juvenile hedgehogs were uniquely marked with five numbered and coloured heat-shrink tubes (10 mm in length for adults, 7 mm for juveniles; Reeve, Bowen and Gurnell, 2019; Printasleeve: Somerset, UK). Each heat-shrink tube on an individual had the same number and colour, unique to the individual, and located in the same area on the hedgehog. Tubes were attached using a portable soldering iron (six watts, manufacturer: Weller) on the upper half of individual spines in different areas on the hedgehog's dorsal surface. As such, individuals could be identified, whether recaptured alive or dead, based on the combination of different numbers, colours, and positions of the heat-shrink tubes. The reliability of this marking system, particularly over relatively long periods of time (<18 months), was validated during previous long-term studies (Reeve et al., 2019). Hedgehogs were classed as being healthy if they had less than five visible external parasites (e.g., ticks, Order Ixodida), no physical injuries, and natural behaviour (e.g., curling into a tight ball). No hedgehogs were marked unless they met these criteria. GPS co-ordinates were taken to record the location of every hedgehog found using a handheld GPS device (Garmin GPS 60). All hedgehogs were released at the location of capture and were observed from a distance until the resumption of normal movement.

To gather comprehensive insight into hedgehog mortality and to give context to the roadkill counts, data from hedgehogs killed from non-road related causes within the four populations were also recorded. These were either encountered during nocturnal surveys or reported by members of the public (including individuals and rescue centres). The public were informed of the study and data requirements via social media, local newspaper articles, workshops, and letters. All animals recovered dead regardless of cause were examined comprehensively to determine whether they had been tagged.

All data were collected under license from Natural England (ref: 2018-36011-SCI-SCI-8 and 2018-36011-SCI-SCI-11). Ethical approval was granted by Nottingham Trent University’s Animal, Rural and Environmental Science Ethical Review Group (code: ARE192014a).

5.2.4 Data analysis

5.2.4.1 Roadkill records

To estimate road mortality rates, λ (individuals/km/day), for each site, Equation 1 was used (see section 3.2.2.1 in Chapter 3). Average carcass persistence time was taken as 4.68 days (±0.08 SE) as calculated in Chapter 3. When the number of survey repeats is large such as in this study, carcasses have a high probability of detection due to comprehensive coverage of the road network across time, and so detectability was input as one (Wembridge et al. 2016). Incorporating the total length of the road surveyed for each site accounts for the differing road lengths, and hence survey effort, between the study sites. To estimate annual road mortality, and account for a largely inactive hibernation period, daily mortality rates were multiplied by 214 (representing 214 days, equivalent to an active period of seven months from April to October; Bearman-Brown et al., 2020). However, it is important to note that hedgehogs vary in the onset, duration, and end of their hibernation period and hence when they could potentially be killed on roads (Bearman-Brown et al., 2020). Therefore, annual estimates are probably conservative.

5.2.4.2 Population demographics

To create the spatial encounter histories required for population density estimation using SCR, each spotlight transect was divided into 50 m 'trap' sections using ArcGIS 10.3.1 (ESRI, 2015). Trap sections of 50 m are considered small enough in relation to hedgehog movements to allow detection at multiple traps (i.e., spatial recaptures), but also large enough to be efficiently solved in a continuous space model (Dupont et al., 2020). The location of each hedgehog's (re)capture was fixed to the closest 'trap' along the transect. Population densities were obtained using multi-session SCR. Eight SCR models were fitted: the null model (no co-variates) and all additive combinations of constant and session-specific density (D), sex-specific detection (p, an estimate of detection at a certain distance from the activity centre) and sex-specific space use (σ, extent of area used by an individual under study). Models were fitted using the package '*oSCR'* (version 0.42.0; Sutherland et al., 2016) in R (version 3.6.1; R Core Development Team, 2017) and were ranked according to Akaike's Information Criterion (AIC) value (Burnham and Anderson, 2004). The best fitting SCR model for each site and age group included constant density (see Section 5.3.2.1). Therefore, the constant population density estimates from the SCR models were used to calculate population sizes. Constant estimates treat all parameters (density, sex-specific detection, and sex-specific space use) the same and so combines all records across the survey sessions. This allows for a much larger sample size to be analysed. In comparison, session-specific estimates stratifies each session and estimates the parameters separately. Chi-squared tests were used to quantify the presence or absence of sex- or age-biases in the roadkill records relative to the source population. A linear regression was used to estimate the rate of heat-shrink tube loss on adult and juvenile hedgehogs over time to explore whether the spotlight surveys adhered to the SCR assumption that animals must not lose their marks over the course of the study.

Sex-specific annual survival rates were computed using right-censored Kaplan–Meier analysis for adults and juvenile hedgehogs for each site (Kaplan and Meier, 1958). Kaplan–Meier analysis was used as it allows for a staggered entry method to be adopted, which was important because individuals were captured and marked on different surveys. Moreover, this analysis was chosen above alternatives such as life tables as it uses event and censoring times. This in turn accounts for individuals that are not recaptured during the surveys, providing more robust results on a larger sample size (i.e., not only those that were recaptured). The differences in males and females at each site were quantified using a log-rank test. All analyses were conducted in R (version 3.6.1; R Core Development Team, 2017) using the packages '*survival*' (Therneau, 2015) and '*survminer*' (Kassambara and Kosinki, 2018). Reproductive rates were calculated by dividing the number of juveniles by the number of adult females present in each local population based on constant SCR densities (Hubert et al., 2011). These estimates are based on juveniles that were independent from their mother and are an average across females in the population.

5.3 Results

5.3.1 Road mortality

Between May 2020 and November 2021, inclusive, 269 roadkill surveys were conducted within the four study sites. Forty-two roadkilled hedgehogs were found within the four study sites; Farnsfield – 19 (♂9, ♀7, 3 juveniles); Southwell – 13 (♂6, ♀4, 2 juveniles, 1 unknown adult); Kirklington – 8 (♂4, ♀2, 2 juveniles); and Halam - 2 (♂1, ♀1). Of the 42 road-killed hedgehogs found, 32 carcasses (76%) had identifiable heat-shrink tubes on their spines that were attached during the spotlight surveys conducted at each site. It is important to note that the roadkill surveys started one month before the spotlight surveys due to national COVID-19 lockdown restrictions and at least three hedgehogs carcasses were found within the study sites before spotlight surveys began. Of the unmarked roadkill, 80% (n = 9) were male. Road mortality rates within each site ranged from 0.26 to 1.30 carcasses/km/year (Table 5.2). Per road type, 0.61 carcasses/km/year were estimated on main roads, 1.05 carcasses/km/year on intermediate roads, and 0.54 carcasses/km/year on minor roads.

Table 5.2: Summary of diurnal roadkill surveys conducted from May 2020 to November 2021, inclusive, in the four study sites in Nottinghamshire.

		Farnsfield	**Southwell**	**Kirklington**	**Halam**
Survey effort of roadkill surveys (total km driven)		1922	1828	1278	1011
Road mortality rates (individuals/km/year)	**Total**	1.30	0.94	0.82	0.26
	Adult male	0.62	0.43	0.31	0.13
	Adult female	0.48	0.29	0.31	0.13
	Juvenile	0.21	0.14	0.21	0.00

5.3.2 Population dynamics

5.3.2.1 Population size

The nocturnal spotlight surveys detected hedgehogs at all sites. Differing predictor variables were included in the best fitting SCR model for hedgehog densities for each site and age group, although each best-fitting model included constant density rather than session-specific density (Table 5.3; Appendix VIII). This infers that there were no differences between population densities between sessions. Collectively, a survey effort of 838.20 km of transects on foot were realised (Table 5.4). Overall, 237 unique individuals (202 adults, 35 juveniles) were caught across 723 capture events, with average recapture rates ranging from 1.5 to four times per individual (Table 5.4). The hedgehog densities were greatest in Farnsfield, followed by Southwell, Kirklington and Halam (Figure 5.3). Population sex ratios differed between survey sessions, with an increase in males during the pre-reproduction survey (April - June 2021) for each local population (Table 5.4). Out of the five heat-shrink tubes originally attached to each hedgehog, the mean number that remained after 12 months on recaptured adult hedgehogs was 3.10 (±0.57 SD, n = 10 individuals) and 2.0 (±0 SD, n = 3 individuals) on juvenile hedgehogs (Appendix X).

Table 5.3: Best fitting Spatial Capture-Recapture models (ΔAIC < 2) estimating hedgehog densities across the four study sites in Nottinghamshire. D = density, p = detection, sig (σ) = space use. AIC = Akaike's Information Criterion, Δi = delta AIC, ω = AIC weighting, Cum ω = cumulative weighting.

		Model	**AIC**	**Δi**	**ω**	**Cum ω**
Farnsfield	**Adult**	D(~1) p(~1) sig(~sex)	3308.30	0.00	0.42	0.42
		D(~session) p(~1) sig(~sex)	3309.91	1.61	0.19	0.61
		D(~1) p(~sex) sig(~sex)	3310.29	1.99	0.16	0.77
	Juvenile	D(~1) p(~1) sig(~1)	912.15	0.00	0.34	0.34
		D(~1) p(~1) sig(~sex)	913.81	1.66	0.15	0.48
		D(~1) p(~sex) sig(~1)	913.85	1.69	0.14	0.63
		D(~session) p(~1) sig(~1)	914.15	2.00	0.12	0.75
Southwell	**Adult**	D(~1) p(~sex) sig(~sex)	1698.17	0.00	0.64	0.64
	Juvenile	D(~1) p(~1) sig(~sex)	279.33	0.00	0.34	0.34
		D(~1) p(~sex) sig(~sex)	280.67	1.34	0.18	0.52
		D(~1) p(~1) sig(~1)	281.13	1.80	0.14	0.66
		D(~session) p(~1) sig(~sex)	281.33	2.00	0.13	0.78
Kirklington	**Adult**	D(~1) p(~1) sig(~sex)	889.31	0.00	0.53	0.53
		D(~1) p(~sex) sig(~sex)	890.22	0.91	0.34	0.86
	Juvenile	D(~1) p(~1) sig(~1)	206.92	0.00	0.36	0.36
		D(~1) p(~sex) sig(~1)	208.70	1.78	0.15	0.51
		D(~session) p(~1) sig(~1)	208.72	1.80	0.15	0.66
		D(~1) p(~1) sig(~sex)	208.74	1.82	0.145	0.80
Halam	**Adult**	D(~1) p(~sex) sig(~sex)	255.72	0.00	0.48	0.48

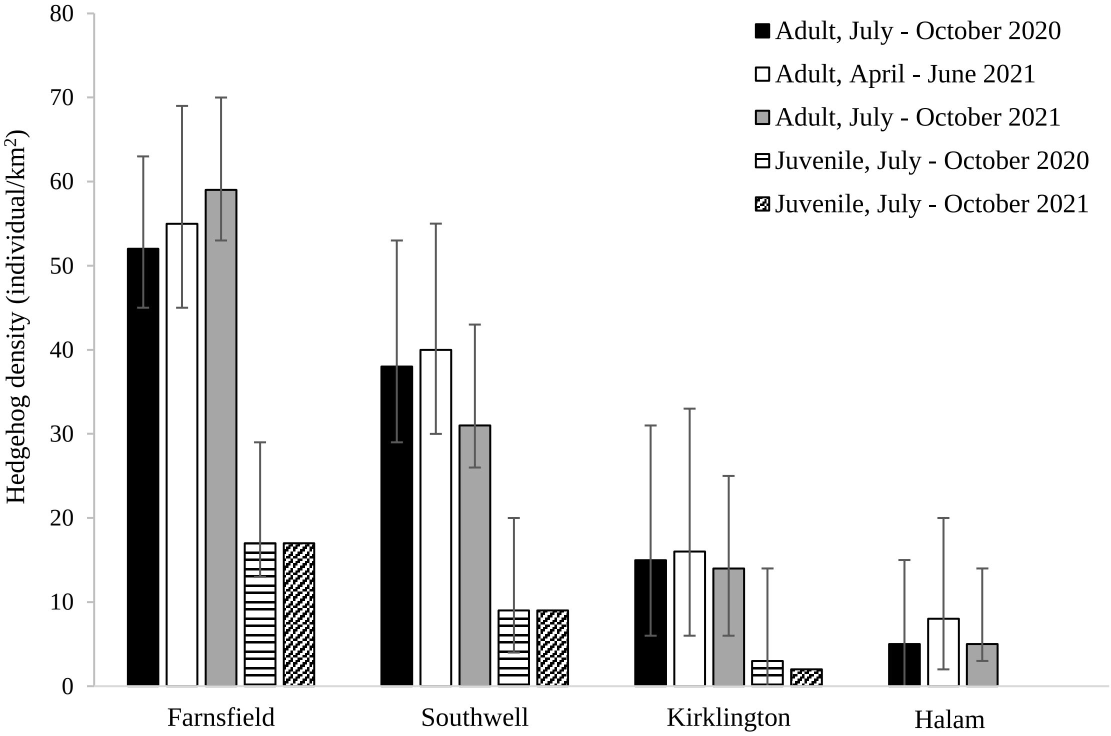


Figure 5.3: Population density estimates (hedgehogs per km^2) for adults and juveniles within the four study sites in Nottinghamshire. Error bars represent 95% confidence intervals where calculable.

Table 5.4: Summary of spotlight surveys across the three survey occasions. The recapture rate refers to the number of times an individual was recaught after the initial capture and marking.

Study site			**Farnsfield**	**Southwell**	**Kirklington**	**Halam**
Number of survey sessions			30	30	30	30
Survey effort (total km walked)			230.40	251.40	172.20	184.20
Number of hedgehogs captured, and marked if new (ratio of adults: juveniles)	**July - October 2020**		48 adults 14 juveniles (1:0.29)	21 adults 5 juveniles (1:0.24)	11 adults 3 juveniles (1:0.27)	2 adults (1:0.00)
	April - June 2021		50 adults	27 adults	11 adults	3 adults
	July - October 2021		54 adults 14 juveniles (1:0.26)	23 adults 5 juveniles (1:0.22)	9 adults 2 juveniles (1:0.22)	2 adults (1:0.00)
Average recapture rate (± SD)	**July - October 2020**	Adult	2.27 (1.58)	2.67 (1.46)	2.27 (0.90)	4.00 (1.41)
		Juvenile	3.43 (2.10)	2.00 (0.71)	3.00 (1.00)	NA
	April - June 2021	Adult	2.46 (1.61)	1.81 (0.92)	1.91 (1.04)	3.00 (1.00)
	July - October 2021	Adult	2.46 (2.05)	2.04 (1.36)	2.22 (0.67)	1.50 (0.71)
		Juvenile	2.57 (1.65)	2.00 (1.22)	3.50 (0.71)	NA
% new adult entrants	**April - June 2021**		88%	63%	64%	100%
	July - October 2021		74%	39%	0%	0%
Sex ratio of adult hedgehogs marked (M:F)	**July - October 2020**		1:1.18	1:0.62	1:1.20	1:1.00
	April - June 2021		1:0.92	1:0.50	1:0.57	1:0.50
	July - October 2021		1:2.00	1:1.09	1:0.80	1:1.00
Constant adult population size			55	29	14	5
Constant adult male population size			22	15	8	3
Constant adult female population size			33	14	7	2
Constant juvenile population size			17	7	3	0

When the recorded road mortality and constant population size figures are combined (i.e., based on marked *and* unmarked individuals), they indicate that 13.2–28.6% of the studied local populations were killed on roads annually (Table 5.5). Considering the marked population and marked roadkill only, between 7.4 and 40.0% of the local populations were killed on roads annually

(Appendix IX). Moreover, two out of the four local populations showed a significant bias in roadkill records towards males relative to their prevalence in the population (Appendix XI). The largest population of Farnsfield showed a bias in roadkill records to adults compared to juveniles, but such biases are difficult to detect in small populations (Appendix XI). Based on the adult female and juvenile population size estimates, the number of juveniles per female was 0.52 in Farnsfield, 0.50 in Southwell, and 0.43 in Kirklington. No juveniles were found in Halam.

Table 5.5: Percentage of the total population and separate cohorts killed on roads in 2020 and 2021 in the four study sites, using constant density estimate from multi-session SCR analyses (i.e., based on marked and unmarked individuals). Data in parenthesis denote 95% confidence intervals.

		Farnsfield	**95% CI**	**Southwell**	**95% CI**	**Kirklington**	**95% CI**	**Halam**	**95% CI**
Total population	**2020**	13.9	10.0 - 18.9	16.7	9.0 – 26.8	30.9	15.9 - 61.7	28.6	8.9 – 50.0
	2021	12.5	9.0 - 17.0	19.4	10.5 – 31.3	18.5	9.5 - 37.0	28.6	8.9 – 50.0
	Average	**13.2**	9.5 - 17.9	**18.1**	9.8 - 29.0	**24.7**	12.7 - 49.4	**28.6**	8.9 – 50.0
Adult population	**2020**	16.4	12.7 – 20.9	17.4	11.6 - 25.0	29.6	17.8 – 55.6	28.6	8.9 – 50.0
	2021	12.7	9.9 - 16.3	20.8	13.9 – 30.0	14.8	8.9 – 27.8	28.6	8.9 – 50.0
	Average	**14.5**	11.3 - 18.6	**19.1**	12.7 - 27.5	**22.2**	13.3 - 41.7	**28.6**	8.9 – 50.0
Juvenile population	**2020**	5.9	3.4 – 10.0	13.9	4.3 - 41.7	33.3	11.1 – 100.0	n/a	n/a
	2021	11.8	6.9 – 20.0	13.9	4.3 - 41.7	33.3	11.1 – 100.0	n/a	n/a
	Average	**8.8**	5.2 - 15.0	**13.9**	4.3 - 41.7	**33.3**	11.1 – 100.0	n/a	n/a
Adult male population	**2020**	22.7	17.2 – 29.4	19.7	13.4 - 28.8	25.0	13.1 - 44.4	0.0	0.0
	2021	18.2	13.8 – 3.5	19.7	13.4 - 28.8	12.5	6.5 - 22.2	47.6	15.9 - 100.0
	Average	**20.5**	15.5 - 26.5	**19.7**	13.4 - 28.8	**18.8**	9.8 - 33.3	**23.8**	7.9 - 71.4
Adult female population	**2020**	12.1	9.5 - 15.4	14.7	9.6 - 20.8	28.6	27.8 - 74.1	71.4	20.4 – 100.0
	2021	9.1	7.1 - 11.5	14.7	9.6 - 20.8	14.3	13.9 - 37.0	0.0	0.0
	Average	**10.6**	8.33 - 13.5	**14.7**	9.6 - 20.8	**21.4**	20.8 - 55.6	**35.7**	10.2 - 71.4

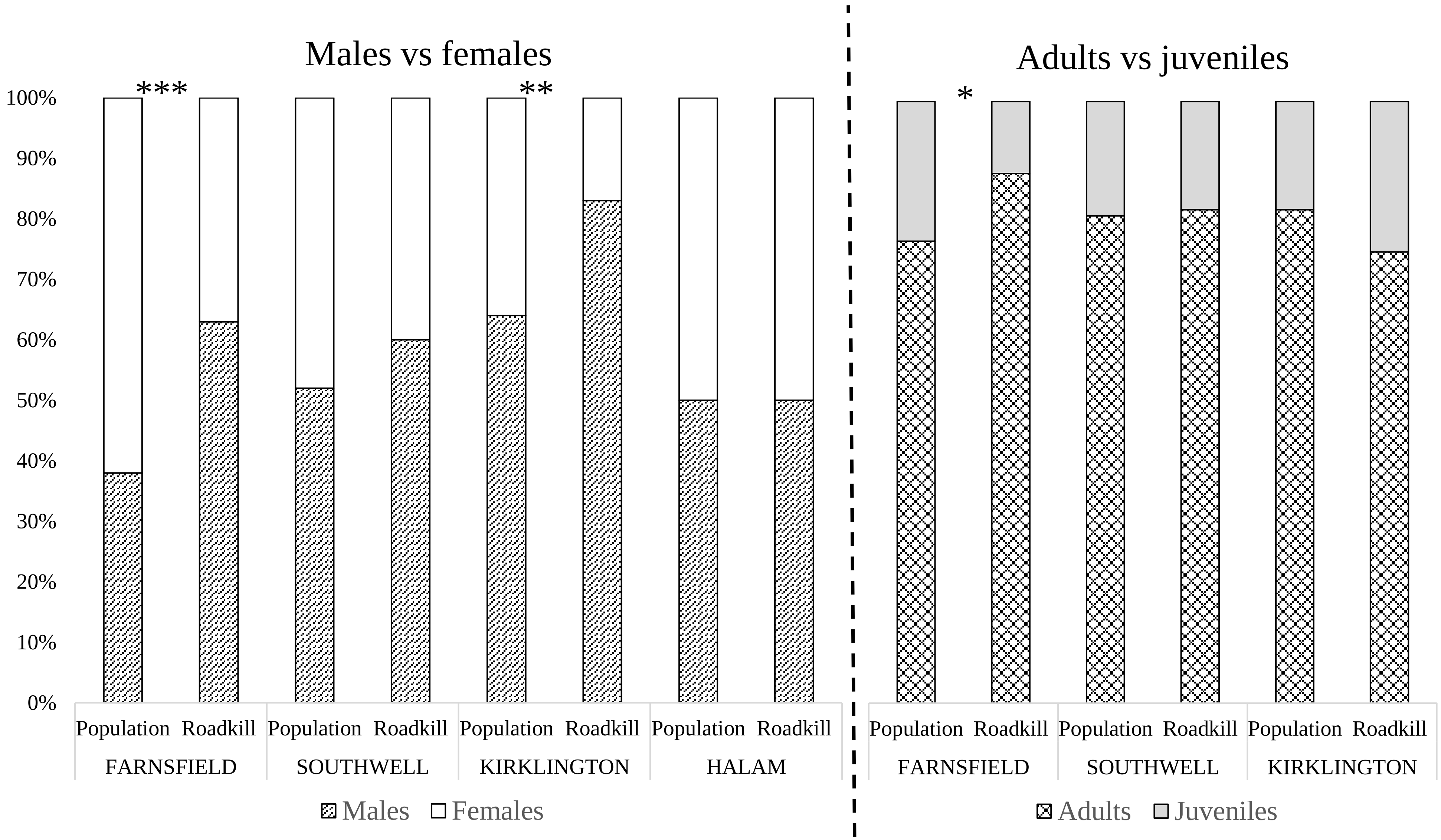


Figure 5.4: The sex and age structure of the four studied populations in Nottinghamshire and of the road mortality within each population. * denotes a significant bias at $p \leq 0.05$, ** $p \leq 0.01$. *** $p \leq 0.001$.

5.3.2.2 Survival and non-road mortality

In addition to the 42 road-killed hedgehogs, 24 known non-road mortalities within the study populations were recorded between May 2020 and November 2021 (Table 5.6). Across all four sites, this comprised of eight known mortalities from disease/illness, five known mortalities from badger predation, two known mortalities from entanglement in sports netting, one from drowning in a garden pond, and four were from unknown causes. Note that this is unlikely to be an exhaustive list of non-road deaths, which leads to the disparity in the contribution of road mortality to total mortality based on known mortality (Table 5.6) and total mortality derived from Kaplan-Meier estimates that also include unrecorded deaths (Table 5.7). Road mortality accounted for more than one third of total mortality (i.e., known and unknown mortality) per annum for each local population, ranging from 37.7% to 41.0% (Table 5.7).

Table 5.6: Causes of known hedgehog mortality for the four study populations. Percentages are of total population mortality.

	Farnsfield (n = 34)	**Southwell (n = 17)**	**Kirklington (n = 12)**	**Halam (n = 3)**
Vehicles	55.9	76.5	66.7	66.7
Badger predation	n/a	11.8	16.7	33.3
Disease (including starvation)	23.5	5.9	8.3	n/a
Entanglement in sports netting	5.9	n/a	n/a	n/a
Drowning	2.9	n/a	n/a	n/a
Unknown	11.8	5.9	8.3	n/a

For both adults and juveniles, annual survival probability was highest in Farnsfield and lowest in Kirklington (Table 5.7). Annual survival was not significantly different between adult males and females at any site (Farnsfield: Log-rank test: $X^2_1 = 9$, $p = 0.08$; Southwell: Log-rank test: $X^2_1 = 9$, $p = 0.31$; Kirklington: Log-rank test: $X^2_1 = 9$, $p = 0.62$; Halam: Log-rank test: $X^2_1 = 9$, $p = 0.80$), nor juvenile males and females (Farnsfield: Log-rank test: $X^2_1 = 9$, $p = 0.44$; Southwell: Log-rank test: $X^2_1 = 9$, $p = 1.00$; Kirklington: Log-rank test: $X^2_1 = 9$, $p = 0.32$).

Table 5.7: Summary table of the demography and road mortality of the four study populations in Nottinghamshire. SE = standard error.

	Farnsfield	**Southwell**	**Kirklington**	**Halam**
Constant adult density (hedgehogs km^{-1})	55 (22♂:33♀)	36 (19♂:17♀)	15 (8♂:7♀)	5 (3♂:2♀)
Constant juvenile density (hedgehogs km^{-1})	17 (10♂:7♀)	9 (4♂:5♀)	3 (2♂:1♀)	0
Adult annual survival rate	0.69 SE 0.07 (0.67♂:0.73♀)	0.61 SE 0.09 (0.58♂:0.67♀)	0.44 SE 0.13 (0.42♂:0.44♀)	0.53 SE 0.25 (0.70♂:0.50♀)
Juvenile annual survival rate	0.64 SE 0.12 (0.51♂: 0.71♀)	0.50 SE 0.35 (0.50♂:0.50♀)	0.38 SE 0.76 (0.50♂:0.50♀)	n/a
Contribution of road mortality to total mortality based on Kaplan-Meier estimates	40.0%	41.0%	39.9%	37.7%
Percentage of the population killed on roads per annum	13.2%	18.1%	24.7%	28.6%

5.4 Discussion

Using in-depth demographic context in addition to detailed road mortality surveys, this is one of the most comprehensive studies on road mortality impacts on wildlife populations to date. Importantly, this study shows that the negative impacts of road mortality are not constant amongst roadside populations of different size. The variation in impact magnitude amongst the four studied populations appears to be largely driven by one or a combination of key life-history traits: population density, reproductive rate, and juvenile survival. In turn, these traits should be key factors for future study and impact assessments of new roads. Whilst road mortality is likely to be demographically compensated in the larger hedgehog populations and/or those with sufficient breeding cohorts, it appears to have significant detrimental impact on small populations that are already vulnerable to demographic and environmental stochasticity. These results emphasise the importance of recognising the interplay between various intrinsic and extrinsic threats and how their combination can drive local depletion and population extinction events. In the case of British hedgehogs more widely, road mortality is likely a significant factor in the decline of rural (e.g., Kirklington and Halam) rather than (peri)urban (e.g., Farnsfield and Southwell) hedgehog populations. This is because hedgehog densities are often lower in rural areas and thus are at higher risk from additional mortality. This, in turn, provides justification for the implementation of conservation strategies, including in relation to road networks, that are targeted towards threatened rural local populations as well as urban local populations that can disperse into rural areas (i.e., source-sink dynamics).

5.4.1 Percentage of the populations killed on roads annually

The estimation of the percentage of each local population killed on roads annually is gaining recognition as a simple yet effective method of examining the relative importance of road mortality in the context of whole populations (Barrientos et al., 2021). As hypothesised, an estimated 13.2 - 28.6% of the studied local hedgehog populations were killed annually in the four sites. These results are in line with previous estimates in Europe that similarly used capture-recapture methods. For instance, an annual loss of 6 - 9% was reported for a rural local population in the Netherlands (Huijser et al., 1997), a 17 – 22% (Goransson, Karlsson and Lindgren, 1976) and 3 – 22% (Kristiansson, 1990) loss was reported for several Swedish populations in rural villages, as well as a 24% loss of a rural local Polish population (Orłowski and Nowak, 2004). These figures approximate estimations of proportional loss from roads of an array of mammal species, including 58% and 49% of the nationwide red fox (*Vulpes vulpes*; Harris and White, 1994) and Eurasian badger (*Meles meles;* Clarke, White and Harris, 1998) populations in the UK, respectively, 10% of the regional Eurasian otter population in Germany (Kubasch, 1992), and 12 – 25% of local post-breeding Eurasian badger populations in Sweden (Seiler, 2003) and The Netherlands (Bekker and Canters, 1997). The threshold for road mortality rates that can be demographically compensated is likely to be species and population specific. Despite having the greatest amounts of road mortality in terms of individuals, the two largest populations in this study had estimated proportional losses that were approximately half of those experienced by the smaller populations due to densities that were 2 – 11 times greater. As a result, it is likely that the breeding cohorts (i.e., effective population size) in larger populations are able to remain sizeable enough for sufficient recruitment and genetic admixing despite road mortality. Larger populations are also more capable of persisting through demographic stochasticity, such as annual fluctuations in population size (Reeve, 1981; Kristiansson, 1990). For example, Jackson (2007) found that hedgehog densities on South Uist, UK, fluctuated 21–25% above and below the mean density between 1998 and 2001. Annual population increases, albeit short-term, likely compensate for losses on roads and prevent ongoing population declines (Ruiz-Capillas, Mata and Malo, 2015).

The greater proportional losses in the smallest populations in this study (Kirklington and Halam), despite lower road mortality rates, reinforces the notion that low road mortality rates do not necessarily equate to low proportional loss (Jaeger and Holderegger, 2005). In areas where population densities are lower, the relative contribution of an individual to population stability is greater (Seiler, 2003). These smaller hedgehog populations, often in rural areas, are already more vulnerable to environmental and demographic stochasticity. As such, they may become increasingly dependent upon new recruits (births or immigrants) to offset the threat that road mortality poses to their persistence. This could indicate that the smaller 'at risk' populations are acting as demographic sinks, as surmised for hedgehogs close to motorways and main roads (up to 25,000 vehicles per day) in New Zealand (Sadleir and Linklater, 2016). In fact, Orłowski and Nowak (2004) and Hubert et al. (2011) also suggest that road mortality is a regulating factor that maintains low hedgehog densities. Beyond the consequences for long-term population trends, wildlife-vehicle collisions are increasingly being considered an ethical issue due to being an unnatural source of mortality and potential form of suffering due to the deaths not necessarily being instantaneous (Moore et al., 2021). Specifically, road mortality has previously been placed in the concept of 'One Welfare'; an approach used to highlight the inter-relatedness between the humane treatment of animals, human wellbeing, and the environment (Englefield et al., 2020). This approach raises the profile for welfare as a key mitigation target, applicable to the estimated 167,000–335,000 hedgehogs killed on British roads each year (Wembridge et al., 2016).

5.4.2 Mortality and survival rates by cohort

The demographic cohort most impacted by road mortality is as important, if not more so, than proportional loss of the whole population. The road mortality records in two of the four studied populations were significantly male-biased, which is a likely function of the greater home ranges, nightly movements and yearly activity levels of males compared to females (Schaus-Calderón, 2021). A male-bias of road mortality raises less concern for population viability of species with a polygamous mating system, such as hedgehogs, as the number of males in a population is not a limiting factor for population growth. Furthermore, hedgehog-vehicle collisions likely operated as a compensatory source of mortality for other mortality causes. Male hedgehogs were recorded as roadkill almost twice as often as females in the two larger populations, a pattern also observed by Haigh et al. (2014b) and Rasmussen et al. (2023). Simultaneously, males are considered to have the highest risk of accidental deaths (Rautio et al., 2016) and lower annual survival probabilities compared to females (this study; Kristiansson, 1990; but see Rasmussen et al., 2023), a likely function of greater activity levels and intra-specific fighting of males. For instance, Rautio et al. (2016) found that 80% of the observed wounds on hedgehogs were on males and male hedgehogs are often more infected with parasites compared to females (Egli, 2004; Haigh et al., 2014a). The high likelihood of male mortality, which is common amongst mammals (see summary by Gantchoff et al., 2020), suggests that the impact of roadkill may be lessened by vehicle collisions largely removing males as the 'doomed surplus' of the population (i.e., compensatory mechanisms).

In animal populations with a small number of reproducing adult females responsible for rearing young, road mortality of a few females may curtail population growth. This is especially the case when females have higher survival rates compared to males (as shown for hedgehogs: this study; Kristiansson, 1990; Huijser and Bergers, 1997). The negative repercussions of female road mortality were shown for giant anteaters (*Myrmecophaga tridactyla*), whereby female-only roadkill produced a 46.1% probability of extinction in 100 years, compared to a 0.1% chance from male-only roadkill (Desbiez, Bertassoni and Traylor-Holzer, 2020). Notably, the two smallest local populations in our hedgehog study had 21.4 – 35.7% of their female cohorts killed on roads annually. Smaller populations are inherently more likely to have a skewed sex ratio in the population or roadkill records by chance, rather than a systematic difference, leading to a disproportionate vulnerability of certain demographic groups.

Adults were significantly more likely to be killed on roads than juveniles, corroborating previous roadkill records in Sweden (Kristiansson, 1990) and Ireland (Haigh et al., 2014b). Importantly however, both age groups were killed as frequently as expected by chance when compared to their proportions in the population. Juvenile hedgehogs (<12 months of age) have smaller home ranges than adults (Kristiansson, 1990; Rasmussen et al., 2019) and do not appear to move far from their natal nests (Rasmussen et al., 2019). As such, juvenile roadkill is likely to be a result of routine movements to forage before hibernation, rather than dispersal like other mammals (e.g., GPS-tracked squirrels; Fey et al., 2016). It is unlikely that road mortality will affect hedgehog population age-specific survival rates or age-structure, especially as no age-biases were found to the road mortality records.

The conclusions of this study rely on robust data on population structure. To collect this data, the encounter histories for each population needed for SCR analyses were collected by spotlight surveys. Previous concerns surrounding the efficacy of spotlight surveys centre on the searches relying on roads and road verges, which hedgehogs have been shown to avoid, although they do not avoid crossing roads per se (Dowding et al., 2010; Schaus-Calderón, 2021). The inclusion of public green space, many private fields, and gardens in the spotlight survey route is likely to have, at least partially, minimised this limitation. Moreover, no significant differences in capture probability have been found between sexes or age groups (Huijser et al., 1997; Pettett et al., 2020). In turn, confidence can be held in the population structure recorded, and so the inferences of road mortality bias and proportional loss. However, small samples sizes were recorded in Halam and, to a lesser extent, Kirklington. Caution should therefore be taken when interpreting the population demographics as differences by cohort and biases are difficult to detect.

5.4.3 Reproductive rates

For relatively short-lived animals, reproduction may have more importance for population growth than survival, and reproduction is likely to be a significant factor in a population's vulnerability to road mortality (Mumme et al., 2000). Rytwinski and Fahrig (2012) and González-Suárez, Zanchetta Ferreira and Grilo (2018) found that traits associated with faster, more frequent reproduction predicted population resilience to additional mortality. The presence of juveniles in three of the four populations confirmed that they are breeding populations with rates comparable to the literature (Farnsfield: 0.52 juveniles per female, Southwell: 0.50 juveniles per female, Kirklington: 0.43 juveniles per female). For example, Hubert et al. (2011) recorded 0.6 and 0.42 juveniles per female in urban and rural area of France, respectively. Reproductive rates are not thought to be wholly density-dependent in hedgehogs and may largely be controlled by predation and food availability during spring to early autumn (Hubert et al., 2011; Moorhouse, 2013). The number of juveniles in the larger populations of Farnsfield and, to a lesser extent, Southwell approximate the number of individuals killed on roads annually in each population. Due to this replacement of many road-killed individuals on an annual basis, road mortality is unlikely to affect the persistence of these populations unless future environmental or demographic changes cause road mortality to rise above recruitment (for example, due to higher traffic and increased road mortality or lower reproductive rates; González-Suárez et al., 2018).

The comparatively high reproductive rates in Kirklington's hedgehog population, despite its relatively rural location, may evidence partial compensation for the large percentage of the population killed on roads annually. However, 33.3% of Kirklington's juvenile population is killed on roads annually, compared to 8.8 – 13.9% for Farnsfield and Southwell. Hubert et al. (2011) surmised that the low survival of juveniles may be a factor in the decrease in local hedgehog abundance in France. The non-existent or very low levels of reproduction and low adult survival rate observed in the smallest density population of Halam, yet coupled with high annual proportional loss from roads, suggest additive mechanisms to road mortality. The lack of juveniles found in Halam is more likely to be a true lack of reproduction rather than not observing juveniles present given the lack of differences in capture probability between adults and juveniles (Pettett et al., 2020). However, the possibility for stochastic error at low sample sizes should be acknowledged. The proximity of populations to their carrying capacity, which is dependent on food availability and space, is likely to affect the extent to which populations are regulated by density-dependent (compensatory) or density-independent (additive) processes (Péron et al., 2016). Reduced per capita growth rate at low population density (i.e., the Allee effect) may result from difficulties in finding mates and/or unbalanced sex ratios in smaller populations (Jaeger and Fahrig, 2001).

It is difficult to make definitive conclusions due to the relatively short-term nature of this study. However, it is possible that the data presented here are a first step at demonstrating inter-specific population differences in compensatory mortality amongst hedgehogs that have been recognised in other species (Murray et al., 2010). It is unlikely that either Kirklington or Halam are fully compensating for the high road mortality rates via reproduction. This, coupled with a slow population growth rate and a high percentage of adult and female roadkills, may be responsible for the sensitivity to road mortality of these small populations. The findings from this thesis can aid evidence-based action towards vulnerable hedgehog populations in rural landscapes. This prioritisation additionally supports cost-effective action for the conservation field that already has limited resources.

5.5 Limitations of the study

Although intense and systematic, this 1.5-year study was not long enough to explore inter-annual variability or a subset of key factors influencing road mortality impact, such as migration and changes in mortality factors over time. For example, Keymer et al. (1991) reported a variable road mortality rate of hedgehogs in Norfolk, UK, of 2.04 km^{-2} in 1979 and 0.52 km^{-2} in 1984. Moreover, it is possible that the road mortality rate calculated in this study is an underestimate as hedgehog–vehicle collisions may not result in instantaneous death. As such, traffic-induced deaths off the road are unlikely to be observed and counted. In addition, whilst main roads, intermediate roads and minor roads were in relative proportion to the British road network, the road mortality rate estimates did not include data from motorways or dual carriageways as there were no such roads within or near the study areas. Although motorways and dual carriageways only represent 1% and 2%, respectively, of the road network (Department for Transport, 2022a) and are reported to have the least amount of hedgehog roadkill across all road types (Rautio et al., 2016), these busy road categories could still make large contributions to road impacts at the population-level.

5.6 Future research directions

For many species, rescue centres play a central role in increasing the survival chances of certain individuals. However, there is little research into how the care and release of hedgehogs from rescue centres may affect a populations ability to cope in the face of anthropogenic mortality such as roads. In this present study, Farnsfield had a relatively high population density compared to previous literature in similar habitats (Dowding, 2007; Schaus-Calderón et al., 2020; L. Moore report for Natural England, unpublished). This in turn resulted in a low proportion of the population being killed per annum. Whether this high population density was ‘average’ for the habitat type or a result of an active rescue centre in the village releasing hedgehogs (from the village and possibly elsewhere) remains unknown. Future road ecology analyses must consider confounding factors such as these.

Whether road mortality is compensatory or additive to other sources of mortality will dictate the urgency and scale of road mitigation required. Therefore, further studies are first needed to elucidate any association between changes in population dynamics and causes of mortality over time, including road mortality. This, in turn, can provide more evidence for or against compensatory mortality in hedgehog populations and help understand if these mechanisms differ between populations. Models such as from population viability analyses, matrix population models and life-equation analyses can be used to project different population and management strategies (Desbiez et al., 2020). Doing so can identify what mitigation option or combination of options may be most cost-effective for population-level impacts. This further helps to develop opportunities for evaluating and modifying mitigation (i.e., adaptive management) that addresses the natural changes in populations, ongoing and planned road construction. Secondly, many pressing management issues cover both local and landscape scales, for example involving source-sink dynamics. Meta-population modelling bridges this gap to determine priority areas based on population sensitivity to road mortality and the dependencies of populations in the wider landscape (Ramp and Ben-Ami, 2006). Finally, a natural development of the research presented here is to examine road mortality impacts at the genetic-level. Specifically, using microsatellite techniques such as multi-generation pedigree and parentage tests could reveal if the reproductive potential of populations is sufficient to counter-balance road mortality and prevent a reduction in genetic diversity. These techniques estimate the breeding population size and relatedness in a population from DNA samples, such as non-invasive hair samples (e.g., Reynolds-Hogland et al., 2022). In turn, this quantifies whether birth rates and offspring survival are sufficient enough to diversify the breeding population and prevent inbreeding.

5.7 Conclusion

Using a combination of repeated population surveys and high-intensity road mortality surveys, this is one of the most comprehensive studies on road mortality impacts on wildlife populations to date. It is likely that up to one third of local hedgehog individuals are killed on roads annually in different populations. However, demographic context was critical to the appropriate interpretation of the impact of mortality rates on local populations, particularly their relationship with population density, reproductive rates, and juvenile survival. The omission of population data in other studies therefore presents a key limitation for understanding and addressing the true impact of roads, which risks inadequate or misplaced mitigation effort. For example, this study supports the assumption that a large amount of road mortality does not necessarily equate to negative impacts on population viability, all other conditions being equal. By contrast, even a low but uncompensated road mortality rate may have detrimental effects for small populations that have low per-capita growth and are already vulnerable to demographic stochasticity.

Understanding when road mortality should and can be mitigated requires focused demographic research over several generations to better identify the link between road mortality and population trends. Moving forward, demographic context and the associated labour costs of population surveys should be included in the research planning stages to maximise scientific output. Doing so alongside interdisciplinary discussions among ecologists, decision makers, and the public has the potential to fundamentally change the way in which road mitigation is planned, implemented, and evaluated. In turn, meeting goals for sustainable transport infrastructure amidst expanding road networks becomes more achievable.

5.8 References

Barrientos, R., Ascensão, F., D'Amico, M., Grilo, C., & Pereira, H. M. (2021). The lost road: Do transportation networks imperil wildlife population persistence? *Perspectives in Ecology and Conservation*, *19*(4), 411–416. https://doi.org/10.1016/J.PECON.2021.07.004

Bearman-Brown, L. E., Baker, P. J., Scott, D., Uzal, A., Evans, L., & Yarnell, R. W. (2020). Over-winter survival and nest site selection of the West-European hedgehog (*Erinaceus europaeus*) in arable dominated landscapes. *Animals*, *10*(9), 1449. https://doi.org/10.3390/ani10091449

Bearman-Brown, L.E., Wilson, L., Evans, L., & Baker, P. Comparing non-invasive surveying techniques for elusive, nocturnal mammals: a case study of the West European hedgehog (*Erinaceus europaeus*). *Journal of Vertebrate Biology*, *69*(3). https://doi.org/10.25225/jvb.20075

Bekker, G. J., & Canters, K. J. (1997). *The continuing story of badgers and their tunnels.* In K. J. Canters, A. Piepers, & D. Hendriks-Heersma (Eds.) Habitat fragmentation, infrastructure and the role of ecological engineering (pp. 344–353). Ministry of Transport, Public Works and Water Management, Road and Hydraulic Engineering Division. The Netherlands : Hague.

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference understanding AIC and BIC in model selection. *Sociological Methods and Research*, *33*(2), 261–304. https://doi.org/10.1177/0049124104268644

Burroughes, N. D., Dowler, J., & Burroughes, G. (2021). Admission and survival trends in hedgehogs admitted to RSPCA wildlife rehabilitation centres. *Proceedings of the Zoological Society*, *74*, 198-204. https://doi.org/10.1007/s12595-021-00363-9

Clarke, G. P., White, P. C. L., & Harris, S. (1998). Effects of roads on badger *Meles meles* populations in south-west England. *Biological Conservation*, *86*(2), 117–124. https://doi.org/10.1016/S0006-3207(98)00018-4

Department for Transport. (2019). *Road traffic estimates in Great Britain: 2019*. Government of the United Kingdom. Retrieved from https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/916749/road-traffic-estimates-in-great-britain-2019.pdf.

Department for Transport. (2022a). *Road lengths in Great Britain (2021)*. Government of the United Kingdom. Retrieved from https://www.gov.uk/government/statistics/road-lengths-in-great-britain-2021/road-lengths-in-great-britain-2021

Department for Transport. (2022b). *Road traffic estimates in Great Britain: 2021*. Government of the United Kingdom. Retrieved from https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/1107056/road-traffic-estimates-in-great-britain-2021.pdf.

Desbiez, A. L. J., Bertassoni, A., & Traylor-Holzer, K. (2020a). Population viability analysis as a tool for giant anteater conservation. *Perspectives in Ecology and Conservation*, *18*(2), 124–131. https://doi.org/10.1016/j.pecon.2020.04.004

Dowding, C. V. (2007). *An investigation of factors relating to the perceived decline of European hedgehogs (*Erinaceus europaeus*) in Britain.* [PhD Thesis, University of Bristol].

Dowding, C. V., Harris, S., Poulton, S., & Baker, P. J. (2010). Nocturnal ranging behaviour of urban hedgehogs, *Erinaceus europaeus,* in relation to risk and reward. *Animal Behaviour*, *80*(1), 13–21. https://doi.org/10.1016/j.anbehav.2010.04.007

Dulac, J. (2013). *Global land transport infrastructure requirements. Estimating road and railway infrastructure capacity and costs to 2050.* International Energy Agency. Retrieved from https://www.iea.org/reports/global-land-transport-infrastructure-requirements

Dupont, G., Royle, J. A., Nawaz, M. A., & Sutherland, C. (2020). Optimal sampling design for spatial capture-recapture. *BioRxiv*, *102*(3), e03262. https://doi.org/doi.org/10.1002/ecy.3262

Egli, R., 2004. Comparison of physical condition and parasite burdens in rural, suburban and urban hedgehogs *Erinaceus europaeus*: implications for conservation. [BSc Thesis, University of Bern].

Efford, M. (2019). *openCR 1.4-open population capture-recapture*. Retrieved from https://cran.microsoft.com/snapshot/2020-04-13/web/packages/openCR/vignettes/openCR-vignette.pdf

Englefield, B., Starling, M., Wilson, B., Roder, C., & McGreevy, P. (2020). The Australian roadkill reporting project— applying integrated professional research and citizen science to monitor and mitigate roadkill in Australia. *Animals*, *10*(7), 1–20. https://doi.org/10.3390/ani10071112

ESRI. (2015). *ArcGIS Desktop: 10.3.1.* Environmental Systems Research Institute. USA : California

Fey, K., Hämäläinen, S., & Selonen, V. (2016). Roads are no barrier for dispersing red squirrels in an urban environment. *Behavioral Ecology*, *27*(3), 741–747. https://doi.org/10.1093/beheco/arv215

Gantchoff, M. G., Hill, J. E., Kellner, K. F., Fowler, N. L., Petroelje, T. R., Conlee, L., … Belant, J. L. (2020). Mortality of a large wide-ranging mammal largely caused by anthropogenic activities. *Scientific Reports*, *10*(1), 1–11. https://doi.org/10.1038/s41598-020-65290-9

González-Suárez, M., Zanchetta Ferreira, F., & Grilo, C. (2018). Spatial and species-level predictions of road mortality risk using trait data. *Global Ecology and Biogeography*, *27*(9), 1093–1105. https://doi.org/10.1111/geb.12769

Goransson, G., Karlsson, J., & Lindgren, A. (1976). Road mortality of the hedgehog Erinaceus europaeus in southern Sweden. *Fauna Flora*, *71*(1), 1–6. https://agris.fao.org/agris-search/search.do?recordID=SE19760115214

Haigh, A., O’Keeffe, J., O’Riordan, R. M., & Butler, F. (2014a). A preliminary investigation into the endoparasite load of the European hedgehog (*Erinaceus europaeus*) in Ireland. *Mammalia*, *78*(1), 103–107. https://doi.org/10.1515/MAMMALIA-2013-0032/HTML

Haigh, A., O’Riordan, R. M., & Butler, F. (2014b). Hedgehog *Erinaceus europaeus* mortality on Irish roads. *Wildlife Biology*, *20*(3), 155–160. https://doi.org/10.2981/wlb.12126

Harris, S., & White, P. (1994). *The red fox*. London : Mammal Society.

Hill, J. E., DeVault, T. L., & Belant, J. L. (2019). Cause-specific mortality of the world’s terrestrial vertebrates. *Global Ecology and Biogeography*, *28*(5), 680–689. https://doi.org/10.1111/geb.12881

Hof, A., & Bright, P. W. (2009). The value of green-spaces in built-up areas for western hedgehogs. *Lutra*, *52*(2), 69–82. https://zoogdierwinkel.nl/sites/default/files/imce/nieuwesite/publicatie%20fotos/Lutra/downloads/52_2_Hof%20&%20Bright.pdf

Hubert, P., Julliard, R., Biagianti, S., & Poulle, M. L. (2011). Ecological factors driving the higher hedgehog (*Erinaceus europaeus*) density in an urban area compared to the adjacent rural area. *Landscape and Urban Planning*, *103*(1), 34–43. https://doi.org/10.1016/j.landurbplan.2011.05.010

Huijser, M. P., Bergers, P. J. M., Nolet, B. A., & Meuwissen, L. T. J. (1997). *Traffic mortality in a hedgehog population.* In M. Huijser & P. Bergers (Eds.) Hedgehogs and traffic: the effects of roads and traffic on hedgehog populations. Ministry of Transport, Public Works and Water Management. Directorate-General for Public Works and Water Management. Road and Hydraulic Engineering Division. The Netherlands : Hague. Retrieved from https://puc.overheid.nl/PUC/Handlers/DownloadDocument.ashx?identifier=PUC_50960_31&versienummer=1.

Jackson, D. B. (2007). Factors affecting the abundance of introduced hedgehogs (*Erinaceus europaeus*) to the Hebridean island of South Uist in the absence of natural predators and implications for nesting birds. *Journal of Zoology*, *271*(2), 210–217. https://doi.org/10.1111/j.1469-7998.2006.00204.x

Jaeger, J. A. G., & Fahrig, L. (2001). Modeling the effects of road networks patterns on population persistence: relative importance of traffic mortality and 'fence effect'. In *Proceedings of the 2001 International Conference on Ecology and Transportation,* 24 – 29 September 2001, North Carolina State University (pp. 298 – 312). USA : Colorado.

Jaeger, J.A.G., & Holderegger, R. (2005). Thresholds of landscape fragmentation. *GAIA*, *14*(2), 113–118. https://doi.org/10.14512/gaia.14.2.10

Johnson, H. (2015). *Conservation strategy for hedgehogs in the United Kingdom.* People's Trust for Endangered Species & the British Hedgehog Preservation Society. London: UK. Retrieved from https://www.hedgehogstreet.org/wp-content/uploads/2018/02/Hedgehog-10-year-strategy-master-document-v5.pdf.

Kaplan, E. L., & Meier, P. (1958). Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association*, *53*(282), 457–481. https://doi.org/10.1080/01621459.1958.10501452

Kassambara, A., & Kosinki, M. (2018). *Survminer: drawing survival curves using 'ggplot2'.* (version 04.2). Retrieved from https://cran.r-project.org/package=survmine.

Keymer, I. F., Gibson, E. A., & Reynolds, D. J. (1991). Zoonoses and other findings in hedgehogs (*Erinaceus europaeus*): a survey of mortality and review of the literature. *The Veterinary Record*, *128*(11), 245–249. https://doi.org/10.1136/vr.128.11.245

Kristiansson, H. (1990). Population variables and causes of mortality in a hedgehog (*Erinaceous europaeus*) population in southern Sweden. *Journal of Zoology*, *220*(3), 391–404. https://doi.org/10.1111/j.1469-7998.1990.tb04314.x

Kubasch, H. (1992). Otterschutz in Sachsen. In C. Ruether (Ed.) *Otterschutz in Deutschland* (pp. 109–112).

Met Office. (2022). *Climate summaries.* Retrieved from https://www.metoffice.gov.uk/research/climate/maps-and-data/summaries/index

Moore, L. J., Arietta, A. Z. A., Spencer, D. T., Huijser, M. P., Walder, B. L., & Abra, F. D. (2021). On the road without a map: Why we need an "ethic of road ecology". *Frontiers in Ecology and Evolution*, *9*, 774286. https://doi.org/10.3389/FEVO.2021.774286

Moore, L. J., Petrovan, S. O., Bates, A. J., Hicks, H. L., Baker, P. J., Perkins, S. E., & Yarnell, R. W. (2023). Demographic effects of road mortality on mammalian populations: a systematic review. *Biological Reviews*. doi: 10.1111/brv.12942.

Moorhouse, T. P. (2013). *Population viability analysis of hedgehogs in rural and urban habitats.* People's Trust for Endangered Species & the British Hedgehog Preservation Society. Retrieved from: http://www.wlgf.org/Moorhouse%20(2013)%20Population%20viability

%20analysis%20of%20hedgehogs.pdf.

Morris, P. A. (2018). *Hedgehog* (1st ed.). New York : Harper Collins Publishers.

Mumme, R. L., Schoech, S. J., Woolfenden, G. E., & Fitzpatrick, J. W. (2000). Life and death in the fast lane: demographic consequences of road mortality in the Florida Scrub-Jay. *Conservation Biology*, *14*(2), 501–512. https://doi.org/10.1046/j.1523-1739.2000.98370

Murray, D. L., Smith, D. W., Bangs, E. E., Mack, C., Oakleaf, J. K., Fontaine, J., … Asher, V. J. (2010). Death from anthropogenic causes is partially compensatory in recovering wolf populations. *Biological Conservation*, *143*(11), 2514–2524. https://doi.org/10.1016/j.biocon.2010.06.018

Ordnance Survey. (2020). *EDINA Digimap*. University of Edinburgh. Retrieved from https://digimap.edina.ac.uk/os

Orłowski, G., & Nowak, L. (2004). Road mortality of hedgehogs *Erinaceus* spp. in farmland in Lower Silesia (south-western Poland). *Pol. J. Ecol, 52*(3), 377-382. https://miiz.waw.pl/pliki/article/ar52_3_14.pdf

Parkes, J. (1975). Some aspects of the biology of the hedgehog (*Erinaceus europaeus* l.) in the Manawatu, New Zealand. *New Zealand Journal of Zoology*, *2*(4), 463–472. https://doi.org/10.1080/03014223.1975.9517887

Péron, G. (2013). Compensation and additivity of anthropogenic mortality: Life-history effects and review of methods. *Journal of Animal Ecology*, *82*(2), 408–417. https://doi.org/10.1111/1365-2656.12014

Pettett, C., Macdonald, D. W., Al-Hajiri, A., Al-Jabiry, H., & Yamaguchi, N. (2020). Characteristics and demography of a free-ranging Ethiopian hedgehog, *Paraechinus aethiopicus*, population in Qatar. *Animals*, *10*(6), 1–17. https://doi.org/10.3390/ani10060951

Pettett, C. E., Moorhouse, T. P., Johnson, P. J., & Macdonald, D. W. (2017). Factors affecting hedgehog (*Erinaceus europaeus*) attraction to rural villages in arable landscapes. *European Journal of Wildlife Research*, *63*(54). https://doi.org/10.1007/s10344-017-1113-6

Prange, S., Gehrt, S. D., & Wiggers, E. P. (2003). Demographic factors contributing to high raccoon densities in urban landscapes. *Journal of Wildlife Management*, *67*(2), 324. https://doi.org/10.2307/3802774

R Core Development Team. (2017). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/

Ramp, D., & Ben-Ami, D. (2006). The effect of road-based fatalities on the viability of a peri-urban Swamp Wallaby population. *The Journal of Wildlife Management*, *70*(6), 1615–1624. https://doi.org/10.2193/0022-541X(2006)70[1615:TEORFO]2.0.CO;2

Rasmussen, S. L., Berg, T. B., Martens, H. J., & Jones, O. R. (2023). Anyone can get old—all you have to do is live long enough: understanding mortality and life expectancy in European hedgehogs (*Erinaceus europaeus*). *Animals*, *13*(4), 626. https://doi.org/10.3390/ANI13040626

Rasmussen, S. L., Jones, O. R., Berg, T. B., & Dabelsteen, T. (2019). The ecology of suburban juvenile European hedgehogs (*Erinaceus europaeus*) in Denmark. *Ecology and Evolution, 9*(23), 1-14. https://doi.ord/ 10.1002/ece3.5764

Rautio, A., Isomursu, M., Valtonen, A., Hirvelä-Koski, V., & Kunnasranta, M. (2016). Mortality, diseases and diet of European hedgehogs (*Erinaceus europaeus*) in an urban environment in Finland. *Mammal Research*, *61*(2), 161–169. https://doi.org/10.1007/s13364-015-0256-7

Reeve, N., Bowen, C., & Gurnell, J. (2019). An improved identification marking method for hedgehogs. *Mammal Communications*, *5*, 1–5. https://www.mammal.org.uk/wp-content/uploads/2019/01/HedgehogMarking.pdf.

Reeve, N. J. (1981). *A field study of the hedgehog (Erinaceus europaeus) with particular reference to movements and behaviour*. [PhD Thesis, University of London].

Reynolds-Hogland, M. J., Ramsey, A. B., Muench, C., Pilgrim, K. L., Engkjer, C., & Ramsey, P. W. (2022). Age-specific, population-level pedigree of wild black bears provides insights into reproduction, paternity, and maternal effects on offspring apparent survival. *Ecology and Evolution*, *12*(4), 8770. https://doi.org/10.1002/ECE3.8770

Roedenbeck, I. A., Fahrig, L., Findlay, C. S., Houlahan, J. E., Jaeger, J. A. G., Klar, N., … van der Grift, E. A. (2007). The Rauischholzhausen agenda for road ecology. *Ecology and Society*, *12*(1). http://www.ecologyandsociety.org/vol12/iss1/art11/

Roos, S., Johnston, A., & Noble, D. (2012). *UK hedgehog datasets and their potential for long-term monitoring* (BTO Research Report No. 598). The British Trust for Ornithology, commissioned and funded by People’s Trust for Endangered Species and the British Hedgehog Preservation Society. Retrieved from https://www.bto.org/our-science/projects/gbw/publications/papers/monitoring/btorr598

Royle, J. A., Fuller, A. K., Sutherland, C., Royle, J. A., & Sutherland, C. (2017). Unifying population and landscape ecology with spatial capture-recapture. *Ecography*, *41*(3), 444-456. https://doi.org/10.1111/ecog.03170

Ruiz-Capillas, P., Mata, C., & Malo, J. E. (2015). How many rodents die on the road? Biological and methodological implications from a small mammals’ roadkill assessment on a Spanish motorway. *Ecological Research*, *30*(3), 417–427. https://doi.org/10.1007/s11284-014-1235-1

Rytwinski, T., & Fahrig, L. (2012). Do species life history traits explain population responses to roads? A meta-analysis. *Biological Conservation*, *147*(1), 87–98. https://doi.org/10.1016/j.biocon.2011.11.023

Sadleir, R. M. F. S., & Linklater, W. L. (2016). Annual and seasonal patterns in wildlife road-kill and their relationship with traffic density. *New Zealand Journal of Zoology*, *43*(3), 275–291. https://doi.org/10.1080/03014223.2016.1155465

Schaus-Calderón, J. S., Uzal, A., Gentle, L. K., Baker, P. J., Bearman-Brown, L., Bullion, S., … Yarnell, R. W. (2020). Application of the Random Encounter Model in citizen science projects to monitor animal densities. *Remote Sensing in Ecology and Conservation*, *6*(4), 514–528. https://doi.org/10.1002/rse2.153

Schaus-Calderón, J. S. (2021). *Responses of the West European hedgehog to urbanisation: impact on population dynamics, animal movement and habitat selection.* [PhD Thesis, Nottingham Trent University].

Seiler, A. (2003). *The toll of the automobile: Wildlife and roads in Sweden.* [PhD Thesis, Swedish University of Agricultural Sciences].

Sutherland, C. S., Royle, J., & Linden, D. (2016). *oSCR: Multi-session sex-structured spatial capture–recapture models.* (version 0.42.0.). Retrieved from https://rdrr.io/github/jaroyle/oSCR/

Therneau, T. (2015). *Package "survival". Survival Analysis* (version 3.3-1). Retrieved from https://cran.r-project.org/package=survival

Turner, J., Freeman, R., & Carbone, C. (2021). Using citizen science to understand and map habitat suitability for a synurbic mammal in an urban landscape: the hedgehog *Erinaceus europaeus*. *Mammal Review, 52*(2), 291-303. https://doi.org/10.1111/mam.12278

van der Grift, Seiler, A., Rosell, C., van der Grift-Simeonova, V.S. (2016). *Safe roads for Wildlife and People: Final report of the SAFEROAD project*. Conference of European Directors of Roads. Retrieved from https://www.saferoad-cedr.org/upload_mm/4/6/b/80eb4659-f6e6-4327-8358-f692b98f3419_CEDR_finalreport.pdf

Wembridge, D. E., Newman, M. R., Bright, P. W., & Morris, P. A. (2016). An estimate of the annual number of hedgehog (*Erinaceus europaeus*) road casualties in Great Britain. *Mammal Communications*, *2*, 8–14. https://www.mammal.org.uk/wp-content/uploads/2016/04/MC1605_HedgehogsRoads_Wembridge.pdf

Williams, B., Mann, N., Neumann, J., Yarnell R. W., & Baker, P. (2018). A prickly problem: developing a volunteer-friendly tool for monitoring populations of a terrestrial urban mammal, the West European hedgehog (*Erinaceus europaeus*). *Urban Ecosystems, 21*(6), 1075-1086. https://doi.org/ 10.1007/s11252-018-0795-1

Young, R. P., Davison, J., Trewby, I. D., Wilson, G. J., Delahay, R. J., & Doncaster, C. P. (2006). Abundance of hedgehogs (*Erinaceus europaeus*) in relation to the density and distribution of badgers (*Meles meles*). *Journal of Zoology*, *269*(3), 349–356. https://doi.org/10.1111/j.1469-7998.2006.00078.x

Appendices VII – XI

Appendix VII: Walking routes (in yellow) used during the spotlight surveys within the four study sites (outlined in red) surveyed between May 2020 and November 2021 in central Nottinghamshire, Great Britain. Source: Esri. "World Imagery" [basemap].

a) Farnsfield b) Southwell

c) Kirklington d) Halam

Appendix VIII: Ranked Spatial Capture-Recapture models estimating hedgehog densities across the four study sites.

K = number of parameters, AIC = Akaike’s Information Criterion, Δi = delta AIC, ω = AIC weighting, Cum ω = cumulative weighting

Farnsfield

	Model	K	AIC	Δi	ω	Cum ω
Adults	D(~1) p(~1) sig(~sex)	5	3308.30	0.00	0.42	0.42
	D(~session) p(~1) sig(~sex)	7	3309.91	1.61	0.19	0.61
	D(~1) p(~sex) sig(~sex)	6	3310.29	1.99	0.16	0.77
	D(~session) p(~sex) sig(~sex)	8	3311.90	3.60	0.07	0.84
	D(~1) p(~sex) sig(~1)	5	3312.10	3.80	0.06	0.90
	D(~1) p(~1) sig(~1	4	3312.65	4.35	0.05	0.95
	D(~session) p(~sex) sig(~1)	7	3313.71	5.41	0.03	0.98
	D(~session) p(~1) sig(~1)	6	3314.26	5.96	0.02	1.00
Juveniles	D(~1) p(~1) sig(~1)	4	912.15	0.00	0.34	0.34
	D(~1) p(~1) sig(~sex)	5	913.81	1.66	0.15	0.48
	D(~1) p(~sex) sig(~1)	5	913.85	1.69	0.14	0.63
	D(~session) p(~1) sig(~1)	5	914.15	2.00	0.12	0.75
	D(~1) p(~sex) sig(~sex)	6	914.45	2.30	0.11	0.85
	D(~session) p(~1) sig(~sex)	6	915.81	3.66	0.05	0.91
	D(~session) p(~sex) sig(~1)	6	915.85	3.69	0.05	0.96
	D(~session) p(~sex) sig(~sex)	7	916.45	4.30	0.04	1.00

Southwell

	Model	K	AIC	Δi	ω	Cum ω
Adults	D(~1) p(~sex) sig(~sex)	6	1698.17	0.00	0.64	0.64
	D(~session) p(~sex) sig(~sex)	7	1701.36	3.19	0.13	0.77
	D(~1) p(~1) sig(~sex)	5	1701.74	3.57	0.11	0.89
	D(~1) p(~1) sig(~1)	4	1703.03	4.87	0.06	0.93
	D(~1) p(~sex) sig(~1)	5	1704.51	6.34	0.08	0.96
	D(~session) p(~1) sig(~sex)	7	1704.92	6.75	0.02	0.98
	D(~session) p(~1) sig(~1)	6	1706.22	8.05	0.01	0.10
	D(~session) p(~sex) sig(~1)	7	1707.70	9.53	0.01	1.00
Juveniles	D(~1) p(~1) sig(~sex)	5	279.33	0.00	0.34	0.34
	D(~1) p(~sex) sig(~sex)	6	280.67	1.34	0.18	0.52
	D(~1) p(~1) sig(~1)	4	281.13	1.80	0.14	0.66
	D(~session) p(~1) sig(~sex)	6	281.33	2.00	0.13	0.78
	D(~1) p(~sex) sig(~1)	5	282.41	3.09	0.07	0.86
	D(~session) p(~sex) sig(~sex)	7	282.67	3.34	0.07	0.92
	D(~session) p(~1) sig(~1)	5	283.13	3.80	0.05	0.97
	D(~session) p(~sex) sig(~1)	6	284.41	5.09	0.03	1.00

Kirklington

	Model	K	AIC	Δi	ω	Cum ω
Adults	D(~1) p(~1) sig(~sex)	5	889.31	0.00	0.53	0.53
	D(~1) p(~sex) sig(~sex)	6	890.22	0.91	0.34	0.86
	D(~session) p(~1) sig(~sex)	7	893.13	3.82	0.08	0.94
	D(~session) p(~sex) sig(~sex)	8	894.04	4.73	0.05	0.99
	D(~1) p(~1) sig(~1)	4	899.38	10.07	<0.01	0.10
	D(~1) p(~sex) sig(~1)	5	899.43	10.12	<0.01	0.10
	D(~session) p(~1) sig(~1)	6	903.20	13.89	<0.01	1.00
	D(~session) p(~sex) sig(~1)	7	903.25	13.94	<0.01	1.00
Juveniles	D(~1) p(~1) sig(~1)	4	206.923	<0.01	0.36	0.36
	D(~1) p(~sex) sig(~1)	5	208.698	1.78	0.15	0.51
	D(~session) p(~1) sig(~1)	5	208.721	1.80	0.15	0.66
	D(~1) p(~1) sig(~sex)	5	208.743	1.82	0.15	0.80
	D(~session) p(~sex) sig(~1)	6	210.497	3.57	0.06	0.86
	D(~session) p(~1) sig(~sex)	6	210.541	3.62	0.06	0.92
	D(~1) p(~sex) sig(~sex)	6	210.682	3.76	0.06	0.98
	D(~session) p(~sex) sig(~sex)	7	212.481	5.56	0.02	1.00

Halam

	Model	K	AIC	Δi	ω	Cum ω
Adults	D(~1) p(~sex) sig(~sex)	6	255.72	0.00	0.48	0.48
	D(~1) p(~1) sig(~1)	4	257.95	2.23	0.16	0.64
	D(~1) p(~sex) sig(~1)	5	258.48	2.76	0.12	0.76
	D(~1) p(~1) sig(~sex)	5	258.77	3.05	0.11	0.87
	D(~session) p(~sex) sig(~sex)	8	259.45	3.73	0.08	0.94
	D(~session) p(~1) sig(~1)	6	261.67	5.95	0.03	0.97
	D(~session) p(~sex) sig(~1)	7	262.21	6.49	0.02	0.98
	D(~session) p(~1) sig(~sex)	7	262.50	6.77	0.02	1.00

Appendix IX: Percentage of the total population and separate cohorts killed on roads in the four study sites based on the marked population only.

	Farnsfield	Southwell	Kirklington	Halam
Total population	9.4	15.8	31.8	20.0
Adult population	9.8	17.0	27.8	20.0
Adult male population	13.1	17.9	33.3	33.3
Adult female population	7.0	15.8	25.0	0.0
Juvenile population	7.4	10.0	40.0	n/a

Appendix X: Heat-shrink tube loss for adult and juvenile hedgehogs over the course of the study

Adult mark loss

Of the initial five heat-shrink tubes (marks) attached to adult hedgehogs across all four sites, the mean number of marks remaining after the first two-week survey period was 4.82 (±0.03 SD, n = 149 individuals). After an average 8.5 months (7 – 10 months) between the survey sessions in autumn 2020 and spring 2021, the mean number of marks remaining was 4.21 (±0.28 SD, n = 24 individuals). After an average 3.8 months (3 – 5 months) between survey sessions in spring 2021 and autumn 2021, the mean number of marks remaining was 4.36 (±0.34 SD, n = 32 individuals). Ten individuals were captured in autumn 2020 and not recaptured again until autumn 2021. In these cases, the mean number of marks remaining was 3.11 (±0.19 SD, n = 10 individuals). Mark loss did not significantly differ between the four study sites (F-stat = 0.22, df = 3, p-value = 0.88).

Juvenile mark loss

Of the initial five heat-shrink tubes (marks) attached to juvenile hedgehogs across all four sites, the mean number of marks remaining after the first two-week survey period was 4.57 (±0.18 SD, n = 31 individuals). After an average 8.5 months (7 – 10 months) between the survey sessions in autumn 2020 and spring 2021, the mean number of marks remaining was 2.95 (±0.43 SD, n = 14 individuals). After an average 3.8 months (3 – 5 months) between the survey sessions in spring 2021 and autumn 2021, the mean number of marks remaining was 3.42 (±0.38 SD, n = 7 individuals). After 12 months, the mean number of marks remaining was 2.0 (±0 SD, n = 3 individuals). There was no significant difference in the mark loss between adults and juveniles (t = 1.38, df = 1, p-value = 0.22) or between the four study sites (F-stat = 0.04, df = 2, p-value = 0.96).

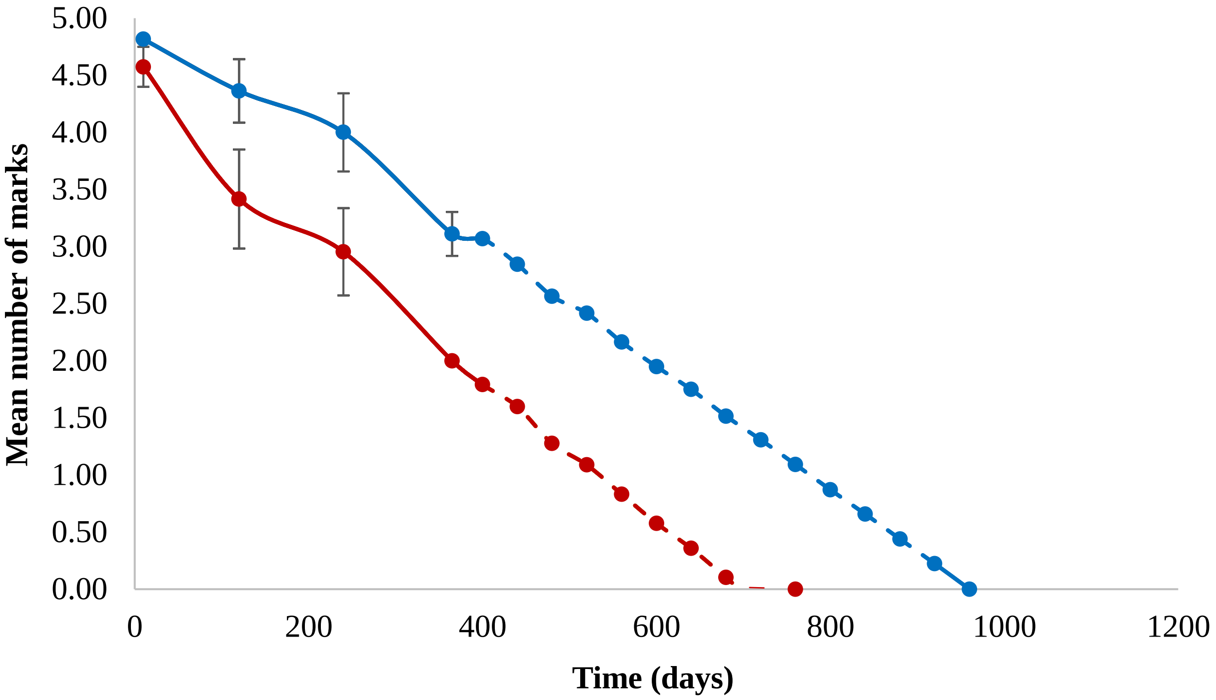


Figure above: The mean number of marks remaining on re-captured hedgehogs (solid line) during the first survey session and at subsequent survey periods after 120 days (4 months), 240 days (8 months) and 365 days (12 months), as well as projected mark loss rate for adults and juvenile hedgehogs across the four study populations surveyed. Error bars represent standard error where calculable.

Appendix XI: Chi-squared (X^2) results comparing the sex and age structure of the four studied populations in Nottinghamshire to the sex and age structure of the road mortality within each population.

	Male vs female		**Adult vs juvenile**	
	X^2 statistic	**p-value**	**X^2 statistic**	**p-value**
Farnsfield	12.501	<0.001	4.330	0.037
Southwell	1.299	0.254	0.033	0.856
Kirklington	9.267	0.002	1.452	0.228
Halam	0.000	1.000	n/a	n/a

CHAPTER 6: Life in the Danger Zone: Understanding Road Avoidance, Barrier Effects and Road Mortality Impacts on Hedgehogs Using Multisite Animal Telemetry

6.1 Introduction

Animal movement patterns are moderated by decision-making centred on several, simultaneous behavioural trade-offs. These trade-offs are contingent on both intrinsic components such as hunger and reproductive status, and extrinsic components such as resource availability at different spatiotemporal scales (Neumann et al., 2012). Animal populations are increasingly exposed to anthropogenic obstacles, such as roads or railways, as human development continues to encroach on the environment. These obstacles have the potential to strongly influence how animals navigate the landscape (Ditmer et al., 2018) and the probability of survival during these movements. For some species, roads can severely restrict free-flowing movement, and this is known as the barrier effect. This phenomenon can manifest through road avoidance behaviour, where animals are deterred from going near or crossing a road; through mortality during road crossing attempts; or both (Proulx et al., 2014). If the barrier effect continually prohibits movement, roads can cause some species to adjust their foraging and travelling behaviours, potentially leading to inaccessibility of resource-rich areas and subsequently lower reproductive and survival rates (Prokopenko et al., 2017). Moreover, if mortality rates or behavioural avoidance are substantial enough to isolate populations on opposite sides of the road, the barrier effect can lead to reduced connectivity between populations, genetic isolation, disruption of metapopulation structure, and even local extinction without the possibility to recolonise (Ceia-Hasse et al., 2018; Ditmer et al., 2018).

Road avoidance behaviour has been documented in an array of taxa, including amphibians (Hels & Buchwald, 2001); small mammals (Rico, Kindlmann and Sedláček, 2007; Brehme et al., 2013); large carnivores (Schwab and Zandbergen, 2011); birds (McClure et al., 2013); reptiles (Hibbitts et al., 2017, Paterson et al., 2019); and ungulates (Beyer et al., 2016, D'Amico et al., 2016). To address variation in animal responses to different road attributes and traffic patterns, Jaeger et al. (2005) identified three types of road avoidance behaviour: road surface avoidance (road substrate and width), traffic-emissions avoidance (noise and light), and vehicle avoidance. Solitary and smaller species such as west European hedgehogs (*Erinaceus europaeus*) are considered to be road surface avoiders, expected to show high deterrence from crossing roads even when traffic volume is low (Mulder, 1999; Rondinini and Doncaster, 2002; McGregor, Bender and Fahrig, 2008). Conversely, large species such as American black bears (*Ursus americanus*) and wolves (*Canis lupus*) generally avoid roads during the day when human activity is greatest but use roads for travelling at night, suggesting an avoidance of vehicles and/or noise rather than the road itself (Kautz et al., 2021).

The magnitude of road avoidance and its relationship with road mortality remain important questions in conservation biology. Central to these questions is that whilst road avoidance behaviour can fragment populations, a lack of road avoidance can result in a large number of wildlife-vehicle collisions (Brehme et al., 2013). Several authors contend that there is a threshold level of traffic volume above which road avoidance will be so extreme that the amount of roadkill will plateau (Clark et al., 2001; Seiler, 2003; Aresco, 2005). This phenomenon, known as the traffic flow theory, is shown by some, but not all, species groups. In general, smaller species are documented to be more sensitive to greater traffic volumes. For instance, Hels & Buchwald (2001) and Litvaitis & Tash (2008) found that the road mortality rates of amphibians and Blanding's turtles (*Emydoidea blandingii*), respectively, plateaued above taxa-specific thresholds of annual average daily traffic (AADT; 15,000 vehicles/day for amphibians, 40,000 vehicles/day for Blanding's turtles). By contrast, the roadkill probability of capybara (*Hydrochoerus hydrochaeris*; Da Silva et al., 2022), moose (*Alces alces)* and bobcat (*Lynx rufus*; Litvaitis and Tash, 2008) showed a positive relationship with traffic volume that did not plateau. The range of behavioural responses to roads, such as road avoidance, likely have a substantial role in explaining the barrier effect and are crucial to accurately interpret road mortality data (Jacobson et al., 2016).

Accurate modelling of road avoidance and road mortality risk is crucial in the early stages of effective mitigation planning, yet inaccurate analysis could waste resources and cause more harm than good (Ascensão et al., 2019). Most wildlife–vehicle collision studies assess road mortality risk using collision data only, such as using a Maxent approach or occurrence distribution modelling (Garrote et al., 2018; Santos et al., 2018; Wright et al., 2020). However, Clevenger & Ford (2010) contend that using only road mortality data omits biologically important information about where animals safely cross roads. Consistent with this idea, Neumann et al. (2012) found that using collision data alone over-predicted road mortality risk in certain areas. If collision and movement data are available, the relative frequency of mortality and successful road crossings can be compared in space and time to ascertain the 'true' road mortality risk i.e., where animals are disproportionately killed based on their movements. Only recently has the full potential for combining these data been considered (e.g., Ditmer et al., 2018). Neumann et al. (2012) highlighted that moose roadkill and successful road crossings do not necessarily occur in the same locations, whilst Zeller et al. (2018) used a multi-scale resource selection function (RSF) to identify areas with both high probability of successful crossing and a high road mortality risk. A detailed level of analysis that combines these data allows targeted mitigation that considers both population connectivity and survival around roads. This is particularly important as both Teixeira et al. (2017) and Ascensão et al. (2019) revealed that mitigation based on road mortality alone ignores population viability as areas of low mortality may mask previous population depression caused by vehicle collisions.

As a generalist small mammal that exhibits complex interactions with roads, the west European hedgehog (hereafter termed ‘hedgehog’) is a useful case study to investigate the overall barrier effect from roads. Hedgehogs have been shown to avoid large, but not small, roads (Rondinini and Doncaster, 2002; Dowding et al., 2010) and they suffer substantial road mortality impacts across their range (Moore et al., 2020). Whilst valuable, previous road avoidance studies were limited to a small sample size, only two local study sites, and/or lacked analysis of explanatory variables for observed factors other than sex. Contrary to documented avoidance, however, hedgehog presence is positively related to traffic volume (Turner, Freeman and Carbone, 2021) and road density (Williams, 2018) as an artefact of high abundances in urban areas (Schaus-Calderón, 2021). Hedgehogs also tend to be attracted to road verges as suitable nesting spots (Bearman-Brown et al., 2020), yet other research has reported an avoidance of road verges altogether (Rondinini & Doncaster, 2002; Schaus-Calderón, 2021). Despite previous research interest, there is no scientific consensus regarding hedgehog behaviour around roads and how this translates to ‘true’ road mortality risk. Given the often-cited role of roads in the ongoing population declines of hedgehogs in Great Britain (Wright et al., 2020; Wembridge et al., 2016), an intensive assessment that combines road mortality counts and high-resolution movement models can provide better understanding of population-level impacts of roads (Bencin et al., 2019).

Using hedgehogs as a case study, this study explored whether the interplay between animal behaviour and survival contributes to any level of barrier effect from roads. Specifically, the objectives of this study were to (1) determine the presence or absence of road avoidance behaviour by hedgehogs and if present, quantify individual, seasonal and road characteristic predictors of the avoidance behaviour, (2) identify predictors of ‘true’ road mortality risk relative to road crossing locations, and (3) quantify the annual road mortality probability of hedgehogs across typical British road networks. Based on previous literature, albeit with small samples sizes, it is hypothesised that hedgehogs will avoid large, but not small, roads (Rondinini and Doncaster, 2002; Dowding et al., 2010). Due to a plethora of literature of sex differences in the activity levels of hedgehogs (see summary in Schaus-Calderón, 2021), it is hypothesised that females will show greater avoidance of roads than males and that males will have a greater risk of road mortality in the long-term. If the traffic flow theory is valid, it is expected that road mortality will plateau at higher traffic volumes. Finally, it is hypothesised that the locations of high road mortality risk for hedgehogs will relate, directly or indirectly, to traffic volume and speed (van Langevelde & Jaarsma, 2009; Cruzado & Donnell, 2010). By focusing on the behavioural responses to roads, this study will aid the theoretical underpinning and development of demographic and movement models. This, in turn, is a critical step in building a large and diverse toolkit for species-specific management around roads.

6.2 Methods and materials

6.2.1 Study sites

Hedgehogs were tracked at 11 study sites in the UK between June 2020 and October 2021, inclusive. The 11 sites are associated with varying extents of urbanisation, such as residential dwellings or industrial sites, and surrounded by a lowland and agricultural landscape. These study sites were chosen (1) for a range of road types and densities that reflect the British road network, and so allowing the results to be generalised beyond the study sites, and (2) if landowner permission was granted during a simultaneous movement study for assessing the efficacy of road mitigation. The four study sites in Nottinghamshire (Sites 1 – 4, Figure 6.1) were the same as those detailed in Chapter 5 and GPS tracking took place three times at each site, approximately six months apart. At the seven remaining study sites (Sites 5 – 11, Figure 6.1), GPS tracking took place once at each site. Road types (a mix of A-roads, B-roads, minor and local roads) and habitat configuration of the 11 study sites are shown in Table 6.1. To reflect the range in AADT and the road classifications of European road networks, herein A-roads will be referred to as main roads, B-roads as intermediate roads, and both minor and local roads as minor roads. Main roads (also known as principal roads) connect major destinations such as cities, with an annual average daily traffic (AADT) of 19,000 vehicles/day. Intermediate roads are distributor roads often located between towns or villages with an AADT of 7,000 vehicles/day. Minor roads often link residential areas or villages to the rest of the road network, with an AADT of 3,000 vehicles/day, whilst local roads serve short distances within neighbourhoods, such as residential streets, with an AADT of 1,000 vehicles/day (Department for Transport, 2022b). Note that these AADT values are a snapshot and averaged from automatic traffic counters that are strategically placed to record every vehicle travelling along a section of road (Sfyridis and Agnolucci, 2020). As per British Standards for road lighting (BS5489-3:1992), the light intensity around the residential areas of the study sites was relatively uniform ranging from 3.5 – 10 lux (Fotios, Uttley and Cheal, 2013), although light intensity reduced outside of the site boundaries. Moreover, the road widths were similarly invariable ranging from 3.5 – 7.0 m.

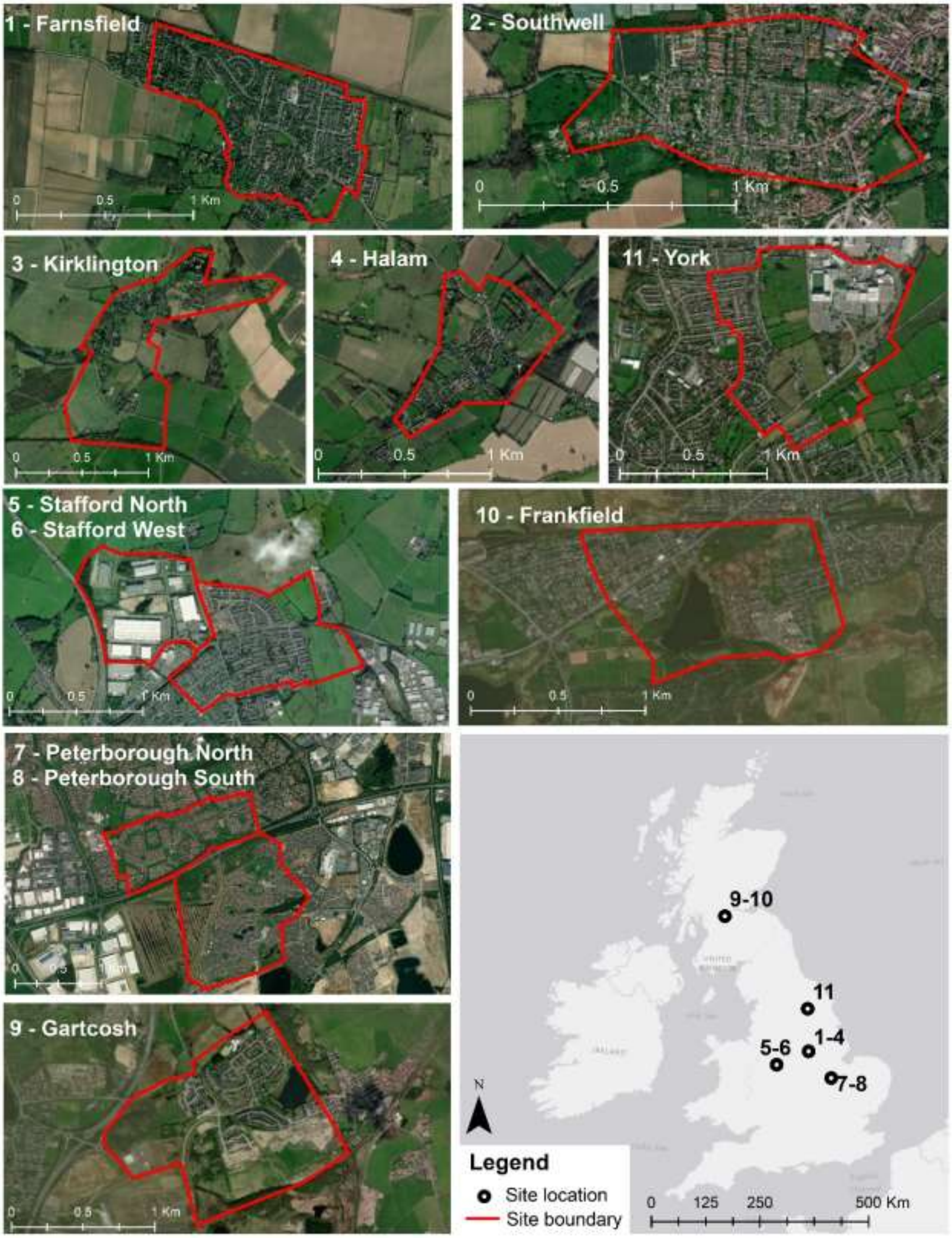


Figure 6.1: Eleven study sites where hedgehogs were surveyed between June 2020 and November 2021, inclusive.

Table 6.1: Description of the size and characteristics of the 11 study sites surveyed between June 2020 and October 2021, inclusive.

	Centroid coordinates	Study site area (km²)	Road density (km/ km²)	Road types	Habitat composition (percentage)							
					Amenity grassland	**Arable**	**Built area***	**Garden**	**Grassland†**	**Pasture**	**Water**	**Woodland**
Farnsfield, Nottinghamshire	53.10437 -1.03483	1.00	15.12	Minor and local roads	10.91	0.00	27.08	58.62	1.10	0.07	0.05	2.17
Southwell, Nottinghamshire	53.07746 -0.96415	0.80	12.21	Intermediate, minor, and local roads	14.90	0.00	28.03	52.58	1.82	0.00	<0.01	2.67
Kirklington, Nottinghamshire	53.10835 -0.98983	0.91	5.80	Main, minor, and local roads	3.64	29.04	9.87	17.33	3.83	27.62	1.12	7.56
Halam, Nottinghamshire	53.08334 -0.98966	0.70	9.80	Minor and local roads	15.16	10.62	13.33	29.66	3.44	18.15	0.85	8.79
Stafford North	52.83667 -2.13912	0.64	6.61	Local roads	10.89	0.00	65.57	0.00	0.00	0.00	0.75	22.78
Stafford West	52.83204 -2.12768	0.83	12.53	Main and local roads	10.88	0.00	28.29	36.73	0.00	22.43	0.12	1.54
Peterborough North	52.54337 -0.28510	1.06	14.85	Minor and local roads	23.93	0.00	31.38	24.98	0.00	0.00	<0.01	19.70
Peterborough South	52.53842 -0.27954	1.71	16.14	Main, minor, and local roads	16.95	0.00	23.18	23.87	15.18	0.00	5.59	15.24
Frankfield	55.88620 -4.14894	0.97	7.04	Main, minor, and local roads	13.96	0.00	15.22	22.83	19.38	0.00	10.55	18.05
Gartcosh	55.89138 -4.06162	1.31	4.90	Intermediate, minor, and local roads	1.44	7.32	13.13	20.14	29.67	10.17	4.18	13.95
York	53.98366 -1.05744	1.22	9.52	Main, minor, and local roads	4.97	11.97	36.73	16.12	8.99	18.38	1.20	1.63

** Built area includes buildings, roads, and hardstanding. †Grassland includes improved, semi-improved and un-improved grasslands of acid, neutral or calcareous soil, not including amenity grassland.*

6.2.2 Animal telemetry

Hedgehogs were searched for by spotlight survey (see Section 5.2.3 in Chapter 5 for methodology) and tracked using Global Positioning System with Very High Frequency (GPS/VHF) tags (hereafter termed ‘tags’; model: PinPoint Beacon 240; Lotek ltd). GPS tags were attached to a subset of healthy adult hedgehogs weighing >600 g to monitor their movements. GPS tags were glued to a patch of clipped spines located on the lower dorsal midline of the hedgehog so to not disrupt animal movement (Glasby and Yarnell, 2013). Tags weighed 10 g and were <5% of the hedgehog’s body mass (av. 1.19% ±0.14 SD, n = 127), following the guidelines of the American Society of Mammologists (Gannon and Sikes, 2007). The weight and overall health of each tagged hedgehog was checked within four days of tag attachment and then every ten days until tag removal (up to 21 days) to ensure the individual’s welfare was unharmed. Tagged hedgehogs were recaptured for health check and eventual tag removal via VHF. No individual was tracked more than once over the course of the study in order to obtain a large sample size and therefore independence between each GPS data set is assumed.

All data were collected under license from Natural England (ref: 2018-36011-SCI-SCI-8 and 2018-36011-SCI-SCI-11). Ethical approval was granted by Nottingham Trent University’s Animal, Rural and Environmental Science Ethical Review Group (code: ARE192014a).

6.2.2.1 GPS tag programming and data cleaning

To obtain fine-scale movement data, the tags were programmed to record geographic co-ordinates (fixes) every ten minutes via a ‘swift’ search for satellites. Ten-minute fixes was deemed appropriate to balance battery life and to obtain accurate road crossing counts (i.e., it was expected that hedgehogs are unlikely to cross a road twice in a ten-minute period). This decision was based on explorations of GPS-data from published papers of the same or similar study sites (e.g., Schaus-Calderón, 2021). The tags started recording fixes one hour before sunset until sunrise to cover the entirety of a hedgehog’s expected active hours and to adapt to changing night lengths throughout the year. Prior to the analysis of the data, fixes were screened for inaccuracies and the fixes that had obtained with ≤4 satellites were removed as per manufacturer’s guidelines. In addition, the distance travelled between two consecutive fixes was calculated using Euclidean distance to remove locations based on implausible hedgehog speeds (over 1 m/s; Braaker et al., 2014). When data was available for less than whole nights (e.g., if the tag was attached or removed in the middle of the night), fixes of those nights were removed to standardise the road crossing frequencies across complete nights only.

6.2.3 Data analysis

6.2.3.1 Road avoidance behaviour

Curated GPS data were analysed using Correlated Random Walk analysis (Fagan and Calabrese, 2014) to determine if hedgehogs exhibited road avoidance behaviour within their activity areas. Correlated Random Walk analysis compares observed movements (e.g., from GPS-tagged animals) to simulated movements from parameterised movement models using specified step length (distance between consecutive points), step number, and turn angle. Random walk models, a type of random search model, are prominent in the animal movement literature. Here, a Correlated Random Walk model was chosen over alternatives such as a Lévy walk model as it allows greater personalisation of the random simulations to match the GPS-tagged individuals (Auger-Méthé et al., 2015). Correlated Random Walk models also present a key advancement upon *un*correlated random walk models as they model a more ecologically realistic successive step orientation (i.e., considering that the direction of movement is not completely independent from the previous direction; Fagan and Calabrese, 2014).

The mean road crossing frequency (number of road crossings per night) of each tracked hedgehog based on the GPS fixes was calculated by intersecting the observed movement paths with the road network (Ordnance Survey Open Road Map; Ordnance Survey, 2022). The same process was completed for random walks generated for each individual. Both analyses were performed in ArcGIS 10.3.1 (ESRI, 2015). Random walks were simulated for each animal with a turn angle drawn from a uniform distribution and a step length distribution, starting location and number of steps that were the same as the observed data. To characterise potential movement more robustly, ten times as many random walks than observed movements were simulated per individual and the mean road crossing rate was taken. The simulated movements were bound to the individual's home range across the entire tracking period to produce the same site fidelity and road type availability as the observed animal. To set the home range boundary, the internationally accepted and standard method was used; 100% Minimum Convex Polygons (MCP; Laver and Kelly, 2008). This method captures the full area of activity, and hence all road crossing opportunities, whilst being less sensitive to the density of locations than alternatives such as kernel estimates (Bianchi et al., 2016). In turn, 100% MCP was appropriate for the greater sampling effort in the present study compared to previous studies over shorter time periods (e.g., up to 6 days tracking – Rodriguez Recio et al., 2013). Furthermore, the observed movement paths were linear interpolations of paths and thus did not represent the actual route taken from one point to the next. As such, 100% MCP home range boundary does not constrain the simulated road crossings to a smaller area, as with kernel estimates, in a manner that might produce biased comparisons between observed and simulated road crossings. However, 100% MCP are susceptible to artificial increases in size by extreme locations or rarely visited areas and so the suitability of this method relies on thoroughly cleaned data points (i.e., removing outliers; Laver and Kelly, 2008). Any simulated locations that fell in impossible places, such as inside buildings, were shifted to the nearest plausible location. The random walks were simulated using the '*animal movement*' function in the program Geographic Modelling Environment (GME; Beyer, 2012). T-tests, Mann-Whitney U tests and chi-squared tests were used to compare movements and home ranges in relation to roads between males and females, between observed and simulated movement trajectories, and to the prevalence of different road types in the study sites.

A combination of road type, sex, and day were chosen to explore differences between the mean observed and simulated road crossing rates based on previous studies (Table 6.2). Following Zuur et al. (2010), assumptions of a linear regression were examined, including zero-inflation and a linear relationship between predictor and outcome variables. Normality was tested using a normal Q-Q plot because formal statistical tests such as Shapiro-Wilk or Kolmogorov-Smirnov were inappropriate due to their over-sensitivity to sample size effects. Homoscedasticity was visually examined via a scatterplot whilst outliers and influential values were tested using standardised residuals and Cook's distance. No outliers in the explanatory or response variables were detected. Road avoidance was first modelled by fitting a maximum likelihood Gaussian Generalised Linear Mixed Model (GLMM) with site as a random effect. Site was used as the random effect to account for the varying context within which the tracked hedgehogs were found. However, as the component variance of the random effect (site) was indistinguishable from zero, a Generalised Linear Model (GLM) was fitted to better account for the normal and independent data with no effect on the variable estimates (Zhang and Lin, 2008). The known avoidance of larger roads by hedgehogs could have biased the overall results if all roads were analysed together (Rondinini and Doncaster, 2002), yet the large number of zeros in crossing rates precluded the use of a multi-variate multiple regression. Therefore, a GLM was run for all road types together, to allow comparisons to previous studies (e.g., Rondinini and Doncaster, 2002), and for each road type separately. The models were adjusted for the availability of each road type in the home ranges of GPS tracked hedgehogs i.e., only hedgehogs that had the possibility of encountering a certain road type were included in the respective model, as not every site contained all road types. Models were run in R (version 3.6.1; R Core Development Team, 2022) and fitted using the package '*lme4'* (version 1.1-21; Bates et al., 2015). The best-fitting model was identified using Akaike's Information Criterion (AICc; corrected for small sample sizes; Burnham & Anderson, 2004). Deviance and the distribution of residuals were checked after fitting the model to ensure unbiased estimates.

GPS data of hedgehogs close to a motorway in Stafford North were not included in this analysis as a concrete central median (also known as central reservation or median strip, used to separate opposing lanes of traffic) was present along the motorway. This physical barrier would likely restrict hedgehog movements in a way that could not be attributed to road avoidance behaviour directly. All remaining roads included in this analysis were free from physical barriers. In addition, less than five days of GPS data were acquired for two hedgehogs (one in Frankfield, one in Peterborough North) due to animal translocation by a member of the public or badger predation, although both individuals (alive or dead) were retrieved. These individuals were not included in the analysis to maintain an accurate depiction of home range and movements.

Table 6.2: *A priori* models for the road avoidance behaviour of west European hedgehogs.

	Model	**Justification**	**Reference**
M0	**Null**	-	-
M1	**Sex (male, female)**	Male and female hedgehogs have shown different movement patterns and activity levels	Riber, 2006 ; Haigh et al., 2014
M2	**Sex + day**	Seasonal differences have been shown in the activity levels of male and female hedgehogs	Rautio et al. (2013) ; Haigh et al. (2014)
M3	**Day**	Hedgehogs show defined activity periods of pre-hibernation, post-hibernation, and breeding with associated differences in activity levels	Rautio et al. (2013)

6.2.3.2 'True' road mortality risk

To assess the 'true' risk of road mortality in relation to road information, a resource selection function (RSF) was fitted to individuals for which data on both road crossings and road mortality within their population were recorded. This included the four study sites in Nottinghamshire (sites 1 – 4, Figure 6.1), compromising 82 hedgehogs (42 ♂, 40 ♀) and 5,891 road crossings. Two female hedgehogs did not cross any roads whilst being tracked and were not included in the analysis to avoid an over-estimation of road avoidance behaviour. RSF is commonly used to explore habitat selection of animals by relating environmental information to location data (Manly et al., 2004). A RSF was identified as the most appropriate and powerful model due to the availability of fine-scale roadkill data, meaning that there was no need to account for imperfect detection as per previously used methods such as occupancy detection modelling (Santos et al., 2018). Likewise, the availability of road crossing data suits a RSF to identify the 'true' road mortality risk as opposed to a proxy of road mortality risk based on the presence or absence of road mortality as per habitat suitability models (Garrote et al., 2018; Wright et al., 2020). Given the extensive dataset available here, RSF can improve the assessment of road mortality risk along roads. Contrary to the standard 'used-available' design of RSFs, i.e., comparing used locations of interest to random available locations, this present study compared successful road crossing locations to roadkill locations in the same four study sites using a binomial logistic regression. This estimates the relative probability of a road segment being the site of a successful road crossing or road mortality. Note that the probability of a successful road crossing and the risk of road mortality describe the inverse outcome and will be used interchangeably hereafter. The road mortality records used in this analysis were collected and detailed in Chapter 3 and Chapter 5 of this thesis (see 5.2.2 in Chapter 5 for full methodological detail).

A combination of traffic, road and seasonal variables were used to analyse 'true' road mortality risk based on existing literature (Table 6.3). Traffic volume and speed were obtained from Nottinghamshire County Council's database. For context, vehicle speeds across the four study sites at night were, on average, 6% (±3.46% SD) faster compared to the day and, on average, 15.22% (±35.94% SD) faster than the signposted speed limit. The locations of streetlamps and signposted traffic speed changes were collected by ground surveys of the study sites. All other spatial queries used to obtain road-related variables were performed in ArcGIS 10.3.1 (ESRI, 2015). A sinuosity index was calculated by dividing 100 m segments of the road by Euclidean distance between the start and finish locations using the 'measure line' tool. Road slope was extracted from a digital elevation model created from a United States Geological Survey (USGS) raster (U.S. Geological Survey, 2022). The presence or absence of road verges and road width were extracted from land cover using Ordnance Survey Mastermap Topography Layers (Ordnance Survey, 2022). The size of the signposted traffic speed change (e.g., whether a 30 mph or 20 mph increase/reduction in speed) and traffic speed were collinear with road slope and traffic volume, respectively, and so were not included in the analysis. Moreover, they were removed from analysis to include a broader range of road and traffic characteristics (i.e., rather than an excessive focus on traffic speed).

Following Zuur et al. (2010), assumptions of a logistic regression were examined, including linearity of independent variables and log-odds based on visualisations from scatterplots, and multicollinearity of the explanatory variables using Variance Inflation Factors (VIF). The VIFs did not exceed 1.06 in the final models and were deemed acceptable (a VIF under three is deemed appropriate; Zuur et al., 2010). Outliers and influential values were tested using standardised residuals and Cook's distance; those that exceeded three standard deviations of the mean were removed (Jones, 2019). Models were run in R (version 3.6.1; R Core Development Team, 2022) and fitted using the package '*lme4*' (version 1.1-21; Bates et al., 2015) The best-fitting model was identified using Akaike's Information Criterion (AICc; corrected for small sample sizes; Burnham & Anderson, 2004). Deviance and the distribution of residuals were checked after fitting the model to ensure unbiased estimates.

Table 6.3: *A priori* models for the road mortality risk of west European hedgehogs.

	Model	Description	Justification	Reference
M0	**Null**	No variables	-	-
M1	**Nightly traffic volume**	Average annual nightly traffic (AADT; average number of vehicles of any type between 9pm – 4am, across a year) taken from the closest year to the tracking period	Hedgehogs have been shown to avoid crossing busy, but not quiet, roads	Rondinini & Doncaster, 2002
M2	**Road slope**	The change in elevation of a road segment (degrees)	Slope has been linked to vehicle speed and, in turn, risk of animal-vehicle collision	de Carvalho, Bordignon, & Shapiro, 2014 ; Kang et al., 2016
M3	**Road sinuosity**	The curvature of 100 m road segments, as a sinuosity index	Curvature of the road can affect the line of sight of both animals and vehicles, as well as vehicle speed	Grilo et al., 2011 ; Girardet et al., 2015
M4	**Road topography**	The road is categorised as either depressed (lower than the banks), flat (level with the bank), raised (higher than the banks and/or ditches are present), or with a combination (the bank of either side of the road differs)	The banks of a road may present physical impediments or barriers to ground-dwelling animals such as hedgehogs trying to cross a road	Clevenger et al., 2002 ; Valero et al., 2015
M5	**Distance to streetlamp**	Euclidean distance (metres) to the nearest permanent streetlamp	Artificial Light at Night (ALAN) has extensive biological implications for nocturnal animals, including changes in behaviour and movements	Gaston & Bennie, 2014 ; Berger et al., 2020
M6	**Road width**	Width of the road (metres) that contains traffic (i.e., excluding pavements)	The width of the road can dictate how long animals are in danger of traffic collision during each road-crossing event	Valero et al., 2015

M7	**Presence or absence of road verge**	Presence or absence of an adjacent grassy road verge	Continuous stretches of grass verges can function as foraging habitat and/or movement corridors for mammals that use habitat edges, such as hedgehogs (particularly in rural landscapes)	Doncaster et al., 2001 ; Schaus-Calderón. 2021
M8	**Distance to signposted traffic speed change**	Linear distance (metres) along the road to the nearest signposted traffic speed change	Speed changes are often implemented on the outskirts of residential areas, producing a ‘transition zone’ between higher-speed rural roads and lower-speed residential roads. Interventions that change vehicle speed have the potential to be cost-effective road mitigation measures	van Langevelde & Jaarsma, 2009 ; Cruzado & Donnell, 2010
M9	**Month**	Month of the year that a road crossing or roadkill was recorded	Hedgehog movements have been shown to change throughout the year depending on proximity to hibernation and breeding	Gagnon et al., 2007 ; Rautio et al., 2013

6.2.3.3 Annual road mortality probability

The annual road mortality probability for hedgehogs across the 11 study sites was quantified by combining the road crossing rates with traffic and road data. The road mortality risk framework developed by Hels & Buchwald (2001) was used to estimate the probability that an individual would be killed (P_{killed}) per single road-crossing event (Equation [2). This equation is better suited to small animals compared to the equation developed by van Langevelde & Jaarsma (1995), for example, that mainly considers large mammals.

[2] $P_{killed} = 1 - \left(e^{\frac{-Na}{v}}\right)$

where N is the number of vehicles/minute, a is the killing width of car (metres, this refers to the area of the vehicle that would kill an animal upon collision), and v is the velocity of the animal moving through the kill zone (metres/minute). For this analysis, the road and traffic measurements of the studied roads were used. The kill width of a car was taken as 1 metre (two sets of tyres each 0.5 m wide) and the animal velocity was taken as 45 metres/minute as per observations and experimental study (Hels and Buchwald, 2001; Carter, Macpherson and Bright, 2010). The number of vehicles per road type was taken as the average of nightly traffic volume between 9pm and 4am.

To calculate the annual road mortality probability (P_{annual}) for an individual, the average number of road crossings per night ($n_{crossings}$) was taken alongside the approximate length of the hedgehog's active season over the year (April to October, inclusive, 214 days) and incorporated as follows:

[3] $P_{annual} = 1 - [(1 - P_{killed})^{(214\ x\ n_{crossings})}]$

6.3 Results

Across the 11 sites and 19 survey sessions, 127 hedgehogs were tagged for an average of 14.12 days (±2.66 days SD), comprising 67 males and 60 females (Table 6.4), from which a total of 64,782 raw (i.e., uncleaned) fixes were recorded. Following data cleaning to remove fixes with low confidence in accuracy and those from incomplete nights, 59,241 fixes remained for analysis. Removed fixes comprised 8.6% of all raw fixes. Whilst wearing a GPS tag, four animals died from either a hedgehog-vehicle collision (two in Southwell) or badger predation (one in Stafford North, one in Frankfield).

Table 6.4: Number of GPS tags deployed on west European hedgehogs, the average and total number of days that a tag was attached. SD = Standard Deviation.

Site	Survey session	Time period	GPS tags deployed			GPS tracking days	
			Male	Female	Total	Average (SD)	Total
Farnsfield	1	June-July 2020	7	7	14	14.86 (1.99)	208
	2	April 2021	7	5	12	13.83 (2.29)	166
	3	September-October 2021	5	6	11	16.00 (2.45)	176
Southwell	4	July-August 2020	5	5	10	15.50 (4.82)	155
	5	June 2021	4	5	9	13.78 (1.48)	124
	6	September 2021	4	4	8	14.13 (3.27)	113
Kirklington	7	September 2020	2	3	5	16.20 (4.82)	81
	8	May 2021	3	2	5	15.00 (1.22)	75
	9	August 2021	2	1	3	14.67 (2.08)	44
Halam	10	September-October 2020	1	1	2	20.00 (1.00)	40
	11	May 2021	1	1	2	17.50 (2.12)	35
	12	August 2021	1	0	1	12.00	12
Stafford North	13	April-May 2021	2	1	3	12.33 (5.56)	37
Stafford West	14	April-May 2021	5	4	9	13.00 (4.13)	119
Peterborough North	15	May-June 2021	2	4	6	11.00 (4.18)	55
Peterborough South	16	May-June 2021	4	4	8	10.88 (3.44)	87
Frankfield, Glasgow	17	July 2021	3	2	5	12.25 (3.40)	49
Gartcosh, Glasgow	18	July 2021	3	1	4	14.00 (1.41)	56
York	19	August 2021	6	4	10	10.10 (1.20)	101
	Total		**67**	**60**	**127**	**14.12 (2.66)**	**1,721**

Male home ranges were significantly larger than female home ranges (♂ : 0.21 km^2 ±0.13 SD, ♀ : 0.06 km^2 ±0.06 SD; Mann-Whitney U test: U-value = 45; p-value = 0.003). The road density within home ranges ranged from 0 to 13.13 km of road/km^2, with an average road density of 8.49 km/km^2 (±3.90 SD). There was no significant difference in the road densities within the home ranges of males and females (Mann-Whitney U test: U-value = 117; p-value = 0.352). Hedgehogs moved a mean of 36.05 m per step length (±13.95 m SD; i.e., between consecutive fixes, corrected for missing fixes), although this was significantly greater in males than females (♂: 41.76 m ±12.72 m SD, ♀: 29.99 m ±12.57 m SD; Mann-Whitney U test: U-value = 59; p-value = 0.006).

There were 8016 road crossings by GPS tagged hedgehogs in total across the 11 study sites and 19 survey sessions. On average, males crossed roads 1.8 times more frequently than females each night. The average number of road crossings per night was 5.63 (±2.52 SD) for males and 3.01 (±1.68 SD) for females (Mann-Whitney U test: U-value = 59.5; p-value = 0.006). For all hedgehogs combined, the average number of road crossings after midnight was significantly greater than before midnight (Mann-Whitney U test: U-value = 24; p-value = <0.001). For whole nights, the road crossing rate was greatest on local roads and lowest on main roads. In fact, main roads were crossed significantly less than expected based on their availability in the study areas (Table 6.5; Appendix XII). Based on the availability of different road types at each site, local and minor roads were included in home ranges significantly more than expected, whilst intermediate roads were included significantly less than expected (Table 6.5; Appendix XII). Main and intermediate roads were 5.06 to 9.09 times less common in home ranges compared to minor and local roads. Furthermore, several individuals located adjacent to roads showed an elongation of their home range and/or had roads acting as the boundary to the home ranges, particularly females and by main roads (see examples in Appendix XIII).

Table 6.5: Details of the road types that were crossed and available for crossing within the home ranges of GPS tracked west European hedgehogs across the 11 study sites, as well as the road types present within the home ranges (corrected for the availability of each road type within the study sites). ** p≤ 0.01 *** p≤ 0.001.

		Local road	Minor road	Intermediate road	Main road
Percentage of roads within the 11 study sites		73.60	16.70	2.61	7.06
Road crossings per night	**Male**	4.06	1.59	0.81	0.37
	Female	2.26	0.97	0.80	0.27
Percentage of total road crossings	**Male**	80.53	17.55	1.20	0.73 **
	Female	79.52	17.04	2.35	1.10
Percentage of home ranges with each road type inside	**Male**	98.46 ***	67.69 ***	13.85 ***	10.77
	Female	100.00	45.76	15.25	6.78

6.3.1 Road avoidance behaviour

Of the 122 hedgehogs analysed, 87.7% (107) of individuals crossed fewer roads than the matched randomly simulated movements. For all hedgehogs and road types combined, the average number of observed road crossings per night (4.36 ±2.52 SD road crossings/night) was significantly lower than the randomly simulated road crossing per night (6.47 ±2.53 SD road crossings/night; t value = -3.140, p value = 0.004; Figure 6.2). As such, hedgehogs exhibited road avoidance behaviour when all roads were combined. That is, the observed hedgehogs behaved differently than the modelled individuals with random movements. There was no significant difference between the road avoidance of males and females when all road types were combined (t value = -1.100, p value = 0.281). Given that a road type was present in an individual’s home range, road avoidance was greatest for main roads, followed by intermediate roads, minor roads and least of all, local roads (Table 6.5; Figure 6.3).

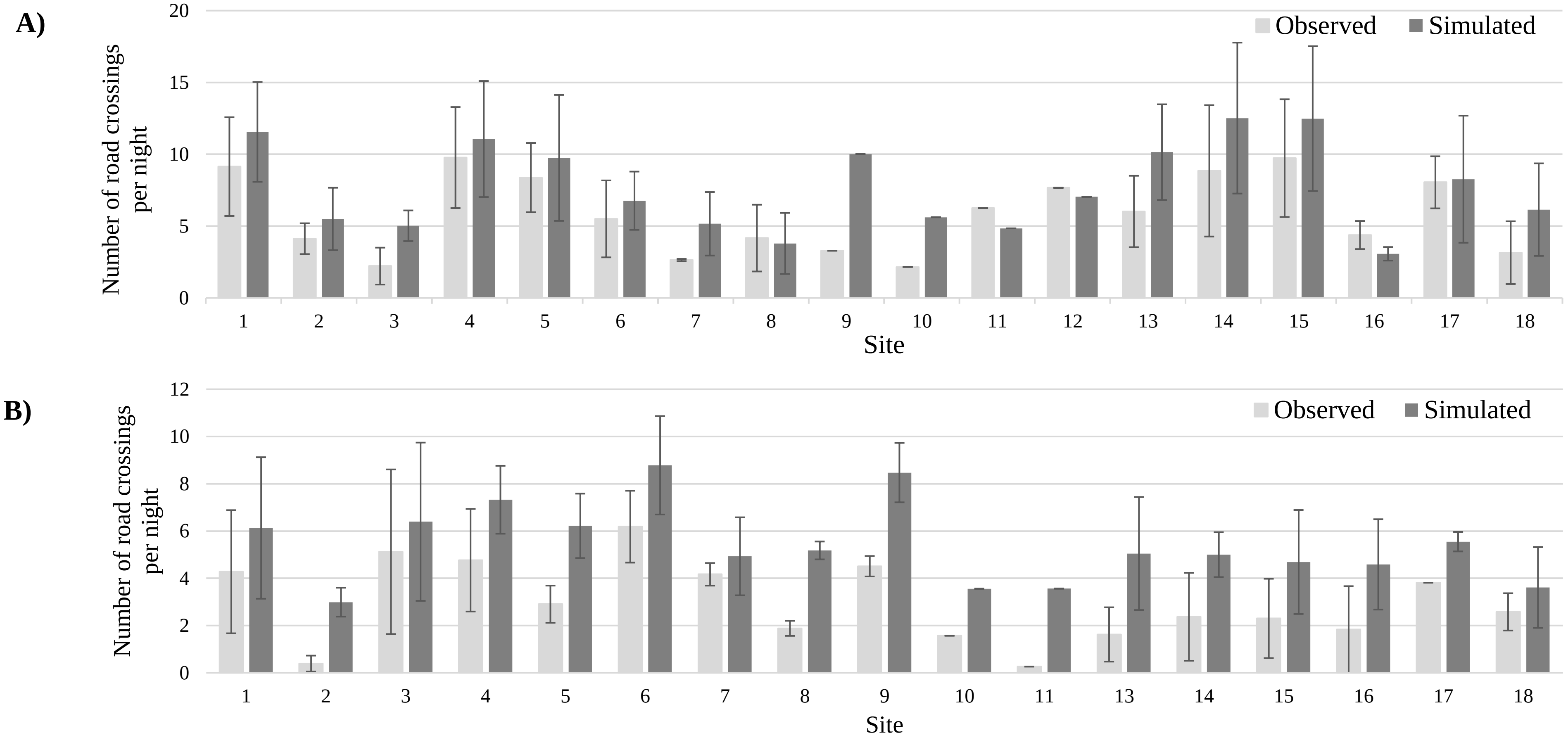


Figure 6.2: Number of observed and simulated road crossings for A) males and B) females. 1: Farnsfield, summer 2020; 2: Farnsfield, spring 2021; 3: Farnsfield, autumn 2021; 4: Southwell, summer 2020; 5: Southwell, spring 2021; 6: Southwell, autumn 2021; 7: Kirklington, autumn 2020; 8: Kirklington, spring 2021; 9: Kirklington, summer 2021; 10: Halam, autumn 2020; 11: Halam, spring 2021; 12: Halam, summer 2021; 13: Stafford, spring 2021; 14: Peterborough North, spring 2021; 15: Peterborough South, spring 2021; 16: Frankfield, summer 2021; 17: Gartcosh, summer 2021; 18: York, autumn 2021. Note: no females were tracked in Halam during summer 2021 and Stafford North individuals were not analysed due to proximity to a motorway. Errors bars represent standard deviation where calculable

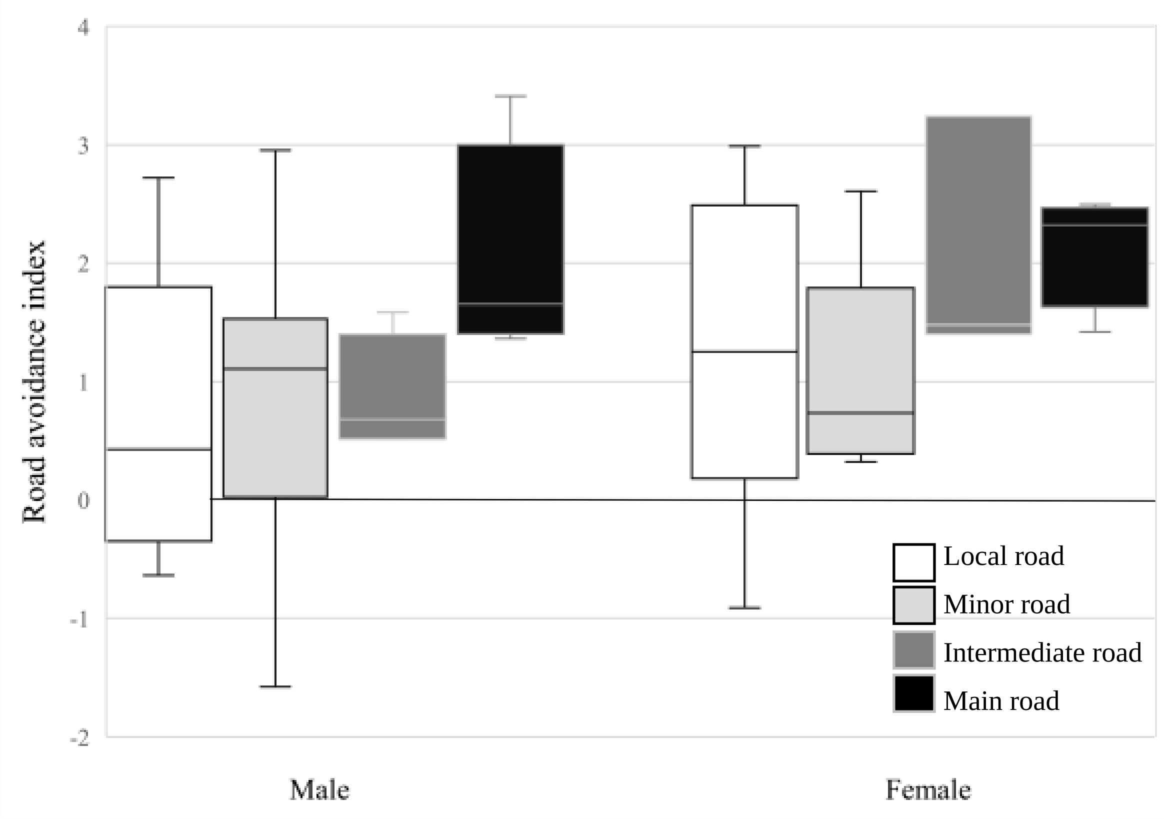


Figure 6.3: The difference between observed and simulated road crossings per night for male and female hedgehogs, by road type. Values >0 indicate road avoidance, i.e., the greater the value, the stronger the avoidance. The horizontal line denotes median values, the boxes extend from the 25th to the 75th percentile of the distribution of values (i.e., inter-quartile range), and the vertical extending lines denote the range.

6.3.2 Predictors of road avoidance behaviour

For all road types combined, the top logistic regression model, with 63% of the cumulative model weight, indicated that 'day' was the most important factor predicting road avoidance behaviour (Table 6.6). That is, road avoidance behaviour increased later in the year. The significance of seasonality was also reflected for both main roads and intermediate roads separately (Table 6.7). For main roads alone, the best fitting model revealed that the increase in road avoidance later in the year was significantly greater for males than females (Figure 6.4). Without the interaction with day, however, females showed significantly greater avoidance of main roads compared to males. There was no significant influence of sex in the avoidance of the other road types (Table 6.7). No significant covariates were found to explain hedgehog interactions with minor or local roads.

Table 6.6: Ranked Generalised Linear Models to predict road avoidance behaviour of west European hedgehogs across 10 study sites and 18 survey sessions in Great Britain. AICc = Akaike's Information Criterion, Δi = delta AIC, ω = AICc weighting.

	Model	AICc	Δi	ω
All road types	**Day**	563.60	0.00	0.63
	Sex*Day	566.25	2.65	0.80
	Null	566.66	3.06	0.93
	Sex	568.13	4.53	1.00
Main roads	**Sex*Day**	22.13	0.00	0.98
	Null	31.11	8.99	0.99
	Day	32.60	10.48	1.00
	Sex	32.74	10.61	1.00
Intermediate roads	**Day**	38.23	0.00	0.57
	Null	39.82	1.58	0.83
	Sex	41.48	3.25	0.94
	Sex*Day	42.79	4.56	1.00
Minor roads	**Day**	248.03	0.00	0.49
	Null	249.05	1.03	0.78
	Sex	250.19	2.16	0.94
	Sex*Day	252.29	4.26	1.00
Local roads	**Null**	515.12	0.00	0.45
	Day	516.03	0.91	0.73
	Sex	516.52	1.40	0.95
	Sex*Day	519.57	4.45	1.00

Table 6.7: Best-fitting Gaussian Generalised Linear Model to predict road avoidance behaviour of west European hedgehogs across the eleven study sites around the UK. * p≤ 0.05, ** p≤ 0.01.

	Covariate	**Estimate**	**Standard Error**	**Z-value**	**p-value**	
All roads	**Intercept**	-23.142	11.403	-2.030	0.045	*
	Day	0.001	0.001	2.278	0.025	*
Main roads	**Intercept**	-20.380	8.510	-2.395	0.038	*
	Sex(male)	-324.700	71.610	-4.534	0.001	**
	Day	0.001	<0.001	2.660	0.024	*
	Sex(male) * Day	0.015	0.003	4.525	0.001	**
Intermediate roads	**Intercept**	-20.450	8.824	-2.317	0.039	*
	Day	0.001	<0.001	2.528	0.027	*

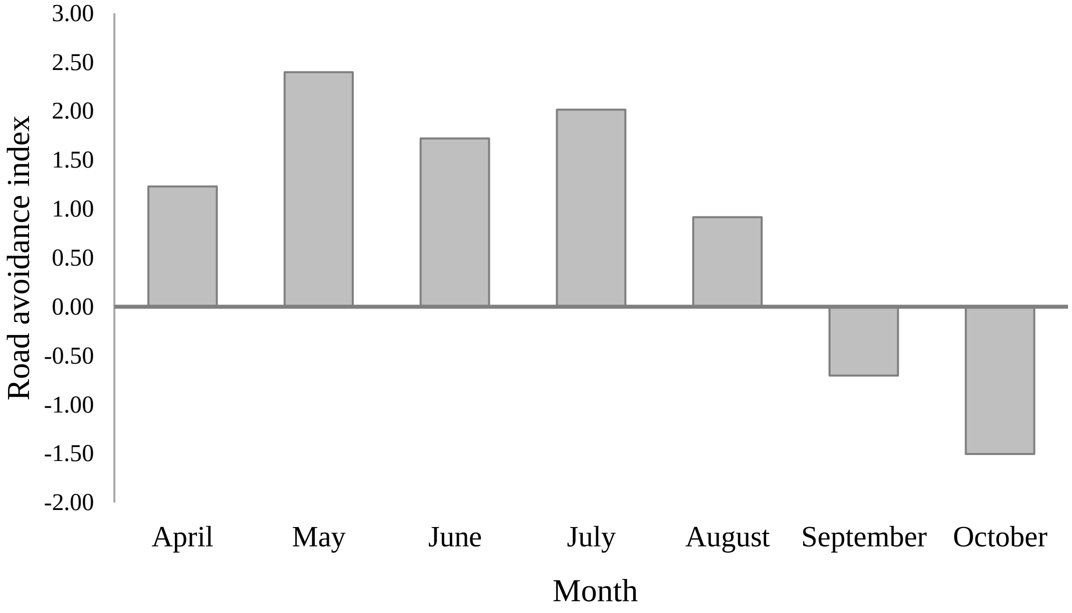


Figure 6.4: The difference in road avoidance between male and female hedgehogs throughout the year (i.e., representing the Sex(male)*Day interaction). Positive values represent a greater road avoidance by females compared to males. Negative values represent a greater road avoidance by males compared to females.

6.3.3 ‘True’ road mortality risk

The most parsimonious RSF model included traffic volume, indicating that the probability of successfully crossing a road decreased with increasing traffic volume (Table 6.8; Table 6.9). Strong, positive relationships indicated that the likelihood of successfully crossing a road increases on roads with a greater slope and with greater distance from the transition zone located at the edge of residential areas.

Table 6.8: Ranked RSF models predicting the likelihood of successfully crossing roads relative to road mortality of west European hedgehogs across the four study sites in Nottinghamshire. AICc = Akaike's Information Criterion, Δi = delta AICc, ω = AICc weighting.

Model	**AICc**	**Δi**	**ω**
Nightly traffic volume	-11791.22	0.00	1.00
Distance to sign-posted speed limit change	-11766.91	24.31	0.00
Slope	-11754.13	37.09	0.00
Road width	-11741.92	49.30	0.00
Month	-11727.53	63.69	0.00
Presence or absence of road verge	-11725.84	65.38	0.00
Sinuosity	-11725.15	66.07	0.00
Topography	-11722.86	68.36	0.00
Null	-11720.97	70.25	0.00
Distance to nearest streetlamp	-11719.28	71.94	0.00

Table 6.9: Best-fitting binomial Resource Selection Function of the likelihood of successfully crossing a road relative to being killed across the four study sites in Nottinghamshire. * p≤ 0.05, *** p≤ 0.001

Covariate	**Estimate**	**Standard error**	**Z-value**	**p-value**	
(Intercept)	5.301	0.188	28.170	<0.001	***
Nightly traffic volume	-0.004	0.001	-7.190	<0.001	***

6.3.4 Annual road mortality probability

For a single road-crossing event, the probability of road mortality ranged from 0.0006 on local roads to 0.0029 on main roads. Based on the risk per crossing and the average number of road crossings per night, males consistently had a greater annual probability of road mortality than females. For both sexes, the annual probability of road mortality was greatest on intermediate roads with moderate traffic volume (Figure 6.5). For a hedgehog in a typical residential area consisting largely of local roads, hedgehogs would expect to make 1,694 road crossings before being killed by a hedgehog-vehicle collision. Based on average road crossing rates, this equates to 526 days, or 2.5 years based on a hedgehogs' spring – autumn active season.

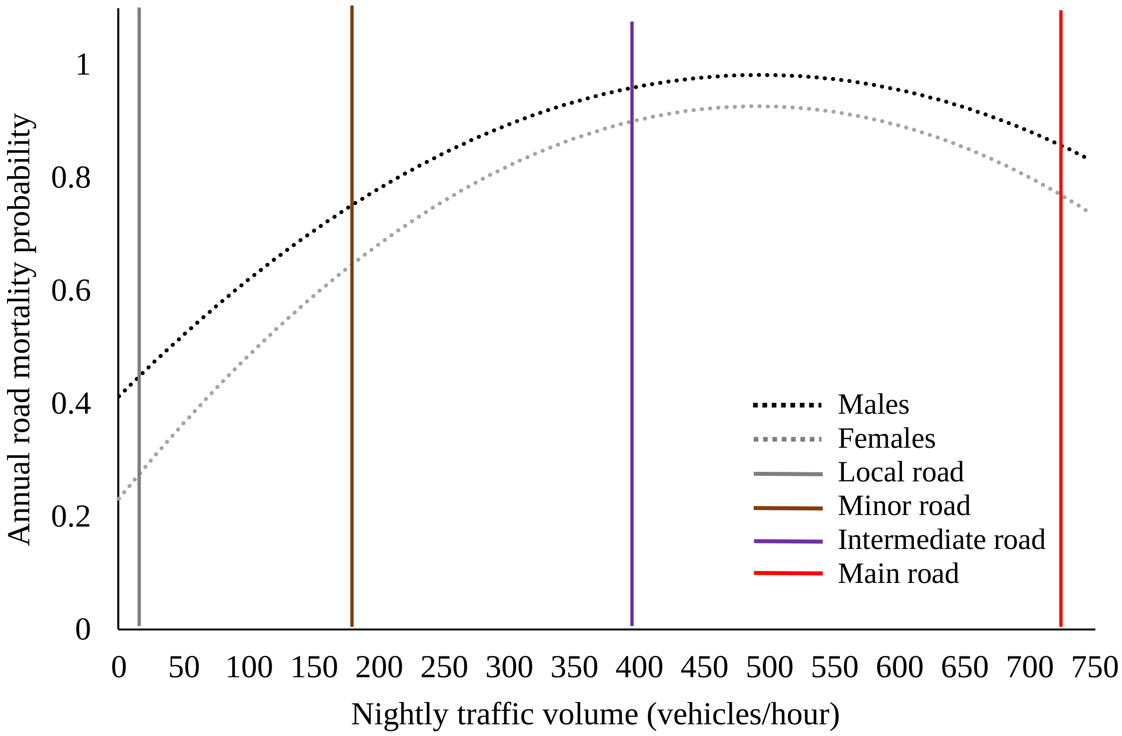


Figure 6.5: Annual roadkill probability of males and females (P_{annual}, as per Equation 3) based on the traffic of studied roads and observed road crossing rates. The average nightly traffic for each studied road type is marked.

6.4 Discussion

This is one of few studies to simultaneously assess intrinsic and extrinsic factors affecting individual probabilities of successful road crossings and mortality using empirical data (e.g., Neumann et al., 2012; Zeller et al., 2018). The findings contribute to an understanding of the multivariate, quantitative, and cumulative effects of roads on hedgehogs and how those effects vary among road networks, months of the year and different sexes. Overall, this study emphasizes that minor and local roads pose relatively little threat to hedgehogs due to either road mortality risk or avoidance behaviour, both of which appear to be low. By contrast, main roads filter hedgehog movements across a landscape, particularly those of females, and intermediate roads may contribute the greatest amount to road mortality rates.

Corroborating findings from other taxa (Kammerle et al., 2017; Dexter et al., 2018; Serieys et al., 2021), sex differences in road crossing rates were observed in this study. The lower road crossing rates of female hedgehogs compared to males may be a function of the significantly smaller step lengths of females, that females spend more time foraging than travelling compared to males

(Schaus-Calderón, 2021), and/or that females select safer habitat to rear young whilst males are not constrained by parental care (Dowding et al., 2010). Collectively, these behaviours result in females reducing their chances of encountering a road, despite having similar road densities within their home ranges as males. This may lessen the impacts of roads on population fitness given the importance of females for population persistence due to hedgehogs adopting a polygamous mating system and maternal care of juveniles. However, female hedgehogs crossed roads an average of 3.01 (±0.68 SD) times per night in relatively residential areas studied here which, while significantly lower compared to males, still remains a very high figure in relation to other small mammals. For example, up to 0.8 crossings per day were made by hazel dormice (*Muscardinus avellanarius*) in agricultural Germany (Kelm et al., 2015), European hares made, on average, 2.7±3.8 SD daily road crossings in mixed landscapes of built-up areas, forest and grassland in Germany and Denmark (Mayer et al., 2022), and several additional rodents (including bank voles *Myodes glareolus* and yellow-necked mice *Apodemus flavicollis*) crossed roads less frequently (Rico, et al., 2007; van der Ree et al., 2010). The high road crossing rates of female hedgehogs are likely to be much lower in areas of farmland or natural habitat with little or no human dwellings, although hedgehog populations are now generally rare and appear to be still declining in such sites (Williams et al., 2018).

6.4.1 Road avoidance behaviour

By analysing fine-scale movement data whilst accounting for the proportion of each road type present in the study area, this study revealed consistent road avoidance behaviour. The road avoidance of hedgehogs is typical of smaller mammals and solitary species (Mulder, 1999; McGregor et al., 2008). The small home ranges of small-bodied species relative to road matrices may play a role in these conclusions. However, small and solitary species are also documented to have a greater predation risk perception and are more cautious of open areas compared to gregarious and/or social species (Duffett et al., 2020), potentially spending less time in resource-rich areas due to greater perceived danger (e.g., white-footed mice *Peromyscus leucopus,* Morris & Davidson, 2000; sand rat *Psammomys obesus,* Tchabovsky et al., 2001; Cape hare *Lepus capensis,* Zaman et al., 2020). In fact, hedgehogs were shown to avoid road verges (i.e., strips of relatively open space) in habitat selection analyses of Rondinini & Doncaster (2002) and Schaus-Calderón (2021) in the UK. Moreover, both this present study and Dowding et al. (2010) observed a significantly greater number of road crossings after, compared to before, midnight. These findings may be explained by the fact that human activity (e.g., traffic, pedestrians, domestic dogs) is lessened at night and so hedgehogs may be adopting acute risk perception, in turn adapting their behaviour accordingly. Therefore, the overall avoidance of roads likely pertains to hedgehogs avoiding areas and times where they are exposed to threats, either natural or anthropogenic. Despite the observed road avoidance behaviour, hedgehogs continued to cross at a high rate of, on average, 4.36 (±2.52 SD) times per night. As a result, roads appear to limit, but not prevent, road crossings by hedgehogs, with the exception of roads with physical barriers such as central medians that were not included in the analysis.

6.4.1.1 Road avoidance behaviour by road type

The assessment of 11 different road networks across the UK highlights that not all roads are perceived by hedgehogs in the same way. The finding that hedgehogs often avoid main roads, but have a tendency to cross minor and local roads, agrees with previous studies by Dowding et al. (2010), Doncaster et al. (2001), Rondinini & Doncaster (2002), and Schaus-Calderón (2021). The analysis of home ranges in this study further supports the greater avoidance of main roads, as the positions and shapes of the home ranges rarely included main and intermediate roads. The comprehensive regression model used here offers a more direct and quantifiable comparison between road types than Doncaster et al. (2001) and Schaus-Calderón (2021), who analysed distance to roads rather than quantified road crossing rates. Moreover, the sample size used here was 2.7 – 7.6 times larger across 5.5 times as many road networks than previous work by Dowding et al. (2010) and Rondinini & Doncaster (2002). Furthermore, the separate analyses for each road type used here revealed that females avoided busier, but not quieter, roads more than males. By contrast, all road types were analysed together in previous studies and sex differences in road avoidance were not found (Rondinini and Doncaster, 2002; Dowding et al., 2010). This difference infers a disparity in risk perception between males and females that may have repercussions for the spatial displacement of individuals. This itself can lead to the exacerbation of resource limitation (Ji et al., 2017) as well as affect the road mortality risk and ultimately population dynamics for this species.

The trend of a decreasing road crossing rate with increasing traffic volume has been shown in several generalist species who have flexibility in resource acquisition on either side of a road (e.g., Dulzura kangaroo rat *Dipodomys simulans*; Brehme et al., 2013). Moreover, the generally accepted hypothesis to explain the road avoidance of small mammals (including hedgehogs; Mulder, 1999; Rondinini & Doncaster, 2002) is an avoidance of the road surface (e.g., temperature, materials;

McGregor et al., 2008). For example, Rico et al. (2007) showed that small mammals did not cross nearby roads regardless of traffic volume in Czechia. However, this assumption is not corroborated here as the strength of hedgehog road avoidance increased from local to main roads, even though all roads were tarmacked with the same surface aspect. That is, roads did not substantially affect the movements of hedgehogs when traffic was low. Moreover, both the light intensity and road widths were relatively invariable across the study sites and so it is unlikely that either of these factors affected the road avoidance behaviour, although further research is warranted. Instead, an avoidance of traffic noise or vehicles themselves is more likely. By further elucidating the type of road avoidance exhibited by hedgehogs, this study presents crucial direction to planning and implementing targeted road mitigation. Crucially, the evidence here indicates that there are a greater number of mitigation options available for counteracting hedgehog road avoidance than previously thought, given that it is not the road surface itself that is avoided. For example, should hedgehogs specifically be avoiding the noise from roads, which can be assessed by a phantom-road experiment (e.g., Schwartz, 2020), measures such as adopting noise-absorbent surfaces or speed limitation could be assessed for efficacy at noise reduction. Importantly, however, reducing the perception of risk (in this case, noise) in order to reduce population fragmentation must be accompanied by a reduction in the *real* risk of vehicle collision, otherwise an ecological trap is introduced and road mortality may increase.

6.4.1.2 Road avoidance behaviour by sex and time of year

The seasonality identified in road crossing probabilities provides novel points of view to long-standing questions surrounding the predictability of animal interactions with roads. The increase in road avoidance throughout the year was likely driven by the increase in traffic volume in late summer/early-autumn (see section 6.4.2; Department for Transport, 2019), and/or males reducing their activity levels after the breeding season. The latter is supported by the fact that the only individuals to cross more roads than expected were males during peak breeding season between May and July (Figure 6.2). In contrast, and likely driving the less extreme seasonality compared to males, females tend to increase their activity levels following juvenile independence in September to build fat reserves for winter hibernation (Doncaster et al., 2001). In fact, the only months where female avoidance was lower than males were September and October (Figure 6.4). Seasonal variations in activity levels by sex are also reflected by changes in home range sizes. In Finland, Rautio et al. (2013) observed that the home range sizes of males during the breeding season (May to July) were, on average, 1.8 times greater than that of females, but this pattern was reversed during the pre-hibernation season (August to September). Moreover, rainfall may also be responsible for the seasonal differences in road crossing rates. This is because rain has been shown to reduce hedgehog activity and is greater during the autumn months (Gazzard, Yarnell and Baker, 2022). These seasonal differences suggest that road crossing events are non-trivial and calculated against the risks and rewards of breeding and survival. The number of males and females tracked for the estimation of road crossing rates was similar (67 males and 60 females; Table 6.4), indicating that sex differences in road avoidance were not due to an unbalanced sampling effort.

6.4.2 'True' risk of road mortality

The significance of traffic volume to the risk of road mortality, as reported in this study, is widely cited across many species and habitats (Gagnon et al., 2007; McCown et al., 2009; Jacobson et al., 2016). On roads with greater traffic volumes, animals have less time to successfully cross the road and drivers have less opportunity to safely avoid animals as the gaps between vehicles decrease. Both factors increase the probability of collision. This study showed that elevated risk of road mortality occurs close to areas of signposted traffic speed change. Cruzado & Donnell (2009) and Riginos et al. (2019) found that most drivers failed to reduce their speeds to the signposted speed limit change from rural to residential transition zones. It is likely that drivers enter or exit low-speed residential areas, where hedgehog activity and densities are high, at excessive speeds that give drivers less time to respond to an animal in the road. This provides useful insight into the complexity of 'true' road mortality risk that varies based on the inextricable link between animal and human behaviour. These principles likely also explain the greater risk of road mortality on flatter roads. Flat roads likely promote increased speed and careless driving, increasing the likelihood of wildlife-vehicle collisions (de Carvalho et al., 2014). Speed limit compliance is variable but driver choice in speed has shown to be largely based on perception of safety, roadway features, and previous speeding convictions (Cruzado and Donnell, 2010). The risk of collision both in the transition zone and on flatter roads may be exaggerated at night when vehicle speeds are greater than in the daytime, which is considered a response to perceived lower human activity (Bassani and Mutani, 2012). In fact, the time between perception and reaction for drivers and animals in the road increases with increasing vehicle speed at night (Rodgers and Robins, 2006). The insights gained from this present study can contribute to the design of high- to low-speed roads and residential transition zones. More specifically, this could entail a more gradual speed reduction or pushing the speed changes further away from the residential area, with measures such as speed bumps or cameras to ensure compliance.

6.4.3 Annual road mortality probability

The effect of traffic on road mortality was not linear, with a greater annual probability of road mortality on intermediate roads compared to main, minor, and local roads. This was similarly observed for different hedgehog species in Bulgaria (*E. roumanicus*, Mikov & Georgiev, 2018) and Turkey (*E. concolor,* Özcan & Özkazanç, 2017), and a suite of taxa including reptiles (Litvaitis & Tash, 2008), carnivores (Clarke, White and Harris, 1998), and ungulates (Seiler, 2005). Collectively, these non-linear relationships suggest that complex interactions between animal behaviour, road, and environmental predictors are at play. The results presented here partially support the traffic flow theory, which states that as traffic volume increases, the probability of an animal-vehicle collision increases steeply until an asymptote is reached (Aresco, 2005). Instead of plateauing, results of this present study indicated that annual road mortality probability of hedgehogs decreased on main roads, which can be explained by the risk-disturbance hypothesis. That is, when traffic has reached a certain species-specific volume, the probability of avoidance becomes greater than the probability of mortality due to a higher perception of risk (Frid and Dill, 2002). This is further reflected in the significant road avoidance of main roads and the greater number of road crossings after midnight when traffic is lower, indicating risk perception by hedgehogs to road traffic. Intermediate roads appear to present a dangerous combination for hedgehogs; the amalgamation of moderate traffic and a lack of substantial deterrence of animals to cross may culminate in relatively high roadkill rates on intermediate roads over time (Clark et al., 2001). By incorporating animal movement data into analyses of road impacts, results such as these can bridge the highly-cited traffic flow theory and species-specific behavioural models such as the risk-disturbance model.

In contrast to findings presented here, a threshold for the probability of hedgehog mortality on roads was not detected by Grilo et al. (2015), nor Hels & Buchwald (2001) who reported an almost linear increase in hedgehog roadkill probability up to 40,000 vehicles per 24 hours. The disparity in results could be due to methodological differences. The greater sensitivity to traffic volume found here may be because Grilo et al. (2015) and Hels & Buchwald (2001) did not incorporate road crossing behaviour into the models. This negates the fact that hedgehogs do not continue to cross roads regardless of traffic volume (this study; Rondinini & Doncaster, 2002). Overall, these findings reinforce the two-fold barrier effect from roads experienced by hedgehogs. Intermediate roads are likely to contribute the most to road mortality rates, whilst main roads limit movements by reducing road crossings attempts due to a higher perception of risk. With the projected increase in traffic volume by up to 50% by 2050 in Great Britain (Department for Transport, 2018), traffic volume on main and intermediate roads may become high enough to invoke such strong road avoidance that these roads are very rarely crossed. Instead, road crossings, and the risk of road mortality, may shift to minor and local roads which too have projected increases in traffic volumes. This is demonstrated in Figure 6.6 where annual road mortality probability was estimated using Equation 3 based on projected increases in traffic volume by 2030 (projected increase of 17%), 2040 (25%), and 2050 (50%; Department for Transport, 2018). The forecasts in roadkill probability for minor and local roads are particularly concerning given that 81% of the British road network is comprised of these road types, raising concern over a possible greater road mortality and road avoidance to curtail population stability.

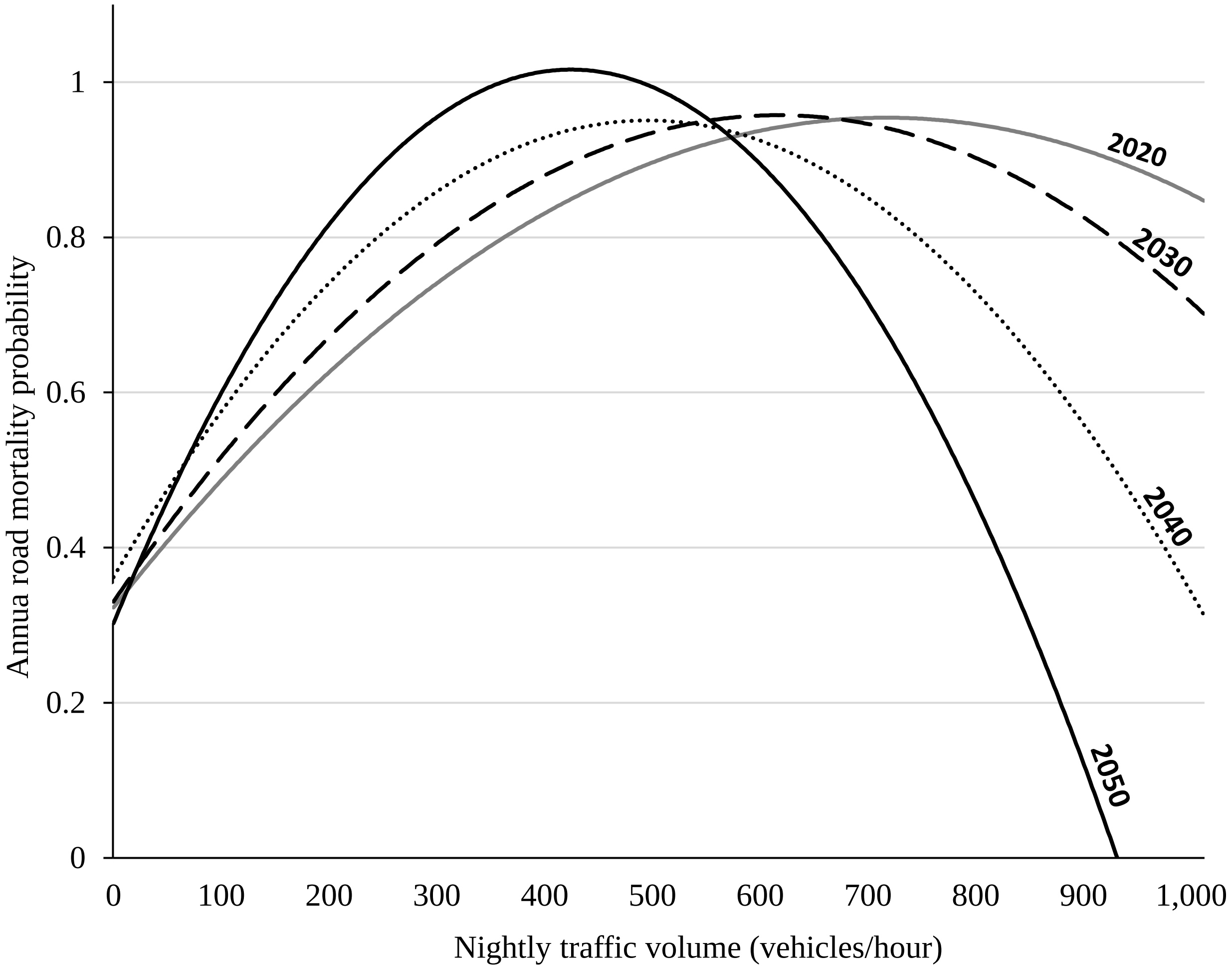


Figure 6.6: Annual roadkill probability of hedgehogs (P_{annual}, as per Equation 3) from 2020 to 2050 based on the projected increases in traffic volume in Great Britain.

6.5 Limitations of the study

The movement paths were linear interpolations between GPS fixes and may not represent the actual route taken from one point to the next. Instead, they represent the shortest distance between two GPS points and may have over-estimated crossing rates. Moreover, although the Correlated Random Walk analysis is an advancement upon *un*correlated random walk analysis, no habitat variables were included in the analysis to explore road avoidance of hedgehogs. This may affect how apt a comparison the random walks were to the observed data. However, Schaus-Calderón (2021) found that the percentage of nightly home range overlap was low (33.8 ± 25.5 %), inferring that over study durations of three weeks, as used here, hedgehogs are likely to show relatively homogenous use of their whole home range. Although not quantified, similar patterns were shown in the GPS data collected in this study. Therefore, habitat preferences within a home range are unlikely to have substantially altered the conclusions. Lastly, the road mortality probability model does not consider the role of the driver in modifying collision probabilities (Litvaitis and Tash, 2008). Driver perception and reaction times to animals in the road can differ by species (Kioko et al., 2015) and time of day (Hobday, 2010) and would be valuable to include in future models.

6.6 Future research directions

Examining the efficacy of road mortality mitigation is an ongoing challenge in the field of road ecology. The methodological approach used here could be used as a robust before-after study for mitigation sites to explore whether the ‘true’ risk of road mortality is lowered once mitigation has been implemented, correcting for changes in the environment such as weather and increases in traffic. Furthermore, appropriate mitigation of the barrier effect depends on the type of road avoidance behaviour exhibited by the species, for example of noise or vehicles (Jaeger et al., 2005). Empirical studies that differentiate between these types of avoidance for hedgehogs, such as by conducting phantom road experiments (Schwartz, 2020) or using study sites with variable noise, light and road widths, may improve interpretation of traffic effects on populations. This, in turn, would help to develop targeted mitigation. Likewise, using genetic approaches to explore the level of gene flow across roads would be a valuable source of information on the degree of road avoidance, providing no physical barriers were present. Previously, Braaker et al. (2017) and Carvalho et al. (2018) used genetic clustering methods and genetic kinship analysis, respectively, in addition to the collection of GPS-data to reveal some degree of fragmentation by roads. Adopting a study design focused on genetic and movement data has the potential to reveal both the extent and effects of road avoidance at the individual and population-level. This present study shows that certain elements of both the traffic flow theory and the risk-disturbance model explain hedgehog movements in relation to roads. Further research could explore which species also adhere to these models and what predicts these differences. In turn, a more universal model can be derived that combines theoretical understanding from the two models.

6.7 Conclusion

By focusing on a large number of individuals across a range of sites using fine-scale telemetry data, this is likely one of the most extensive and detailed study into animal interactions with roads to date. All types of road filter, but do not prevent, hedgehog road crossings. This is a result of road avoidance behaviour that differs by road type, time of year and sex. Overall, however, daily road crossing rates remained very high across the study sites. This suggests that roads are a non-trivial occurrence where road crossings are based on a perception of mortality risk against the benefits of reproduction and survival. To this end, hedgehogs appear to be adapting their behaviour marginally to make the risk acceptable. There are several theoretical and applied implications of this work. This includes support for the risk-disturbance hypothesis and identifying risk factors such as speed and the transition zones around residential areas that can form key mitigation targets. Using species-specific behavioural responses to risk will improve interpretation of traffic effects on populations in the future and lead understanding towards a more universal model based on generalities in animal behaviour around roads. As evidenced in this study, the fact that hedgehogs appear to minimise some of the mortality risks associated with living near road networks supports the notion that hedgehogs are an urban-adapter species. Whether the behavioural adaptations of hedgehogs can cope with the commensurate increase in traffic volumes in the future will be critical for ongoing population viability.

6.8 References

Auger-Méthé, M., Derocher, A. E., Plank, M. J., Codling, E. A., and Lewis, M.A. (2015). Differentiating the Lévy walk from a composite correlated random walk. *Methods in Ecology and Evolution*, *6*(10), 1179-1189. https://doi.org/10.1111/2041-210X.12412

Aresco, M. J. (2005). The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. *Biological Conservation*, *123*(1), 37–44. https://doi.org/10.1016/j.biocon.2004.10.006

Ascensão, F., Kindel, A., Teixeira, F. Z., Barrientos, R., D'Amico, M., Borda-de-Água, L., & Pereira, H. M. (2019). Beware that the lack of wildlife mortality records can mask a serious impact of linear infrastructures. *Global Ecology and Conservation*, *19*. https://doi.org/10.1016/j.gecco.2019.e00661

Bassani, M., & Mutani, G. (2012). Effects of environmental lighting conditions on operating speeds on Urban Arterials. *Transportation Research Record*, *2298*, 78–87. https://doi.org/10.3141/2298-09

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2014). Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.48550/arxiv.1406.5823

Bearman-Brown, L. E., Baker, P. J., Scott, D., Uzal, A., Evans, L., & Yarnell, R. W. (2020). Over-winter survival and nest site selection of the West-European hedgehog (*Erinaceus europaeus*) in arable dominated landscapes. *Animals*, *10*(9). https://doi.org/10.3390/ani10091449

Bencin, H. L., Prange, S., Rose, C., & Popescu, V. D. (2019). Roadkill and space use data predict vehicle-strike hotspots and mortality rates in a recovering bobcat (*Lynx rufus*) population. *Scientific Reports*, *9*(1). https://doi.org/10.1038/s41598-019-50931-5

Berger, A., Lozano, B., Barthel, L. M. F., & Schubert, N. (2020). Moving in the dark—evidence for an influence of artificial light at night on the movement behaviour of European hedgehogs (*Erinaceus europaeus*). *Animals*, *10*(8), 1–16. https://doi.org/10.3390/ANI10081306

Beyer, H. L. (2012). *Geospatial Modelling Environment* (Version 0.6.0.0). http://www.spatialecology.com/gme.

Beyer, H. L., Gurarie, E., Börger, L., Panzacchi, M., Basille, M., Herfindal, I., … Matthiopoulos, J. (2016). "You shall not pass!": Quantifying barrier permeability and proximity avoidance by animals. *Journal of Animal Ecology*, *85*(1), 43–53. https://doi.org/10.1111/1365-2656.12275

Bianchi, R. D. C., Olifiers, N., Gompper, M. E., & Mourão, G. (2016). Niche Partitioning among Mesocarnivores in a Brazilian Wetland. *PLOS ONE*, *11*(9), e0162893. https://doi.org/10.1371/JOURNAL.PONE.0162893

Braaker, S., Kormann, U., Bontadina, F., & Obrist, M. K. (2017). Prediction of genetic connectivity in urban ecosystems by combining detailed movement data, genetic data and multi-path modelling. *Landscape and Urban Planning*, *160*, 107–114. https://doi.org/10.1016/j.landurbplan.2016.12.011

Braaker, S., Moretti, M., Boesch, R., Ghazoul, J., Obrist, M. K., & Bontadina, F. (2014). Assessing habitat connectivity for ground-dwelling animals in an urban environment. *Ecological Applications*, *24*(7), 1583–1595. https://doi.org/10.1890/13-1088.1

Brehme, C. S., Tracey, J. A., Mcclenaghan, L. R., & Fisher, R. N. (2013). Permeability of roads to movement of scrubland lizards and small mammals. *Conservation Biology*, *27*(4), 710–720. https://doi.org/10.1111/COBI.12081

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference understanding AIC and BIC in model selection. *Sociological Methods and Research*, *33*(2), 261–304. https://doi.org/10.1177/0049124104268644

Carter, S., Macpherson, J., & Bright, P. (2010). *Response of hedgehogs to roads and traffic : a field experiment*. People's Trust for Endangered Species.

Carvalho, F., Lourenço, A., Carvalho, R., Alves, P. C., Mira, A., & Beja, P. (2018). The effects of a motorway on movement behaviour and gene flow in a forest carnivore: Joint evidence from road mortality, radio tracking and genetics. *Landscape and Urban Planning*, *178*, 217–227. https://doi.org/10.1016/j.landurbplan.2018.06.007

Ceia-Hasse, A., Navarro, L. M., Borda-de-Água, L., & Pereira, H. M. (2018). Population persistence in landscapes fragmented by roads: Disentangling isolation, mortality, and the effect of dispersal. *Ecological Modelling*, *375*, 45–53. https://doi.org/10.1016/j.ecolmodel.2018.01.021

Clark, B. K., Clark, B. S., Johnson, L. A., & Haynie, M. T. (2001). Influence of roads on movements of small mammals. *The Southwestern Naturalist*, *46*(3), 338-344. https://doi.org/10.2307/3672430

Clarke, G. P., White, P. C. L., & Harris, S. (1998). Effects of roads on badger *Meles meles* populations in south-west England. *Biological Conservation*, *86*(2), 117–124. https://doi.org/10.1016/S0006-3207(98)00018-4

Clevenger, A. P., Chruszcz, B., & Gunson, K. E. (2002). Spatial patterns and factors influencing small vertebrate fauna road-kill aggregations. *Biological Conservation*, *109*(1), 15–26. https://doi.org/10.1016/S0006-3207(02)00127-1

Clevenger, A. P., & Ford, A. T. (2010). Wildlife crossing structures, fencing, and other highway design considerations. In J. Beckmann, A. Clevenger, M. Huijser, & J. Hilty (Eds.) *Safe passages: highways, wildlife, and habitat connectivity.* Washington D.C : Island Press.

Cruzado, I., & Donnell, E. T. (2009). Evaluating effectiveness of dynamic speed display signs in transition zones of two-lane, rural highways in Pennsylvania. *Transportation Research Record*, *2122*(1), 1–8. https://doi.org/10.3141/2122-01

Cruzado, I., & Donnell, E. T. (2010). Factors affecting driver speed choice along two-lane rural highway transition zones. *Journal of Transportation Engineering, 136*(8). https://doi.org/10.1061/ASCETE.1943-5436.0000137

D'Amico, M., Périquet, S., Román, J., & Revilla, E. (2016). Road avoidance responses determine the impact of heterogeneous road networks at a regional scale. *Journal of Applied Ecology*, *53*(1), 181–190. https://doi.org/10.1111/1365-2664.12572

Da Silva, A. C. F, B., Fernando Saraiva De Menezes, J., & Rodrigues Oliveira Santos, L. G. (2022). Roadkill risk for capybaras in an urban environment. *Landscape and Urban Planning*, *222*. https://doi.org/10.1016/J.LANDURBPLAN.2022.104398

de Carvalho, N. C., Bordignon, M. O., & Shapiro, J. T. (2014). Fast and furious: A look at the death of animals on the highway MS-080, Southwestern Brazil. *Iheringia - Serie Zoologia*, *104*(1), 43–49. https://doi.org/10.1590/1678-4766201410414349

Department for Transport. (2018). *Road traffic forecasts 2018: moving Britain ahead.* Government of the United Kingdom. Retrieved from https://www.thenbs.com/PublicationIndex/documents/details?Pub=DFT&DocID=323980

Department for Transport. (2019). *Road traffic estimates in Great Britain: 2019*. Government of the United Kingdom. Retrieved from https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/916749/road-traffic-estimates-in-great-britain-2019.pdf.

Dexter, C. E., Appleby, R. G., Scott, J., Edgar, J. P., & Jones, D. N. (2018). Individuals matter: Predicting koala road crossing behaviour in south-east Queensland. *Australian Mammalogy*, *40*(1), 67–75. https://doi.org/10.1071/AM16043

Ditmer, M. A., Rettler, S. J., Fieberg, J. R., Iaizzo, P. A., Laske, T. G., Noyce, K. V., & Garshelis, D. L. (2018). American black bears perceive the risks of crossing roads. *Behavioral Ecology*, *29*(3), 667–675. https://doi.org/10.1093/beheco/ary020

Doncaster, P. C., Rondinini, C., & Johnson, P. C. D. (2001). Field test for environmental correlates of dispersal in hedgehogs *Erinaceus europaeus*. *Journal of Animal Ecology*, *70*(1), 33–46. https://doi.org/10.1046/j.1365-2656.2001.00471.x

Dowding, C. V., Harris, S., Poulton, S., & Baker, P. J. (2010). Nocturnal ranging behaviour of urban hedgehogs, *Erinaceus europaeus*, in relation to risk and reward. *Animal Behaviour*, *80*(1), 13–21. https://doi.org/10.1016/j.anbehav.2010.04.007

Duffett, D., D'Amico, M., Mulero-Pázmány, M., & González-Suárez, M. (2020). Species' traits as predictors of avoidance towards roads and traffic. *Ecological Indicators*, *115*. https://doi.org/10.1016/J.ECOLIND.2020.106402

ESRI. (2015). *ArcGIS Desktop: 10.3.1*. Environmental Systems Research Institute. USA : California

Fagan, W. F., & Calabrese, J. M. (2014). The correlated random walk and the rise of movement ecology. Bulletin of the Ecological Society of America, 95(3), 204–206. https://doi.org/10.1890/0012-9623-95.3.204

Fotios, S., Uttley, J., & Cheal, C. (2013). What is the right light level for residential roads? *Proceedings of the 7th Lux Pacific*, 6 – 8 May 2023 (pp. 256–259), Thailand : Bangkok.

Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, *6*(1). https://www.jstor.org/stable/pdf/26271862.pdf

Gagnon, J. W., Theimer, T. C., Dodd, N. L., Boe, S., & Schweinsburg, R. E. (2007). Traffic volume alters elk distribution and highway crossings in Arizona. *The Journal of Wildlife Management*, *71*(7), 2318–2323. https://doi.org/10.2193/2006-224

Gannon, W. L., & Sikes, R. S. (2007). Guidelines of the American society of mammologists for the use of wild mammals in research. *Journal of Mammalogy*, *88*(3), 809–823. https://doi.org/10.1644/06-mamm-f-185r1.1

Garrote, G., Fernández-López, J., López, G., Ruiz, G., & Simón, M. A. (2018). Prediction of Iberian lynx road–mortality in southern Spain: A new approach using the MaxEnt algorithm. *Animal Biodiversity and Conservation*, *41*(2), 217–225. https://doi.org/10.32800/abc.2018.41.0217

Gaston, K. J., & Bennie, J. (2014). Demographic effects of artificial night-time lighting on animal populations. *Environmental Reviews*, 22(4). https://doi.org/10.1139/er-2014-0005

Gazzard, A., Yarnell, R. W., Baker, P. (2022). Fine-scale habitat selection of a small mammalian urban adapter: the West European hedgehog (*Erinaceus europaeus*). *Mammalian Biology*, *102*(2), 387-403. https://doi.org/10.1007/s42991-022-00251-5

Girardet, X., Conruyt-Rogeon, G., & Foltête, J. C. (2015). Does regional landscape connectivity influence the location of roe deer roadkill hotspots? *European Journal of Wildlife Research*, *61*(5), 731–742. https://doi.org/10.1007/s10344-015-0950-4

Glasby, L., & Yarnell, R. W. (2013). Evaluation of the performance and accuracy of Global Positioning System bug transmitters deployed on a small mammal. *European Journal of Wildlife Research*, *59*(6), 915–919. https://doi.org/10.1007/s10344-013-0770-3

Grilo, C., Ascensão, F., Santos-Reis, M., & Bissonette, J. A. (2011). Do well-connected landscapes promote road-related mortality? *European Journal of Wildlife Research*, *57*(4), 707–716. https://doi.org/10.1007/s10344-010-0478-6

Grilo, C., Ferreira, F. Z., & Revilla, E. (2015). No evidence of a threshold in traffic volume affecting road-kill mortality at a large spatio-temporal scale. *Environmental Impact Assessment Review*, *55*, 54–58. https://doi.org/10.1016/j.eiar.2015.07.003

Haigh, A., O'Riordan, R. M., & Butler, F. (2014). Hedgehog *Erinaceus europaeus* mortality on Irish roads. *Wildlife Biology, 20*(3), 155–160. https://doi.org/10.2981/wlb.12126

Hels, T., & Buchwald, E. (2001). The effect of road kills on amphibian populations. *Biological Conservation*, *99*(3), 331–340. https://doi.org/10.1016/S0006-3207(00)00215-9

Hibbitts, T. J., Fitzgerald, L. A., Walkup, D. K., & Ryberg, W. A. (2017). Why didn't the lizard cross the road? Dunes sagebrush lizards exhibit road-avoidance behaviour. *Wildlife Research, 44*(3), 194–199. https://doi.org/10.1071/WR16184

Hobday, A. J. (2010). Night-time driver detection distances for Tasmanian fauna: informing speed limits to reduce roadkill. *Wildlife Research, 37*(4), 265–272. https://doi.org/10.1071/WR09180

Jacobson, S. L., Bliss-Ketchum, L. L., Rivera, C. E., & Smith, W. P. (2016). A behavior-based framework for assessing barrier effects to wildlife from vehicle traffic volume. *Ecosphere, 7*(4), e01345. https://doi.org/10.1002/ecs2.1345

Jaeger, J. A. G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., … Von Toschanowitz, K. T. (2005). Predicting when animal populations are at risk from roads: An interactive model of road avoidance behavior. *Ecological Modelling*, *185*(2–4), 329–348. https://doi.org/10.1016/j.ecolmodel.2004.12.015

Ji, S., Jiang, Z., Li, L., Li, C., Zhang, Y., Ren, S., … Chu, H. (2017). Impact of different road types on small mammals in Mt. Kalamaili Nature Reserve. *Transportation Research Part D: Transport and Environment, 50*, 223–233. https://doi.org/10.1016/J.TRD.2016.11.006

Jones, P. R. (2019). A note on detecting statistical outliers in psychophysical data. *Perception, & Psychophysics, 81*, 1189–1196. https://doi.org/10.3758/s13414-019-01726-3

Kammerle, J.-L., Brieger, F., Kroeschel, M., Hagen, R., Storch, I., Suchant, R., … Suchant, R. (2017). Temporal patterns in road crossing behaviour in roe deer (*Capreolus capreolus*) at sites with wildlife warning reflectors. *PLOS ONE, 12*(9), e0184761. https://doi.org/10.1371/journal.pone.0184761

Kang, W., Minor, E. S., Woo, D., Lee, D., & Park, C. R. (2016). Forest mammal roadkills as related to habitat connectivity in protected areas. *Biodiversity and Conservation*, *25*(13), 2673–2686. https://doi.org/10.1007/s10531-016-1194-7

Kautz, T. M., Fowler, N. L., Petroelje, T. R., Beyer, D. E., Svoboda, N. J., & Belant, J. L. (2021). Large carnivore response to human road use suggests a landscape of coexistence. *Global Ecology and Conservation, 30*, e01772. https://doi.org/10.1016/J.GECCO.2021.E01772

Kioko, J., Kiffner, C., Phillips, P., Patterson-Abrolat, C., & Katers, S. (2015). Driver knowledge and attitudes on animal vehicle collisions in northern Tanzania. *Tropical Conservation Science, 8*(2), 352–366. https://doi.org/10.1177/194008291500800206

Kelm, J., Lange, A., Schulz, B., Göttsche, M., Steffens, T., & Rech, H. (2015). How often does a strictly arboreal mammal voluntarily cross roads? New insights into the behaviour of the hazel dormouse in roadside habitats. *Folia Zoologica, 64*(4), 342-348. https://doi.org/10.25225/fozo.v64.i4.a9.2015

Laver, P. N., & Kelly, M. J. (2008). A critical review of home range studies. *Journal of Wildlife Management*, *72*(1), 290–298. https://doi.org/10.2193/2005-589

Litvaitis, J. A., & Tash, J. P. (2008). An approach toward understanding wildlife-vehicle collisions. *Environmental Management*, *42*(4), 688–697. https://doi.org/10.1007/s00267-008-9108-4

Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2004). *Resource Selection by Animals* (2nd ed.). Berlin : Springer Dordrecht.

Mayer, M., Fischer, M., Blaum, N., Sunde, P., Ullmann, W. (2023). Influence of roads on space use by European hares in different landscapes. *Landscape Ecology, 38*(1), 131-146. https://doi.org/10.1007/s10980-022-01552-3

McClure, C. J. W., Ware, H. E., Carlisle, J., Kaltenecker, G., & Barber, J. R. (2013). An experimental investigation into the effects of traffic noise on distributions of birds: Avoiding the phantom road. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1773). https://doi.org/10.1098/rspb.2013.2290

McCown, J. W., Kubilis, P., Eason, T. H., & Scheick, B. K. (2009). Effect of traffic volume on American black bears in central Florida, USA. *Ursus*, *20*(1), 39–46. https://doi.org/10.2192/08GR004R2.1

McGregor, R. L., Bender, D. J., & Fahrig, L. (2008). Do small mammals avoid roads because of the traffic? *Journal of Applied Ecology*, *45*, 117–123. https://doi.org/10.1111/j.1365-2664.2007.01403.x

Mikov, A. M., & Georgiev, D. G. (2018). On the road mortality of the Northern White-Breasted Hedgehog (*Erinaceus roumanicus* Barrett-Hamilton, 1900) in Bulgaria. *Ecologia Balkanica*, *10*(1), 19–23. http://web.uni-plovdiv.bg/mollov/EB/2018_vol10_iss1/19-23_eb.18102.pdf

Moore, L. J., Petrovan, S. O., Baker, P. J., Bates, A. J., Hicks, H. L., Perkins, S. E., & Yarnell, R. W. (2020). Impacts and potential mitigation of road mortality for hedgehogs in Europe. *Animals*, *10*(9), 1523. https://doi.org/10.3390/ani10091523

Morris, D. W., & Davidson, D. L. (2000). Optimally foraging mice match patch use with habitat differences in fitness. *Ecology, 81*(8), 2061–2066. https://doi.org/10.2307/177095

Mulder, J. L. (1999). The behaviour of hedgehogs on roads. *Lutra*, *42*. https://www.mulder-natuurlijk.nl/publicaties/wetenschappelijke%20publicaties/Hedgehog%20behaviour%20on%20roads.pdf

Neumann, W., Ericsson, G., Dettki, H., Bunnefeld, N., Keuler, N. S., Helmers, D. P., & Radeloff, V. C. (2012). Difference in spatiotemporal patterns of wildlife road-crossings and wildlife-vehicle collisions. *Biological Conservation*, *145*(1), 70–78. https://doi.org/10.1016/J.BIOCON.2011.10.011

Ordnance Survey. (2020). *EDINA Digimap*. University of Edinburgh. Retrieved from https://digimap.edina.ac.uk/os

Özcan, A. U., & Özkazanç, N. K. (2017). Identifying the hotspots of wildlife–vehicle collision on the Çankırı–kırıkkale highway during summer. *Turkish Journal of Zoology*, *41*(4), 722–730. https://doi.org/10.3906/zoo-1601-64

Paterson, J. E., Baxter-Gilbert, J., Beaudry, F., Carstairs, S., Chow-Fraser, P., Edge, C. B., … Davy, C. M. (2019). Road avoidance and its energetic consequences for reptiles. *Ecology and Evolution*, *9*(17), 9794–9803. https://doi.org/10.1002/ECE3.5515

Prokopenko, C. M., Boyce, M. S., & Avgar, T. (2017). Characterizing wildlife behavioural responses to roads using integrated step selection analysis. *Journal of Applied Ecology*, *54*(2), 470–479. https://doi.org/10.1111/1365-2664.12768

Proulx, C. L., Fortin, G., & Blouin-Demers, G. (2014). Blanding’s turtles (*Emydoidea blandingii*) avoid crossing unpaved and paved roads. *Journal of Herpetology*, *48*(2), 267–271. https://doi.org/10.1670/12-176

R Core Development Team. (2022). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing. https://www.r-project.org/

Rautio, A., Valtonen, A., & Kunnasranta, M. (2013). The effects of sex and season on home range in European hedgehogs at the northern edge of the species range. *Ann. Zool. Fennici*, *50*(1), 107–123. https://doi.org/10.5735/086.050.0110

Riber, A. B. (2006). Habitat use and behaviour of European hedgehog *Erinaceus europaeus* in a Danish rural area. *Acta Theriologica*, *51*(4), 363–371. https://doi.org/10.1007/BF03195183

Rico, A., Kindlmann, P., & Sedláček, F. (2007). Barrier effects of roads on movements of small mammals. *Folia Zool*, *56*(2), 1-12. https://www.natur.cuni.cz/fakulta/zivotni-prostredi/lide/zamestnanci/pavel-kindlmann/dokumenty/barrier-20effects-20of-20roads-20on-20movements-20of-20small-20mammals.pdf

Riginos, C., Fairbank, E., Hansen, E., Kolek, J., & Huijser, M. P. (2019). Effectiveness of night-time speed limit reduction in reducing wildlife-vehicle collisions (report no. FHWA-WY-1904F). *Wyoming Department of Transportation.* Retrieved from https://rosap.ntl.bts.gov/view/dot/42488%0Ahttps://trid.trb.org/view/1659707

Rodgers, A. R., & Robins, P. J. (2006). Moose detection distances on highways at night. *Alces*, *42*, 75–87. https://alcesjournal.org/index.php/alces/article/view/389

Rodriguez Recio, M., Mathieu, R., Latham, M. C., Latham, A. D. M., & Seddon, P. J. (2013). Quantifying fine-scale resource selection by introduced European hedgehogs (*Erinaceus europaeus*) in ecologically sensitive areas. *Biological Invasions*, *15*(8), 1807–1818. https://doi.org/10.1007/S10530-013-0410-6

Rondinini, C., & Doncaster, C. P. (2002). Roads as barriers to movement for hedgehogs. *Functional Ecology*, *16*(4), 504–509. https://doi.org/10.1046/j.1365-2435.2002.00651.x

Santos, R. A. L., Mota-Ferreira, M., Aguiar, L. M. S., & Ascensão, F. (2018). Predicting wildlife road-crossing probability from roadkill data using occupancy-detection models. *Science of the Total Environment*, *642*, 629–637. https://doi.org/10.1016/j.scitotenv.2018.06.107

Schaus-Calderón, J. S. (2021). *Responses of the West European hedgehog to urbanisation: impact on population dynamics, animal movement and habitat selection.* [PhD Thesis, Nottingham Trent University].

Schwab, A. C., & Zandbergen, P. A. (2011). Vehicle-related mortality and road crossing behavior of the Florida panther. *Applied Geography*, *31*(2), 859–870. https://doi.org/10.1016/j.apgeog.2010.10.015

Schwartz, A. L. W. (2020). *Roads and wildlife*. [PhD Thesis, Cardiff University].

Seiler, A. (2003). *The toll of the automobile: Wildlife and roads in Sweden.* [PhD Thesis, Swedish University of Agricultural Sciences].

Seiler, A. (2005). Predicting locations of moose-vehicle collisions in Sweden. *Journal of Applied Ecology*, *42*(2), 371–382. https://doi.org/10.1111/j.1365-2664.2005.01013.x

Serieys, L. E. K., Rogan, M. S., Matsushima, S. S., & Wilmers, C. C. (2021). Road-crossings, vegetative cover, land use and poisons interact to influence corridor effectiveness. *Biological Conservation*, *253*. https://doi.org/10.1016/j.biocon.2020.108930

Sfyridis, A., & Agnolucci, P. (2020). Annual average daily traffic estimation in England and Wales: An application of clustering and regression modelling. *Journal of Transport Geography*, *83*. https://doi.org/10.1016/j.jtrangeo.2020.102658

Tchabovsky, A. v, Krasnov, B., Khokhlova, I. S., & Shenbrot, G. I. (2001). The effect of vegetation cover on vigilance and foraging tactics in the fat sand rat *Psammomys obesus*. *Journal of Ethology*, *19*(2), 105–113. https://doi.org/10.1007/s101640170006

Teixeira, F. Z., Kindel, A., Hartz, S. M., Mitchell, S., & Fahrig, L. (2017). When road-kill hotspots do not indicate the best sites for road-kill mitigation. *Journal of Applied Ecology*, *54*(5), 1544–1551. https://doi.org/10.1111/1365-2664.12870

Turner, J., Freeman, R., & Carbone, C. (2021). Using citizen science to understand and map habitat suitability for a synurbic mammal in an urban landscape: the hedgehog *Erinaceus europaeus*. *Mammal Review*, *52*(2), 291-303. https://doi.org/10.1111/mam.12278

U.S. Geological Survey. (2022). *EarthExplorer*. https://earthexplorer.usgs.gov/

Valero, E., Picos, J., Lagos, L., & Álvarez, X. (2015). Road and traffic factors correlated to wildlife–vehicle collisions in Galicia (Spain). *Wildlife Research*, *42*(1), 25. https://doi.org/10.1071/WR14060

van der Ree, R., Cesarini, S., Sunnucks, P., Moore, J. L., & Taylor, A. (2010). Large gaps in canopy reduce road crossing by a gliding mammal. *Ecology and Society*, *15*(4). https://doi.org/10.5751/ES-03759-150435

van Langevelde, F., & Jaarsma, C. F. (1995). Habitat fragmentation, the role of minor rural roads and their traversability. In C. Kanters et al. (Eds.) Proceedings of Habitat fragmentation, infrastructure and the role of ecological engineering (pp.171-182). The Netherlands : Hague

van Langevelde, F., & Jaarsma, C. F. (2009). Modeling the effect of traffic calming on local animal population persistence. *Ecology and Society*, *14*(2). https://doi.org/10.5751/ES-03061-140239

Wembridge, D. E., Newman, M. R., Bright, P. W., & Morris, P. A. (2016). An estimate of the annual number of hedgehog (*Erinaceus europaeus*) road casualties in Great Britain. *Mammal Communications*, *2*, 8–14. https://www.mammal.org.uk/wp-content/uploads/2016/04/MC1605_HedgehogsRoads_Wembridge.pdf

Williams, B. M. (2018). *An investigation into the factors influencing hedgehog (Erinaceus europaeus) occupancy throughout rural and urban Britain*. (PhD Thesis, University of Reading].

Williams, B. M., Baker, P. J., Thomas, E., Wilson, G., Judge, J., & Yarnell, R. W. (2018). Reduced occupancy of hedgehogs (*Erinaceus europaeus*) in rural England and Wales: The influence of habitat and an asymmetric intra-guild predator. *Scientific Reports*, *8*(1), 17–20. https://doi.org/10.1038/s41598-018-30130-4

Wright, P. G. R., Coomber, F. G., Bellamy, C. C., Perkins, S. E., & Mathews, F. (2020). Predicting hedgehog mortality risks on British roads using habitat suitability modelling. *PeerJ*, 7: e8154. https://doi.org/10.7717/peerj.8154

Zaman, M., Rakha, B. A., Wrensford, K., Zhu, M., Fan, L., & Jiang, G. (2020). Occurrence of conspecific in the neighboring space influence on flight initiation distance in cape hare *Lepus capensis* under human stimuli. *Open Journal of Ecology*, *10*(06), 380–395. https://doi.org/10.4236/OJE.2020.106024

Zeller, K. A., Wattles, D. W., & DeStefano, S. (2018). Incorporating road crossing data into vehicle collision risk models for moose (*Alces americanus*) in Massachusetts, USA. *Environmental Management*, *62*(3), 518–528. https://doi.org/10.1007/s00267-018-1058-x

Zhang, D., & Lin, X. (2008). Variance component testing in Generalized Linear Mixed Models for longitudinal/clustered data and other related topics. In D. B. Dunson (Ed.) *Random Effect and Latent Variable Model Selection (pp* 19–36). New York : Springer New York

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14. https://doi.org/10.1111/J.2041-210X.2009.00001.X

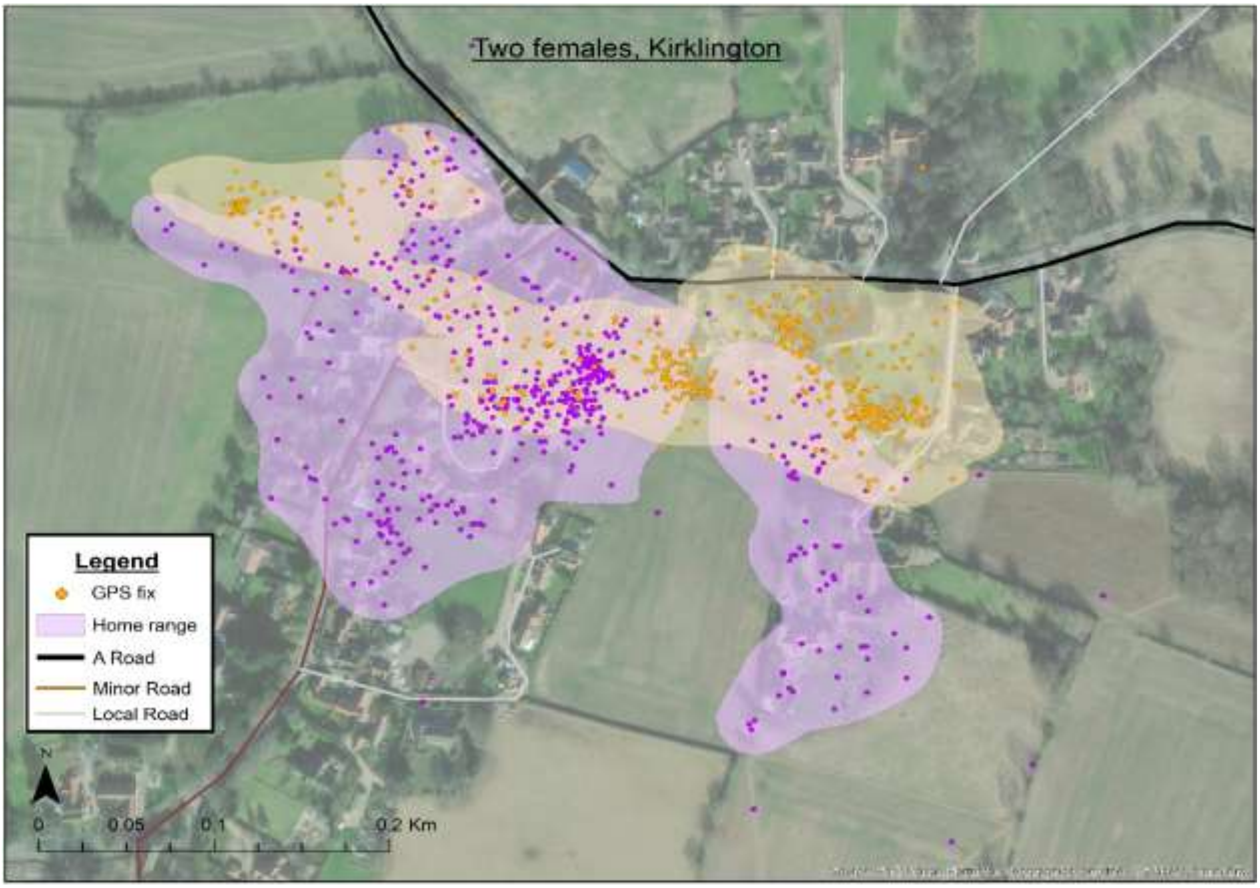
Appendices XII - XIII

Appendix XII: Chi-squared (X^2) results comparing the percentage of total road crossings and home range to the percentage of each road type within the study sites.

	Local road		**Minor road**		**Intermediate road**		**Main road**	
	X^2 statistic	p-value	X^2 statistic	p-value	X^2 statistic	p-value	X^2 statistic	p-value
Total road crossings	1.129	0.288	0.050	0.823	0.788	0.375	10.707	0.001
Home ranges	17.867	<0.001	206.255	<0.001	110.539	<0.001	1.961	0.161

Appendix XIII: GPS fixes and home ranges of nine GPS tracked west European hedgehogs at several sites between June 2020 and October 2021, inclusive.

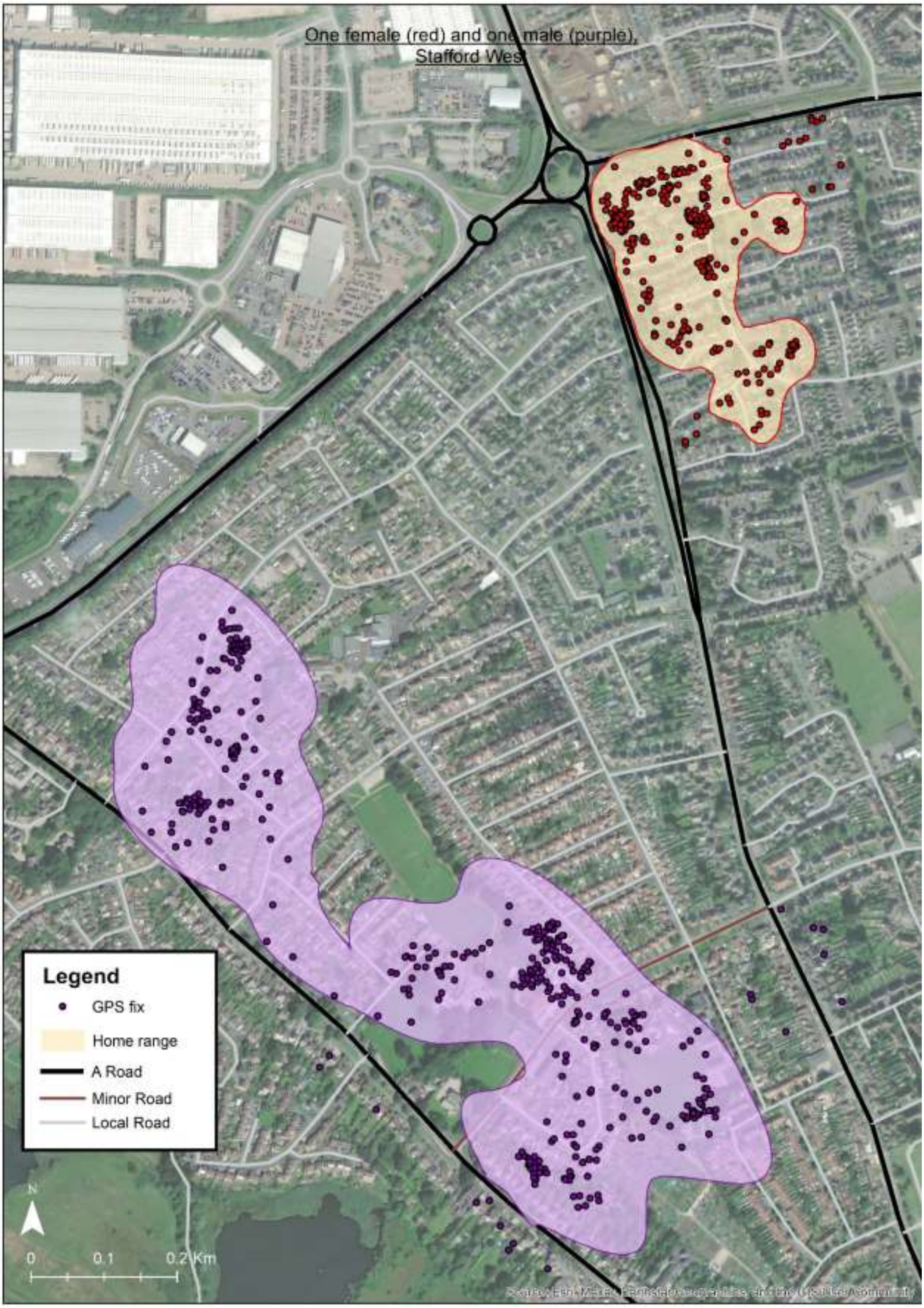
Colours represent GPS fixes recorded by different individuals. Home ranges represent 95% Kernel Density Estimates encompassing all GPS fixes recorded during the tracking period.


Two females, Kirklington
Legend
GPS fix
Home range
A Road
Minor Road
Local Road
N
0
0.05
0.1
0.2 Km


Two females, Southwell
Legend
GPS fix
Home range
B Road
Minor Road
Local Road
N
0
0.05
0.1
0.2 Km


Male, York
Legend
GPS fix
Home range
A Road
Minor road
Local road
N
0
0.05
0.1
0.2 Km


Female, Peterborough North
Legend
GPS fix
Home range
Local road
N
0
0.05
0.1
0.2 Km


One female (red) and one male (purple), Stafford West
Legend
● GPS fix
Home range
A Road
Minor Road
Local Road
N
0
0.1
0.2 Km

CHAPTER 7: General Discussion and Conclusions

7.1 Synopsis

Linear transportation features are globally pervasive and 47% of the Earth's terrestrial surface is currently less than 5 km from a road (Ibisch et al., 2016). Roads are responsible for the advancement of economic and human well-being yet are thought to threaten the viability of many wild populations around the world. Despite widespread concern, robust assessments of road impacts on wildlife at the population-level are lacking and appropriate mitigation remains difficult. Therefore, studies that investigate the multi-faceted impacts of roads, and any links between them, are necessary to inform effective conservation management.

Using novel study designs and contemporary analyses, this thesis aimed to optimise the design of road ecology studies and, using hedgehogs as a case study, to improve understanding of how the survival and movements of individuals are affected by roads. Collectively, these findings underline if, where, and what type of mitigation should be used to reduce road mortality. Using a systematic review protocol, Chapter 2 found that road mortality impacts showed considerable species and intra-specific differences at the local population-level and that female-biased mortality may destabilise population dynamics. Importantly, the demographic effects of road mortality are not limited to the immediate location or time period of the wildlife-vehicle collisions and future study designs that combine methods are best suited to detect demographic changes. Chapter 3 was the first study to quantify biases in road mortality rate estimation for different species in Great Britain, advocating for tailored survey frequency and the application of correction factors in future studies. This chapter also used spatio-temporal modelling based on fine-scale data to reveal that road mortality tracks key life history events, such as breeding and dispersal. Moreover, geographic hotspots were driven by a species-specific combination of urbanity, road design, and traffic volume. Chapter 4 summarised the known and potential consequences of road mortality on the five hedgehog species (*Erinaceus* spp.) in Europe, revealing several knowledge gaps that limit appropriate conservation action. Using west European hedgehog (*Erinaceus europaeus*) in Great Britain as a case study, Chapter 5 was the most comprehensive study on population-level effects of hedgehog road mortality to date. The study highlighted that larger populations are more likely to compensate for road mortality due to greater reproductive and/or survival rates, compared to small populations that are already more susceptible to Allee effects. Finally, Chapter 6 identified that hedgehog road avoidance is greater in females, towards large roads, and later in the year for males. These movements were ground-truthed in the ‘true’ risk of road mortality, which was predicted by human driving behaviours such as speed, particularly on the outskirts of residential areas. This final section, Chapter 7, aims to collate findings from this thesis to progress the overall understanding of population viability around roads. Based on this knowledge, this chapter will discuss the conservation and management implications of the work and suggest avenues for future research.

7.2 Gathering baseline road mortality data

The road mortality records of 49 wild vertebrate species collected in Chapter 3 bolsters previous claims of Hill et al. (2020) that a species’ vulnerability to collision is irrespective of body size, taxonomic group, or conservation status. This is of particular importance for rare and threatened species that (sometimes naturally) have low population densities, such as red squirrels (*Sciurus vulgaris*) and the greater mouse-eared bat (*Myotis myotis*), that find additional mortality difficult to cope with (Mathews et al., 2018). On the other hand, knowledge of mortality rates of some species, such as invasive species, may help understand the spread, appropriate management, and ecosystem impacts of these species at a low cost. For example, 90% of the roadkill of the invasive common racoon dog (*Nyctereutes procyonoides*) in Poland consisted of dispersing juveniles, indicating a healthy population capable of spreading quickly (Kowalczyk et al., 2009). Moreover, based on the relationship between road mortality and roadside population abundance (Bright, George, & Balmforth, 2005; George et al., 2011), road mortality rates can be used to track current and past population trends when corrected for influential factors such as carcass detection and persistence. An example of the value of conducting posterior corrections to past roadkill data is shown in Table 7.1 for west European hedgehogs in Great Britain, allowing comparisons of road mortality rates on a like-to-like basis as survey frequency, length and timing has been accounted for. Two models were developed and used based on the nature of the data collection (i.e., for repeated surveys of the same road section and for unsystematic surveys, often based on citizen science; see Appendix XIV for derivation of these equations). The steady decline in hedgehog road mortality counts between 1959 and 2019 may reflect the nationwide decline of hedgehogs in Great Britain (Wilson and Wembridge, 2018). The possible increase in road mortality since 2019 may reflect the stabilisation or increase in urban hedgehog numbers (Wembridge et al., 2022). However, this explanation is dependent on the accuracy of previous road surveys. Hodson (1966), for example, surveyed a short 2.4 km road section, although over a relatively long period, that is unlikely to be representative of Great Britain. As such, the robustness of previous road mortality rate estimates when extrapolated should be considered carefully. Improving the robustness of historic nationwide hedgehog population size estimates, as a means to provide demographic context, would help to refine confidence in these nationwide road mortality estimations.

Table 7.1: Nationwide road mortality estimates for Great Britain based on the total counts of hedgehog casualties from the study (n), distances surveyed in km (l), number of carcasses per km per day (λ), and the standardised road mortality rate (s) for several roadkill surveys since 1952.

Data	**Survey period**	**Survey months**	**Model**	**Survey interval**	n	l **(km)**	**Casualties per km per day (λ)**	**Standardised casualties per km per day (s)‡**	**Standardised casualties per km per year**	**Standardised casualties per year in Great Britain**
This study*	2020-21	12 months/ year	2	2	86	18,749	0.0035	0.0035	0.7539	300,651
Mammals on Roads (MoR**;** Wembridge et al., 2022)*****	2020-21	3 months/ year†	1	n/a	51	2,971	0.0046	0.0027	0.5753	229,412
MoR; Wembridge et al., 2022	2015-19	3 months/ year†	1	n/a	132	1,7765	0.0020	0.0012	0.2490	99,302
Bright et al. (2005)	2001-04	3 months/ year†	1	n/a	7,009	484,153	0.0039	0.0023	0.4852	193,474
Morris (1993)	1990-93	3 months/ year†	1	n/a	4,625	21,4435	0.0058	0.0034	0.7228	288,247
Hodson (1966)	1959-60	12 months/ year	2	1	15	2,339	0.0071	0.0071	1.5242	607,852
Davies (1957)	1952-54	12 months/ year	1	n/a	112	23,384	0.0013	0.0013	0.2738	109,176

*These data were collected during the national lockdown when traffic volumes were 49% lower than the previous year (Department for Transport, 2022b). †July – September ‡ Estimates of λ from Morris, Bright and MoR were based on surveys undertaken over three of the eight months that hedgehogs are, on average, active for in a year. Therefore, standard lambda (s) was multiplied by 214 (representing 214 days, eight months) of active season to account for the relatively inactive hibernation period of hedgehogs over winter in Britain. This is the same correction applied in Equation 1.

Recording the sex- and age-specific rates, locations, and timing of road mortality, as shown in Chapter 3, provides a broad understanding of the extent of road impacts (Grilo et al., 2009; González-Calderón, 2020). These patterns appear highly dependent on the species, with road avoidance behaviour likely playing a large role in determining susceptibility (Jaeger et al., 2005). As conservation resources remain limited yet road networks continue to expand, targeted action for only the most at-risk populations is placed at a premium. To achieve cost-effective and tailored action, research must focus on understanding the behavioural ecology of animal presence and movements around roads (Roedenbeck et al., 2007). Using hedgehogs as a case study through Chapters 4 – 6, this thesis highlights the value of collecting movement and demographic data for accurately interpreting road mortality impacts.

7.3 The barrier effect; a product of road avoidance, road mortality, or both?

This thesis found substantial sex differences in several aspects of the barrier effect and therefore, road impacts may be more nuanced than previously recognised. Compared to their female conspecifics, male hedgehogs studied in Chapter 5 and 6 had larger home ranges, showed lower avoidance of roads, suffered more road mortality, and had lower overall survival rates. In this way, males appear to be the ‘risk-takers’ within the population, fitting the polygamous lifestyle of the species (Dowding et al., 2010). As such, males are more affected by hedgehog-vehicle collisions than fragmentation from the barrier effect of roads. Conversely, this thesis highlights that females may be more affected by fragmentation effects due to high road avoidance. This may present challenges to long-term demographic rescue of small populations. That is, male movement can rescue a population from genetic isolation, but a viable population requires breeding females for new births, yet females appear to be less prone to dispersal. As such, the re-colonisation or strengthening of a stable breeding cohort in sink populations, as well as the colonisation of unoccupied habitat, may be limited. It should be noted that females who were potentially pregnant at the time of the spotlight surveys were not GPS tracked for ethical reasons and so post-reproduction dispersal in breeding females may have been missed. Future studies that can genotype several neighbouring populations over time from hair samples, for example, could be a less invasive, although relatively expensive, method for tracking movements of females and offspring between populations (Balkenhol & Waits, 2009). In addition, personality may play a role in survival probability near roads. For example, Bremner-Harrison et al. (2004) reported that bolder captive-bred swift foxes (*Vulpes velox*) had a lower likelihood of survival post-release. Of note is that at least two of five swift foxes that died during the study were killed in a wildlife-vehicle collision. By contrast, personality was not found to affect the survival of released hedgehogs in Denmark (Rasmussen et al., 2021), although personality was tested in an artificial environment (i.e., in an enclosure) and whether personality has an effect to more familiar, natural environments such as roadsides remains untested.

Despite the documented road avoidance behaviour of 87.7% of individuals tracked in this study, hedgehogs were observed to cross roads an average of 4.36 times (±2.52 SD) per night. Furthermore, hedgehogs appeared to adjust both their nightly and seasonal movement patterns based on a perception of (road) mortality risk against the benefits of reproduction and survival. For example, hedgehogs made more crossings after midnight, when traffic and human activity was lower, compared to before midnight. To this end, hedgehogs appear to be adapting their behaviour marginally to make the mortality risks acceptable at a population level (Dowding et al., 2010). Consequently, the observed rate of road crossings is likely to prevent complete population fragmentation unless the population is bounded by roads with physical barriers such as concrete central medians.

7.4 A reliance on rescue effects between local hedgehog populations

Combining movement, road mortality, and demographic data across four local hedgehog populations, this thesis reinforces the notion that (local) populations do not respond equally to wildlife-vehicle collisions (Schwab and Zandbergen, 2011; Ceia-Hasse et al., 2017). Little or no compensatory mechanisms for road mortality were identified in the two smaller populations of Kirklington and Halam, yet their population densities remained relatively stable between 2020 and 2021. Therefore, it seems likely that these populations are rescued by immigration. In the case of Halam, the hedgehog population may be acting as a demographic sink within a wider meta-population structure. This is because the population persists with a very small number of individuals (<4 hedgehogs) whilst experiencing a proportional loss of 33% from road mortality annually. A similar conclusion was reached by Roger, Bino and Ramp (2012), who reported that annual common wombat (*Vombatus ursinus*) road fatalities within an Australian protected area matched the total population estimate. The authors considered immigration to be the only explanation for the population's continued existence.

The potential for demographic recovery is supported by the number of new entrants (i.e., immigrants) in each population throughout the roadkill surveys and between survey sessions. As shown in Chapter 5, 26% (n = 11) of roadkilled animals found within the four populations were unmarked, of which 80% (n = 9) were male. Whilst the relatively high number of unmarked roadkill may be a function of the roadkill surveys starting one month before hedgehog marking took place, roadkill within the four study sites during the first month of roadkill surveys was relatively low (n = 3). Moreover, 60 - 83% of the captures during the spotlight surveys were new individuals (i.e., they had not been found in a previous spotlight survey session either six or 12 months prior). This movement of transient individuals was also recorded by Reeve (1981), although the extent of site fidelity appears to be dependent on habitat quality (Pettett et al., 2020). Confidence can be held that the majority of the new entrants were previously unmarked individuals, rather than previously caught individuals whose marks fell off. This is for two reasons: firstly, the longevity of heat-shrink tubes was longer than the study's duration (Chapter 5; Appendix IX), and secondly, the spotlight surveys found 73 - 90% of the population, inferring that the surveys were thorough and robust. Evidence for transient (male) individuals is further provided by the exploratory movements out of the study sites by two males in May 2021, consisting of one male from Halam that made two exploratory trips two days apart, and one male from Kirklington. The routes travelled by these individuals out of the study site were between 3.99 and 6.67 km, with Euclidean distances to the furthest point travelled between 1.53 and 2.52 km (Figure 7.1). These distances are greater than those between the closest neighbouring populations in this study, indicating the possibility of movements between high-quality habitat patches (e.g., built areas, gardens) across the matrix (e.g., arable dominated farmland). Similarly, in a rural landscape in Oxfordshire, Doncaster, Rondinini and Johnson (2001) found that hedgehogs could travel distances of up to 3.8 km from a release point in exploratory movements and that, at small scales, no population was completely isolated from its neighbours.

A relatively high turnover of (both male *and* female) transient individuals may bolster the breeding cohorts of local populations that would otherwise be subject to the Allee effect, i.e., reduced per capita growth rate at low population density (Jaeger and Fahrig, 2001). This safeguards smaller populations from an increased likelihood of both inbreeding effects and local extinction, although the frequency and direction of inter-patch movements warrants further research. In many populations including hedgehogs (Doncaster et al., 2001; Pettett et al., 2020), those in areas of lower habitat quality and resource availability (in this study, Kirklington and Halam) show lower site fidelity, less stability, longer and faster dispersal distances (summarised by Prange, Gehrt, & Wiggers, 2003). A greater understanding of how transient individuals move between low- and high-quality habitat (i.e., either as part of an ideal free distribution population or more traditional source-sink dynamics) could further direct conservation strategies at the landscape-scale. In this current study, it is likely a combination of Allee effects, free distribution and source-sink dynamics is at play in this studied hedgehog metapopulation (Altermatt and Ebert, 2010).

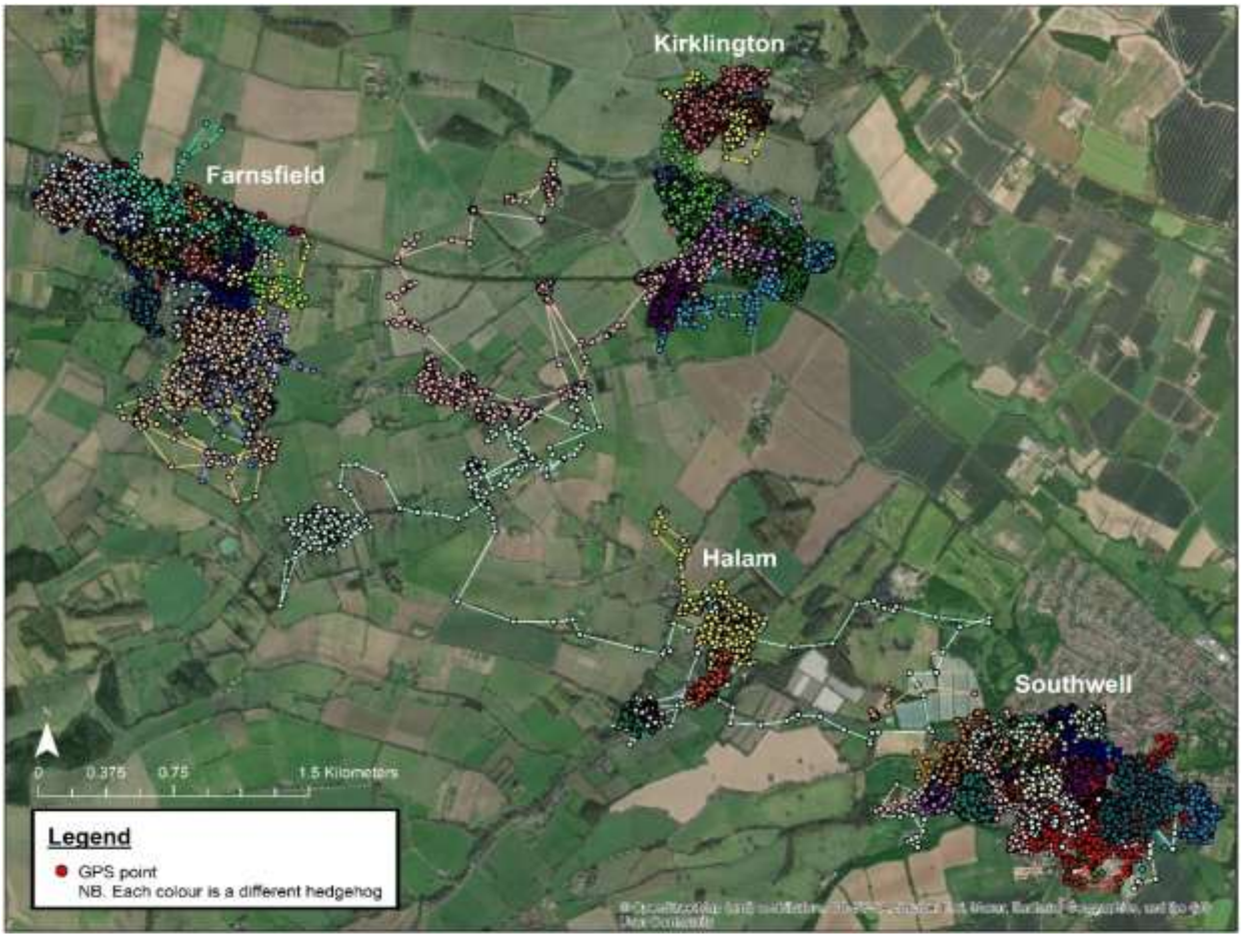


Figure 7.1: GPS points from all hedgehogs (*N* = 82) tracked in the four study sites in Nottinghamshire between June 2020 and October 2021, inclusive. Farnsfield, n = 37; Southwell, n = 27; Kirklington, n = 13; Halam, n = 5.

7.5 The role of roads in the decline of hedgehogs in Great Britain

Previous models on several species (such as red fox *Vulpes vulpes*, European rabbit *Oryctolagus cuniculus*, and round-tailed muskrat *Neofiber alleni*) have suggested that only a very high proportion of individual loss (> 0.90) will lead to species extinction (Grilo et al., 2021). Elsewhere, Seiler (2003) estimated that 25% loss of a badger's (*Meles meles*) breeding population on roads is unsustainable, whilst Ruiz-Capillas, Mata and Malo (2015) suggests that an annual loss of 6 – 10% of a roadside wood mouse (*Apodemus sylvaticus*) population may cause local extinctions on road verges. Based on the results from Chapter 3 and the recent estimate of 879,000 hedgehogs in Great

Britain (Mathews et al., 2018), approximately 33-34% of the British hedgehog population is killed on roads annually. However, it should be noted that both the nationwide population estimate and road mortality estimate have high levels of uncertainty and should be interpreted with caution. Larger local populations in high quality habitat (i.e., peri-urban areas for hedgehogs) may be able to compensate for this loss and so experience few or no negative effects from road mortality (Prange, et al., 2003; Hubert et al., 2011). In this way, urban hedgehog populations may be resilient to road mortality and potential historic population declines – and more recent stabilisation – may be related to non-road factors, such as community-level garden connectivity and/or supplementary feeding (Wembridge et al., 2016).

On the other hand, this thesis suggests that roads have contributed to (but not solely caused) the decline of British hedgehogs in rural areas. Even a low but uncompensated mortality rate may reduce population growth by decreasing the breeding population and increasing the population’s susceptibility to environmental and demographic stochasticity, such as extreme drought and altered hibernation patterns due to climate change (Carvalho and Mira, 2011; Roger et al., 2011). From a population connectivity perspective, road mortality may also be removing the excess individuals from larger, thriving populations (i.e., where births outnumber deaths) that would otherwise rescue smaller populations. However, as discussed in Section 7.4, these effects are likely to be dependent on wider population connectivity and context-specific conditions in Great Britain. For example, local populations are likely to substantially differ in the number of source populations from which they receive immigrants depending on the surrounding landscape. For example, Doncaster et al. (2001) suspected that distances of >10 km severely limit dispersal between nearest neighbour hedgehog populations. Likewise, the east of England has a high proportion of arable land, a habitat type that hedgehogs are reported to avoid (Doncaster et al., 2001; Schaus-Calderón, 2021). Moreover, differences in traffic volume between regions in Great Britain are up to 4.1-fold, with greatest traffic in the south-east and lowest in the northeast of England (Department for Transport, 2022a). The extent that geographical distances and habitat matrix between local populations determine the potential for rescue effects, and so how important this is for the persistence of local populations, would be a insightful focus for future research.

7.6 Wider implications of the research

7.6.1 Optimising road ecology research

Currently, two key trade-offs exist in road ecology research. High financial input and time are set against (1) road survey frequency and hence the accurate detection of carcasses, and (2) collecting comprehensive population data to act as empirical context to road mortality counts. The methods and subsequent findings within this thesis offer several approaches to reduce this trade-off and optimise logistical capacity of future research. Firstly, explicitly considering the characteristics of the focal taxa when determining road survey frequency enables sufficient carcass detection whilst minimising biases and costs. Specifically, the need to correct for carcass persistence due to varying traffic volume and scavenging activity also applies to similar landscapes in Great Britain and, albeit with more caution, to Europe (Santos et al., 2016). Secondly, road ecologists and planners must consider that low rates of road mortality do not necessarily represent low impact from road mortality. Instead, targeted evaluations of one or more of the biological parameters identified and adopted in Chapter 2 and 5, respectively, are critical to obtaining data on the site-specific and cumulative impacts of roadkill at the least cost. In fact, evaluating the ecological effects of roads is considered to be the first step in transparent and effective decision-making frameworks, such as the Evidence to Decision tool developed by Christie et al. (2022). Standardised approaches can also produce studies that are comparable across different study systems and ecological contexts to further benefit cost-efficiency of road ecology research. These take-home messages are not only relevant to roads but can also be applied to mortality from other linear infrastructure such as railways and powerlines.

Chapter 3 and Chapter 6 provide a rare opportunity to compare two analysis methods used to identify mitigation locations, i.e., ‘roadkill hotspots’ and ‘high-risk roadkill areas’. Although these terms are used interchangeably in the literature, slight differences in the results from the analyses suggest that a road of high risk does not necessarily correlate with a large amount of road mortality. For example, Chapter 6 identified that roads with high traffic volume have a significantly greater risk per road crossing for hedgehogs than quiet roads. Conversely, traffic volume alone was ranked in the 5th, 10th and 11th (out of 11) models that analysed roadkill records, all of which were between 4.89 and 13.86 AIC from the top model. Instead, road verges and gardens were consistently included in both models that were < 2 AIC of the top model. To this end, areas of preferential crossings by hedgehogs and areas of roadkill hotspots are not necessarily the same. Hotspot analysis using roadkill data alone can therefore over-predict risk (in this case, the risk near road verges and gardens) as it does not consider where animals attempt or avoid crossing. The identification of both roadkill hotspots and roads with high roadkill risk have value in mitigating the impacts of roads. However, road ecologists and planners must explicitly consider the differences in the potential conclusions from data analyses when designing research objectives and mitigation options.

Chapters 3 presents a regional case study on the spatio-temporal patterns of road mortality. The patterns from the high-intensity surveys in this thesis draw several parallels to those determined by citizen science, such as that road mortality tracks key life history events (Raymond et al., 2021). This suggests that concerns over the spatial and temporal clustering of citizen science records to areas and times of human habituation may not apply to roadkill data. In fact, citizen science road mortality records may be necessary for investigations into the collision patterns for rare or sparsely distributed species. For these species, fine-scale road surveys, as undertaken in this thesis, would need to be particularly long-term, perhaps impractically so, to obtain sample sizes that are large enough for analysis (Périquet et al., 2018). For example, the spatial and temporal patterns could only be analysed for 8% and 47% of recorded species in Chapter 3, respectively, due to small sample sizes. This is because it is recommended to have more than five records per variable included in a model for robust statistical inference (Vittinghoff & McCulloch, 2007). It is important to note, however, that citizen science remains limited to well-known, charismatic species (Balčiauskas et al., 2020). Moreover, exploring road mortality beyond broad spatial and temporal patterns, such as long-term demographic impacts, will require intensive and repeated road surveys conducted at the local scale and ideally by a trained specialist.

7.6.2 Hedgehog conservation near roads

Within a conservation perspective, the objectives for reducing road mortality can be varied. For example, mitigation can be targeted to areas of additive road mortality or vulnerable cohorts of the population (e.g., females; Chapter 2 and 5) to stabilise population dynamics, focused on roadkill hotspots (Chapter 3) to reduce overall mortality levels, or directed to road segments with high mortality risk (Chapter 6) to bolster population connectivity. In addition, the design of road networks and mitigation is often influenced by priorities of human safety and travel efficiency as per both National Highway’s Strategic Road Network priorities (National Highways, 2017) and public demand (Transport Focus, 2021). As such, the recommendations below are intended to be holistic by considering socioeconomic factors such as vehicle and pedestrian travel efficiency (van Strien & Grêt-Regamey, 2016) and the cost-effectiveness of strategies for reduced ecological impact (Helldin & Petrovan, 2019).

Chapter 6 determined that, in contrast to existing understanding, hedgehogs do not avoid the road surface itself but another element of the road zone, such as vehicles, noise or vibrations. This suggests that road avoidance behaviour is short-term and acute which, in turn, affords a greater number of mitigation options to cater for species-specific behavioural traits (Jaeger et al., 2005). It is also clear from Chapter 5 that different mitigation strategies are needed for urban populations that appear stable in the face of road mortality and for rural populations that are particularly susceptible to the negative effects. It is recommended that road mitigation takes a multi-faceted approach to reducing road mortality in smaller populations to benefit the mortality:recruitment ratio and increase the likelihood that these populations become self-sustaining (i.e., these populations change from being sinks to sources). Moreover, reducing road mortality in larger populations and improving landscape connectivity could reinforce the dispersal of transient individuals into, and so also protecting, smaller (more rural) populations. The latter would benefit from agri-environmental schemes that provide conduits of movement through habitat edges such as strips of grassland and hedgerows (Moorhouse et al., 2014; Yarnell and Pettett, 2020).

McClure and Ament (2014) provided a conceptual framework for mitigating road mortality based on the influence of a road segment for population fragmentation and roadkill risk. Applying this conceptual framework to the road crossing and road mortality data in this thesis, mitigation should particularly target roads with high traffic volumes as these areas inhibit connectivity (i.e., high road avoidance) *and* pose high road mortality risk per crossing. It is recommended that measures to combat main roads need only take place when small (more rural) populations are intersected by main roads. The standard approach may be to construct a fence along these roads as very few crossing attempts are made and even fewer are successful (i.e., a fence would be unlikely to lead to a net increase in fragmentation). For example, fencing alone reduced ungulate-vehicle collisions by 80% in Alberta, Canada (Clevenger et al., 2001). However, as mentioned in Section 7.4, migration into small populations is likely to be key to demographic rescue and their long-term persistence. As such, it is recommended that traffic calming measures (see below) or a combination of tunnels and fences are adopted to reduced road mortality in small populations. Hedgehogs have been shown to use tunnels infrequently (Helldin and Petrovan, 2019). However, research on their effectiveness remains limited and unpublished data by L. Moore indicates that rates of tunnel use remain low within local hedgehog populations.

Success in reducing road mortality is likely dependent on changing driver behaviour. Whilst the installation of static road signs that warn of animal presence is the most common strategy to reduce wildlife-vehicle collisions, growing evidence indicates that road signs may be inadequate to achieve significant reductions in road mortality (Dique et al., 2003; Paterson et al., 2019; Riginos et al., 2019). However, enhanced road signs that are accompanied by detection systems that flash when animals are detected or are likely to be present on the roadside show greater success than static signs (Grace et al., 2017; Riginos et al., 2018; Gagnon et al., 2019). Such road signs could be installed for hedgehogs during high-risk periods, such as late summer and autumn, and may be particularly effective for hedgehogs as a charismatic species. However, their effectiveness warrants further research, particularly into whether efficacy is influenced by road conditions and driver familiarisation (i.e., whether the driver is a local resident; Huijser & McGowen, 2010).

Vehicle speed was found to increase the probability of hedgehog road mortality in Chapter 6. As such, the reduction in speed around small populations presents a clear target for road mortality mitigation, with additional benefits of improved human safety (Goniewicz et al., 2016). The transition zone between rural and residential areas present localised areas for measures to improve compliance with speed limits, enabling more effective and inexpensive action than widespread speed reductions. However, the effectiveness of speed limit changes has been mixed (Dique et al., 2003). For example, only 20% of drivers obeyed the new speed limits in the United States of America (USA) and wildlife–vehicle collisions increased following speed limit changes (Bertwistle, 1999; summarised in Huijser and McGowen, 2010). A change in signposted speed limits could be accompanied with traffic calming measures such as speed bumps, enhanced road signs, and, although comparatively more expensive, speed cameras (van Langevelde & Jaarsma, 2009; Jaarsma & van Langevelde, 2011). The latter have proven to be a highly reliable approach to speed enforcement that produces considerable returns on investment through reduced social and economic costs associated with crashes (Pilkington & Kinra, 2005). Further mitigation options may become available with ongoing improvements to vehicle technology. For example, recent advances now enable smart cars to alert drivers before they cross the speed limit and to send speeding offences to the police, both of which aim to encourage speed compliance (Kazmi et al., 2022).

7.7 Limitations of the study

Although this research was conducted rigorously, there are some limitations that should be mentioned. Twenty-four percent of the 1.5 years of data collection experienced reduced traffic volume as a result of COVID-19 related lockdowns. Comparisons made in Chapter 3 and other studies showed, on the most part, a reduction in road mortality when under lockdown restrictions compared to 'normal' traffic conditions (Shilling et al., 2021; Pokorny, Cerri and Bužan, 2022; but see Bíl et al., 2021). Therefore, this study may represent the best-case scenario for road impacts and the influence of this on the conclusions of this study should be treated with caution. In addition, the COVID-19 lockdowns reduced the number of spotlight survey sessions available during the study. Therefore, it was not possible to quantify immigration and emigration from local populations as per Huijser et al. (1997) and Pettett et al. (2020). As such, conclusions on inter-patch movements currently based on the number of new entrants and dispersal of GPS tracked hedgehogs should be interpreted with caution. Similarly, the study designs adopted here aimed to increase sample sizes of GPS tracked hedgehogs in order to provide a more robust insight into hedgehog movements around roads (i.e., opting for many hedgehogs tracked for ~3 weeks rather than a small number of hedgehogs tracked for many months). As such, little long-term data from individuals was obtained, precluding accurate insight into different mortality factors without the bias of method and overall reproductive success. Therefore, the conclusions surrounding the extent of compensation to road mortality remains a tentative, albeit important, first step in developing understanding. For ethical reasons, the GPS tracking of juvenile hedgehogs and female hedgehogs who may have been pregnant was prohibited. As such, the dispersal of these individuals following the breeding season are missing pieces of data that could inform conclusions on the meta-population dynamics of hedgehogs.

7.8 Future research and recommendations

It is considered that wildlife-vehicle collisions kill individuals irrespective of their body condition and overall health. Further research to explore conditions such as disease, starvation and neurological disorders will help to clarify the significance of animal's dying from wildlife-vehicle collisions (Lehnert, Bissonette and Haefner, 1998). Reminiscent of the broader lack of knowledge on the impact of rescue centres on population dynamics, there is little research into the effects of captivity on the vulnerability of released animals. For example, whether the release of animals from captivity has an influence on an individual's perception of vehicles and therefore road mortality risk warrants further research, as conducted for Tasmanian devils (*Sarcophilus harrisii*; Grueber et al., 2017). Additionally, a phantom road experiment that deploys artificial light or noise in non-road environments (e.g., Schwartz, 2020) could further identify the aspect of the road that hedgehogs avoid and refine suitable mitigation options.

Identifying the most cost-effective measures to combat road impacts will require extensive knowledge on the most at-risk populations. To aid this task, results from local population-level studies could be combined in regional and global analyses (e.g., meta-analyses) to further scrutinise available evidence (Hill et al., 2020). If action is needed, platforms such as Conservation Evidence (www.conservationevidence.com) can be used to identify potential actions and evaluate the trade-offs between the financial investment and expected effect size (cost-efficiency).

If mitigation is implemented, subsequent monitoring and evaluations of its effectiveness should be carried out that is tailored to the specific biological parameter(s) that the mitigation sought to affect. These evaluations can benefit from new innovations and technologies, such as automated camera systems with timelapse capabilities, machine learning for pattern recognition, or RFID tags and transponders (L. Moore; unpublished data on detecting hedgehogs using RFID tags). Exploring driver compliance with speed changes or road signs and their effect on road mortality and crossing rates warrants research attention, particularly at the rural-residential transition zone. Given the seasonal variation in hedgehog crossing rates, studies assessing the efficacy of measures should cover at least one full year, although ideally more. Evidence on the effectiveness of different strategies should also include a transparent evaluation of costs, feasibility, and acceptability across socio-economic, ecological, and political paradigms.

Critically, the publication bias towards rejecting articles that show no effectiveness of mitigation leads to amplified cases of mitigation failure and “evidence complacency”, where decisions are not evidence-based, resulting in poor practice and inefficiencies (Sutherland & Wordley, 2017). Moving forward, it is recommended that broad inter-disciplinary participation are prioritised, alongside conservation practitioners examining, testing, and publishing the evidence of mitigation effectiveness (whether successful or not). This could be an important step in building a repertoire of effective conservation actions and has the potential to create a step-change in conservation strategies.

7.9 Conclusion

Transportation planners and road ecologists in the 21st century must balance the increasing need for human development with the need for environmentally-friendly practises. Using an integrated population and movement approach, this thesis strived to provide guidelines on optimal study designs in road ecology and to improve understanding on the survival and movements of animals near roads. It is clear that inter-related factors are at play that may (de)stabilise populations, such as vital rates, meta-population dynamics and risk perception by individuals. This study underlines that even a small amount of road mortality can be concerning for population persistence and that roads filter but do not prevent movements throughout the landscape. This thesis provides a comprehensive argument for multi-faceted conservation efforts that aim to protect larger populations (i.e., potential source populations) and to reduce road mortality within small hedgehog populations (i.e., potential sink populations). Addressing meta-population connectivity, such as through improving the permeability of the habitat matrix, will become increasingly relevant as traffic volumes are set to increase.

Understanding the ecological and cost-effectiveness, social acceptability and feasibility of different mitigation actions, such as speed reduction in rural-residential transition zones, will benefit the theoretical and practical perspectives of road ecology. It is hoped that the guidelines of survey protocol and study design presented here can be further utilised to interpret road mortality data of any terrestrial species more accurately. In light of growing road networks around the world, strategic research planning and collaborative monitoring efforts could substantially improve the options and outcomes of conservation action for roadside populations.

7.10 References

Altermatt, F., & Ebert, D. (2010). Populations in small, ephemeral habitat patches may drive dynamics in a *Daphnia magna* metapopulation. *Ecological Society of America*, *91*(10), 2975-2982. https://doi.org/10.1890/09-2016.1

Balčiauskas, L., Stratford, J., Balčiauskienė, L., & Kučas, A. (2020). Importance of professional roadkill data in assessing diversity of mammal roadkills. *Transportation Research Part D: Transport and Environment*, *87*. https://doi.org/10.1016/j.trd.2020.102493

Balkenhol, N., & Waits, L. P. (2009). Molecular road ecology: Exploring the potential of genetics for investigating transportation impacts on wildlife. *Molecular Ecology, 18*(20), 4151–4164. https://doi.org/10.1111/j.1365-294X.2009.04322.x

Bertwistle, J. (1999). The effects of reduced speed zones on reducing bighorn sheep and elk collisions with vehicles on the Yellowhead Highway in Jasper National Park. In *Proceedings of the International Conference on Wildlife Ecology and Transportation,* 13-16 September 1999, Florida Department of Transportation (pp. 89–97). USA : Florida.

Bíl, M., Andrášik, R., Cícha, V., Arnon, A., Kruuse, M., Langbein, J., … Seiler, A. (2021). COVID-19 related travel restrictions prevented numerous wildlife deaths on roads: A comparative analysis of results from 11 countries. *Biological Conservation, 256*. https://doi.org/10.1016/J.BIOCON.2021.109076

Brenmer-Harrison, S., Prodohl, P.A., & Elwood, R. W. (2004). Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*). *Animal Conservation, 7*, 313-320. https://doi.org/ 10.1017/S1367943004001490

Bright, P., George, L. & Balmforth, Z. (2005). *Mammals on Roads. Development and testing the use of road counts to monitor abundance.* People's Trust for Endangered Species and Joint Nature Conservation Committee.

Carvalho, F., & Mira, A. (2011). Comparing annual vertebrate road kills over two time periods, 9 years apart: a case study in Mediterranean farmland. *European Journal of Wildlife Research*, *57*(1), 157–174. https://doi.org/10.1007/s10344-010-0410-0

Ceia-Hasse, A., Borda-de-Água, L., Grilo, C., & Pereira, H. M. (2017). Global exposure of carnivores to roads. *Global Ecology and Biogeography*, *26*(5), 592–600. https://doi.org/10.1111/geb.12564

Christie, A. P., Downey, H., Frick, W. F., Grainger, M., O'Brien, D., Tinsley-Marshall, P., … Sutherland, W. J. (2022). A practical conservation tool to combine diverse types of evidence for transparent evidence-based decision-making. *Conservation Science and Practice*, *4*(1), e579. https://doi.org/10.1111/CSP2.579

Clevenger, A. P., Chruszcz, B., & Gunson, K. E. (2001). Highway mitigation fencing reduces wildlife-vehicle collisions. *Wildlife Society Bulletin, 29*(2), 646–653. https://doi.org/10.2307/3784191

Davies, J. L. (1957). A hedgehog road mortality index. *Prox. Zool. Soc. Lond., 128*, 606–608.

Department for Transport. (2022a). *Road lengths in Great Britain (2021)*. Government of the United Kingdom. Retrieved from https://www.gov.uk/government/statistics/road-lengths-in-great-britain-2021/road-lengths-in-great-britain-2021

Department for Transport. (2022b). *Road traffic estimates in Great Britain: 2021*. Government of the United Kingdom. Retrieved from https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/1107056/road-traffic-estimates-in-great-britain-2021.pdf.

Dique, D. S., Thompson, J., Preece, H. J., Penfold, G. C., Villiers, D. L. de, & Leslie, R. S. (2003). Koala mortality on roads in south-east Queensland: the koala speed-zone trial. *Wildlife Research*, *30*(4), 419. https://doi.org/10.1071/WR02029

Doncaster, C. P., Rondinini, C., & Johnson, P. C. D. (2001). Field test for environmental correlates of dispersal in hedgehogs *Erinaceus europaeus*. *Journal of Animal Ecology*, *70*(1), 33–46. https://doi.org/10.1111/J.1365-2656.2001.00471.X

Dowding, C. V., Harris, S., Poulton, S., & Baker, P. J. (2010). Nocturnal ranging behaviour of urban hedgehogs, *Erinaceus europaeus*, in relation to risk and reward. *Animal Behaviour*, *80*(1), 13–21. https://doi.org/10.1016/j.anbehav.2010.04.007

Gagnon, J. W., Dodd, N. L., Sprague, S. C., Ogren, K. S., Loberger, C. D., & Schweinsburg, R. E. (2019). Animal-activated highway crosswalk: long-term impact on elk-vehicle collisions, vehicle speeds, and motorist braking response. *Human Dimensions of Wildlife*, *24*(2), 132–147. https://doi.org/10.1080/10871209.2019.1551586

George, L., Macpherson, J. L., Balmforth, Z., & Bright, P. W. (2011). Using the dead to monitor the living: Can road kill counts detect trends in mammal abundance? *Applied Ecology and Environmental Research*, *9*(1), 27–41. https://doi.org/10.15666/aeer/0901_027041

Goniewicz, K., Goniewicz, M., Pawłowski, W., & Fiedor, P. (2016). Road accident rates: strategies and programmes for improving road traffic safety. *European Journal of Trauma and Emergency Surgery*, *42*(4), 433–438. https://doi.org/10.1007/S00068-015-0544-6/TABLES/1

González-Calderón, A. (2020). Seasonal and spatial patterns of mammalian road kill in northeastern Cordoba Province, Argentina. *Studies on Neotropical Fauna and Environment*, *57*(3), 172-180. https://doi.org/10.1080/01650521.2020.1829892

Grace, M. K., Smith, D. J., & Noss, R. F. (2017). Reducing the threat of wildlife-vehicle collisions during peak tourism periods using a Roadside Animal Detection System. *Accident Analysis & Prevention*, *109*, 55–61. https://doi.org/10.1016/J.AAP.2017.10.003

Grilo, C., Bissonette, J. A., & Santos-Reis, M. (2009). Spatial-temporal patterns in Mediterranean carnivore road casualties: Consequences for mitigation. *Biological Conservation*, *142*(2), 301–313. https://doi.org/10.1016/j.biocon.2008.10.026

Grilo, C., Borda-de-Água, L., Beja, P., Goolsby, E., Soanes, K., le Roux, A… González-Suárez, M. (2021). Conservation threats from roadkill in the global road network. *Global Ecology and Biogeography*, *30*(11), 2200–2210. https://doi.org/10.1111/GEB.13375

Grueber, C. E., Reid-Wainscoat, E. E., Fox, S., Belov, K., Shier, D. M., Hogg, C. J., & Pemberton, D. (2017). Increasing generations in captivity is associated with increased vulnerability of Tasmanian devils to vehicle strike following release to the wild. *Scientific Reports*, *7*(1), 2161. https://doi.org/10.1038/s41598-017-02273-3

Helldin, J. O., & Petrovan, S. O. (2019). Effectiveness of small road tunnels and fences in reducing amphibian roadkill and barrier effects at retrofitted roads in Sweden. *PeerJ*, *7*, e7518. https://doi.org/10.7717/peerj.7518

National Highways (formerly Highways England). (2017). *Connecting the Country - Planning for the long term*. Retrieved from https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/666876/Connecting_the_country_Planning_for_the_long_term.pdf

Hill, J. E., DeVault, T. L., Wang, G., & Belant, J. L. (2020). Anthropogenic mortality in mammals increases with the human footprint. *Frontiers in Ecology and the Environment*, *18*(1), 13–18. https://doi.org/10.1002/fee.2127

Hodson, N. L. (1966). A survey of road mortality in mammals (and including data for the Grass snake and Common frog). *Journal of Zoology*, *148*(4), 576–579. https://doi.org/10.1111/j.1469-7998.1966.tb02972.x

Hubert, P., Julliard, R., Biagianti, S., & Poulle, M. L. (2011). Ecological factors driving the higher hedgehog (*Erinaceus europeaus*) density in an urban area compared to the adjacent rural area. *Landscape and Urban Planning*, *103*(1), 34–43. https://doi.org/10.1016/j.landurbplan.2011.05.010

Huijser, M. P., Bergers, P. J. M., Nolet, B. A., & Meuwissen, L. T. J. (1997). *Traffic mortality in a hedgehog population.* In M. Huijser & P. Bergers (Eds.) Hedgehogs and traffic: the effects of roads and traffic on hedgehog populations. Ministry of Transport, Public Works and Water Management. Directorate-General for Public Works and Water Management. Road and Hydraulic Engineering Division. The Netherlands : Hague. Retrieved from https://puc.overheid.nl/PUC/Handlers/DownloadDocument.ashx?identifier=PUC_50960_31&versienummer=1.

Huijser, M. P., & McGowen, P. T. (2010). Reducing wildlife-vehicle collisions. In J. Beckmann, A. Clevenger, M. Huijser, & J. Hilty (Eds.) *Safe passages: highways, wildlife, and habitat connectivity.* Washington D.C : Island Press.

Ibisch, P. L., Hoffmann, M. T., Kreft, S., Pe'Er, G., Kati, V., Biber-Freudenberger, L., DellaSala, D. A., Vale, M. M., … & Selva, N. (2016). A global map of roadless areas and their conservation status. *Science, 354*(6318), 1423–1427. https://doi.org/10.1126/science.aaf7166

Jaarsma, C. F., & van Langevelde, F. (2011). Effects of scale and efficiency of rural traffic calming on safety, accessibility and wildlife. *Transportation Research Part D: Transport and Environment*, *16*(7), 486–491. https://doi.org/10.1016/j.trd.2011.05.009

Jaeger, J. A. G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B., & Von Toschanowitz, K. T. (2005). Predicting when animal populations are at risk from roads: An interactive model of road avoidance behavior. *Ecological Modelling, 185*(2–4), 329–348. https://doi.org/10.1016/j.ecolmodel.2004.12.015

Jaeger, J. A. G., & Fahrig, L. (2001). Modeling the effects of road networks patterns on population persistence: relative importance of traffic mortality and 'fence effect'. In *Proceedings of the 2001 International Conference on Ecology and Transportation,* 24 – 29 September 2001, North Carolina State University (pp. 298 – 312). USA : Colorado.

Kazmi, S. S. A., Ahmed, M., Mumtaz, R., & Anwar, Z. (2022). Spatiotemporal clustering and analysis of road accident hotspots by exploiting GIS technology and kernel density estimation. *Computer Journal, 65*(2), 155–176. https://doi.org/10.1093/comjnl/bxz158

Kowalczyk, R., Zalewski, A., Jędrzejewska, B., Ansorge, H., & Bunevich, A. N. (2009). Reproduction and mortality of invasive raccoon dogs (*Nyctereutes procyonoides*) in the białowieża primeval forest (Eastern Poland). *Annales Zoologici Fennici*, *46*(4), 291–301. https://doi.org/10.5735/086.046.0406

Lehnert, M. E., Bissonette, J. A., & Haefner, J. W. (1998). Deer (Cervidae) highway mortality: using models to tailor mitigative efforts. In *Proceedings of the XXIIIrd Congress of the International Union of Game Biologists*, Office National de la Chasse (pp 835–841). France : Paris.

Mathews, F., Kubasiewicz, L. M., Gurnell, J., Harrower, C. A., McDonald, R. A., & Shore, R. F. (2018). *A review of the population and conservation status of British mammals.* The Joint Nature Conservation Committee Retrieved from http://publications.naturalengland.org.uk/publication/5636785878597632

McClure, M., & Ament, R. (2014). *Where people and wildlife intersect. Prioritising mitigation of road impacts on wildlife connectivity.* Center for Large Landscape Conservation and Great

Northern Landscape Conservation Cooperative.. Retrieved from https://largelandscapes.org/wp-content/uploads/2019/06/Where-People-Wildlife-Intersect-Prioritizing-Mitigation.pdf

Moorhouse, T. P., Palmer, S. C. F., Travis, J. M. J., & Macdonald, D. W. (2014). Hugging the hedges: Might agri-environment manipulations affect landscape permeability for hedgehogs? *Biological Conservation*, *176*, 109–116. https://doi.org/10.1016/j.biocon.2014.05.015

Morris, P. (1993). *Hedgehog Roadkill Report*. Unpublished report.

Paterson, J. E., Baxter-Gilbert, J., Beaudry, F., Carstairs, S., Chow-Fraser, P., Edge, C. B… Davy, C. M. (2019). Road avoidance and its energetic consequences for reptiles. *Ecology and Evolution*, *9*(17), 9794–9803. https://doi.org/10.1002/ECE3.5515

Périquet, S., Roxburgh, L., le Roux, A., & Collinson, W. J. (2018). Testing the value of citizen science for roadkill studies: A case study from South Africa. *Frontiers in Ecology and Evolution*, *6*. https://doi.org/10.3389/fevo.2018.00015

Pettett, C., Macdonald, D. W., Al-Hajiri, A., Al-Jabiry, H., & Yamaguchi, N. (2020). Characteristics and demography of a free-ranging Ethiopian hedgehog, *Paraechinus aethiopicus*, population in Qatar. *Animals*, *10*(6), 1–17. https://doi.org/10.3390/ani10060951

Pilkington, P., & Kinra, S. (2005). Effectiveness of speed cameras in preventing road traffic collisions and related casualties: systematic review. *BMJ*, *330*(7487), 331–334. https://doi.org/10.1136/bmj.38324.646574.AE

Pokorny, B., Cerri, J., & Bužan, E. (2022). Wildlife roadkill and COVID-19: A biologically significant, but heterogeneous, reduction. *Journal of Applied Ecology*, *59*(5), 1291–1301. https://doi.org/10.1111/1365-2664.14140

Prange, S., Gehrt, S. D., & Wiggers, E. P. (2003). Demographic factors contributing to high raccoon densities in urban landscapes. *The Journal of Wildlife Management*, *67*(2), 324. https://doi.org/10.2307/3802774

Rasmussen, S. L., Kalliokoski, O., Dabelsteen, T., & Abelson, K. (2021). An exploratory investigation of glucocorticoids, personality and survival rates in wild and rehabilitated hedgehogs (*Erinaceus* europaeus) in Denmark. *BMC Ecology and Evolution, 21*. https://doi.org/10.1186/s12862-021-01816-7

Raymond, S., Schwartz, A. L. W., Thomas, R. J., Chadwick, E., & Perkins, S. E. (2021). Temporal patterns of wildlife roadkill in the UK. *PLOS ONE*, *16*(10), e0258083. https://doi.org/10.1371/JOURNAL.PONE.0258083

Reeve, N. J. (1981). *A field study of the hedgehog (*Erinaceus europaeus*) with particular reference to movements and behaviour*. [PhD Thesis, University of London].

Riginos, C., Fairbank, E., Hansen, E., Kolek, J., & Huijser, M. P. (2019). Effectiveness of night-time speed limit reduction in reducing wildlife-vehicle collisions (report no. FHWA-WY-1904F). *Wyoming Department of Transportation.* Retrieved from https://rosap.ntl.bts.gov/view/dot/42488%0Ahttps://trid.trb.org/view/1659707

Riginos, C., Graham, M. W., Davis, M. J., Johnson, A. B., May, A. B., Ryer, K. W., & Hall, L. E. (2018). Wildlife warning reflectors and white canvas reduce deer–vehicle collisions and risky road-crossing behavior. *Wildlife Society Bulletin, 42*(1), 119-130. https://doi.org/10.1002/wsb.862

Roedenbeck, I. A., Fahrig, L., Findlay, C. S., Houlahan, J. E., Jaeger, J. A. G., Klar, N., Kramer-Schadt, S., & van der Grift, E. A. (2007). The Rauischholzhausen agenda for road ecology. *Ecology and Society*, *12*(1). http://www.ecologyandsociety.org/vol12/iss1/art11/

Roger, E., Bino, G., & Ramp, D. (2012). Linking habitat suitability and road mortalities across geographic ranges. *Landscape Ecology*, *27*(8), 1167–1181. https://doi.org/10.1007/s10980-012-9769-5

Roger, E., Laffan, S. W., & Ramp, D. (2011). Road impacts a tipping point for wildlife populations in threatened landscapes. *Population Ecology*, *53*(1), 215–227. https://doi.org/10.1007/s10144-010-0209-6

Ruiz-Capillas, P., Mata, C., & Malo, J. E. (2015). How many rodents die on the road? Biological and methodological implications from a small mammals' roadkill assessment on a Spanish motorway. *Ecological Research*, *30*(3), 417–427. https://doi.org/10.1007/s11284-014-1235-1

Santos, R. A. L., Santos, S. M., Santos-Reis, M., Picanço de Figueiredo, A., Bager, A., Aguiar, L. M. S., & Ascensão, F. (2016). Carcass persistence and detectability: Reducing the uncertainty surrounding wildlife-vehicle collision surveys. *PLOS ONE, 11*(11), e0165608. https://doi.org/10.1371/journal.pone.0165608

Schaus-Calderón, J. S. (2021). *Responses of the West European hedgehog to urbanisation: impact on population dynamics, animal movement and habitat selection.* [PhD Thesis, Nottingham Trent University].

Schwab, A. C., & Zandbergen, P. A. (2011). Vehicle-related mortality and road crossing behavior of the Florida panther. *Applied Geography, 31*(2), 859–870. https://doi.org/10.1016/j.apgeog.2010.10.015

Seiler, A. (2003). *The toll of the automobile: Wildlife and roads in Sweden.* [PhD Thesis, Swedish University of Agricultural Sciences].

Shilling, F., Nguyen, T., Saleh, M., Kyaw, M. K., Tapia, K., Trujillo, G… Ham, E. (2021). A reprieve from US wildlife mortality on roads during the COVID-19 pandemic. *Biological Conservation*, *256*, 109013. https://doi.org/10.1016/J.BIOCON.2021.109013

Sutherland, W. J., & Wordley, C. F. R. (2017). Evidence complacency hampers conservation. *Nature Ecology and Evolution*, *1*(9), 1215–1216. https://doi.org/10.1038/S41559-017-0244-1

Transport Focus (2021). *Road users' priorities for improvement*. Retrieved from https://www.transportfocus.org.uk/publication/road-users-priorities-for-improvement/

van Langevelde, F., & Jaarsma, C. F. (2009). Modeling the effect of traffic calming on local animal population persistence. *Ecology and Society*, *14*(2). https://doi.org/10.5751/ES-03061-140239

van Strien, M. J., & Grêt-Regamey, A. (2016). How is habitat connectivity affected by settlement and road network configurations? Results from simulating coupled habitat and human networks. *Ecological Modelling*, *342*, 186–198. https://doi.org/10.1016/j.ecolmodel.2016.09.025

Vittinghoff, E., & McCulloch, C. E. (2007). Relaxing the rule of ten events per variable in logistic and cox regression. *American Journal of Epidemiology*, *165*(6), 710–718. https://doi.org/10.1093/AJE/KWK052

Wembridge, D. E., Newman, M. R., Bright, P. W., & Morris, P. A. (2016). An estimate of the annual number of hedgehog (*Erinaceus europaeus*) road casualties in Great Britain. *Mammal Communications*, *2*, 8–14. https://www.mammal.org.uk/wp-content/uploads/2016/04/MC1605_HedgehogsRoads_Wembridge.pdf

Wembridge, D., Johnson, G., Al-Fulaij, N., & Langton, S. (2022). *The State of Britain's Hedgehogs 2022*. People's Trust for Endangered Species and the British Hedgehog Preservation Society. Retrieved from https://www.hedgehogstreet.org/wp-content/uploads/2022/02/SoBH-2022-Final.pdf

Wilson, E., & Wembridge, D. E. (2018). *The State of Britain's Hedgehogs 2018*. People's Trust for Endangered Species and the British Hedgehog Preservation Society. Retrieved from https://www.hedgehogstreet.org/wp-content/uploads/2018/02/SoBH-2018_final-1.pdf

Yarnell, R. W., & Pettett, C. E. (2020). Beneficial land management for hedgehogs (*Erinaceus europaeus*) in the united kingdom. *Animals*, *10*(9), 1–10. https://doi.org/10.3390/ani10091566

Appendix XIV: A mathematical derivation of a general model for estimating road mortality rates (individuals/km/year) from counts of casualties based on unsystematic road surveys.

Casualties occur at a constant rate, λ ($km^{-1}.day^{-1}$), and are removed at a rate, μ, proportional to the density of casualties, s ($= n/l$), where n is the total number of casualties recorded, l is the total distance surveyed, p be the probability that a carcass is removed in time t, tr is the carcass persistence, and d is the detection probability specific to body size. tr = 4.7 days based on Chapter 3. When surveys were repeated frequently (i.e., Hodson (1996), this study), it was assumed that that all casualties were recorded; for single surveys such as MoR, a detection rate of 0.8 was used.

At time $t = 0$, $s = 0$ and $ds/dt = \lambda$. As t increases, s approaches a maximum value, s' at which $ds/dt = 0$ and $\mu = \lambda$.

MODEL 1 – developed for a single survey of l km, or multiple surveys of independent road sections totalling l km (e.g., *Mammals on Roads*)

For a given number of carcasses, n, the number removed in time, t

$= p.t.n$

and the rate of removal, μ ($km^{-1}.day^{-1}$)

$= p.t.n/(t.l)$ (Equation A)

Substituting for p in Equation A,

$\mu = n/(l.t_r)$

At a 'steady-state', $\mu = \lambda$. If only some carcasses are recorded, with a detection rate, d, and n is the *recorded* number of casualties.

$\lambda = n/(l.t_r.d)$

This is the same as Model 1 in Wembridge *et al*. (2016).

Estimates of λ from Morris, Bright and MoR were based on surveys undertaken over three of the eight months hedgehogs are, on average, active for in a year. Therefore, standard lambda (s) was calculated using 214 days (eight months) of active season to account for the relatively inactive hibernation period of hedgehogs over winter in Britain (i.e., $\lambda*(214/365)$).

MODEL 2 – developed for repeat surveys (i.e., of the same road section, e.g., this study). This Model is used in Chapter 3 and described in Appendix III: A mathematical derivation of a general model for estimating road mortality rates (individuals/km/year) from counts of casualties